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DISTRIBUTION OF THE VELOCITIES OF ABSORPTION OF WATER IN THE ONION ROOT

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(WITH FIVE FIGURES)

Although many investigations have been made there is, up to the present, no available study which furnishes reliable quantitative data on the distribution of the rates of water absorption in any one root. Only recently (**1**, **8**) has there been any attempt to make the investigations strictly quantitative in character but all studies are open to adverse criticism since none were carried out under adequately controlled conditions. It appears that the only method at present available which provides for complete control of conditions using the *intact, uninjured,* and *unstimulated* root is that used in the present study.

Since reviews have been presented by other investigators (**1**, **4**, **8**, **9**) no comprehensive survey of the literature will be attempted. It is important, however, to call attention to certain inadequacies of the methods employed by the more recent investigators. Popesco (**4**) made determinations of the rates of water absorption on single roots of a number of different plants, but his results were only relatively quantitative. He employed both direct and indirect methods which involved: (1) the isolation of given regions of a root by covering these with cocoa-butter and then placing the root in a U-tube, one arm of which, drawn out to a capillary, was graduated in arbitrary units; (2) the use of dyes and microchemical reagents; and (3) plasmolysis. Höhn (**1**) made unsuccessful attempts to use a modified form of Popesco's "cocoa-butter" procedure. He was unable to obtain a perfect seal with rings of cocoa-butter and he points out the impossibility of employing inelastic material to cover the region of elongation. To cover various regions of the root Höhn substituted oil for cocoa-butter. His experiments were carefully carried out under known conditions of temperature and humidity. The chief criticism of his work is given by Sierp and

Brewig (**8**, p. 115) who show that Höhn's conclusions regarding the distribution of the rates of water absorption in a single root are not valid because they are based on comparative measurements of (1) different roots, and (2), on the same root, but at different time periods. Furthermore, as will be shown later, Höhn's tabulated results do not warrant the conclusions that he gives.

Ursprung and Blum (**9**), Höhn (**1**), and Sierp and Brewig (**8**) call attention to the limitations of all methods involving dyes and microchemical reagents, pointing out that it is impossible to determine the rates of water absorption when quantitative relations between the spread of the dyes and the movement of the water are not known. On this basis the results of Popesco (**4**) and Keller (**2**) employing dyes may be questioned. Ursprung and Blum (**9**) based their conclusions on suction-pressure measurements. As pointed out by Sierp and Brewig (**8**, p. 115) their method is limited because such measurements could be evaluated quantitatively only if the suction values remained constant when the root absorbed water and it has not been established that such a relation exists.

Sierp and Brewig (**8**) used a number of micropotometers making simultaneous measurements on the same root. They state that so far as they know this was the first time such a procedure had been followed. However, the method employed in the present investigation, which also involved simultaneous measurements by several micropotometers on the same root, was first reported by Rosene and Lund in 1934 (**6**). The technique followed by Sierp and Brewig has serious limitations. They made measurements on the roots of plants which were in an inverted position with respect to gravity, thus producing conditions of stimulation. In order to insure water-tight connections they wound thread impregnated with wool fat around the root. They maintain that after the experiment no injury to the root was apparent but they do not give the criteria or tests upon which their conclusion was based. Wrapping the roots with thread in this manner would produce mechanical stimulation and would interfere with respiratory activities. The quantitative determinations made by Höhn, and by Sierp and Brewig, were expressed in milligrams per linear length, assuming that the diameter of the root was uniform throughout its length. It is obvious that such a technique furnishes data which is only relatively quantitative. Of far greater value are reliable data on the rate of absorption per unit of surface area.

Determination of the distribution of the velocities of absorption of water in roots should therefore be made on intact, uninjured, unstimulated roots, and under conditions which permit careful control of such conditions as temperature, light, oxygen, and humidity. It should be possible to make simultaneous measurements of water absorption by different regions, and to determine the rates of absorption per unit of surface area. It is believed that the present technique fulfills these requirements.

Apparatus and method

The experiments were conducted at room temperature (25° C.) in a basement room, the temperature of which did not vary more than 2° during the longest experiments, which were of several days' duration. The observations were made on the roots of *Allium cepa,* which for the most part were grown either in tap water, or in a saturated atmosphere in vessels through which air was continuously passed.[1] In certain experiments, observations were made on roots which had developed when a given onion was growing in the experimental apparatus. Several experimental chambers were constructed, making it possible to run controls while varying the conditions in one or more chambers.

The details of one experimental chamber are shown in figure 1. The removable glass cover (A, fig. 1) rests in a groove (F) in the transite base (B) which is attached to a rack and pinion stand providing vertical adjustment for the base and cover. The base has four perforations lined with bakelite tubing through which connections pass from the interior to the exterior of the chamber. The onion bulb rests upon a cork ring which is placed in a hole in a swivel attachment (C). The swivel attachment is supported by the glass tube (G), which is cemented to a brass rod (D). The brass rod passes through a perforation and is supported on the outside by a three-way mechanical micromanipulator. With this arrangement the onion bulb may be moved to any desired position by manipulation from the outside. Each micropotometer (H) consists of a calibrated glass tube made from carefully selected millimeter pyrex tubing of uniform bore. One end of each tube (a, b, c, d, fig. 1) was ground down on two opposite sides of the bore and a hole was bored through to permit passage of the root. One or more micropotometers were cemented with DeKhotinsky to a glass rod (E) which was supported by a three-way mechanical manipulator which provided delicate adjustments and accurate placing of the micropotometers around the root. The potometers varied in length from 25 to 40 millimeters but were the same for any one experiment. Glass tubes (I and O), which pass through rubber stoppers fitted into perforations of the base, provide for inlet and outlet of glass. Moisture and airtight seals at the perforations through which the rods (D and E) passed were made with finger stalls designated as M in figure 1. These were filled with water. By packing plasticene around the base of the chamber where it fits into the groove, the interior could be completely sealed off from the exterior.

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[1] The experiments reported in this paper were carried out in the fall of 1934 on onion sets grown the preceding spring. Observations on onion sets procured this spring (1935) show slightly higher rates of water absorption.

Throughout all of the experiments reported in this paper, air saturated with moisture was continuously passed through the chamber. Both inlet and outlet tubes (I and O) were connected to wash bottles. The latter connection served as a test to determine any leakage of air through the apparatus and as a means of gauging the relative rate of gas flow by counting the bubbles per unit time.

Most of the experiments were made on a single intact root after the sister roots had been cut off. Removing the onion from the vessel in which it grew, cutting the sister roots, and placing it in the experimental chamber, required such a short period of exposure that the root had no time to dry out in any region. This was determined by microscopic examination in a

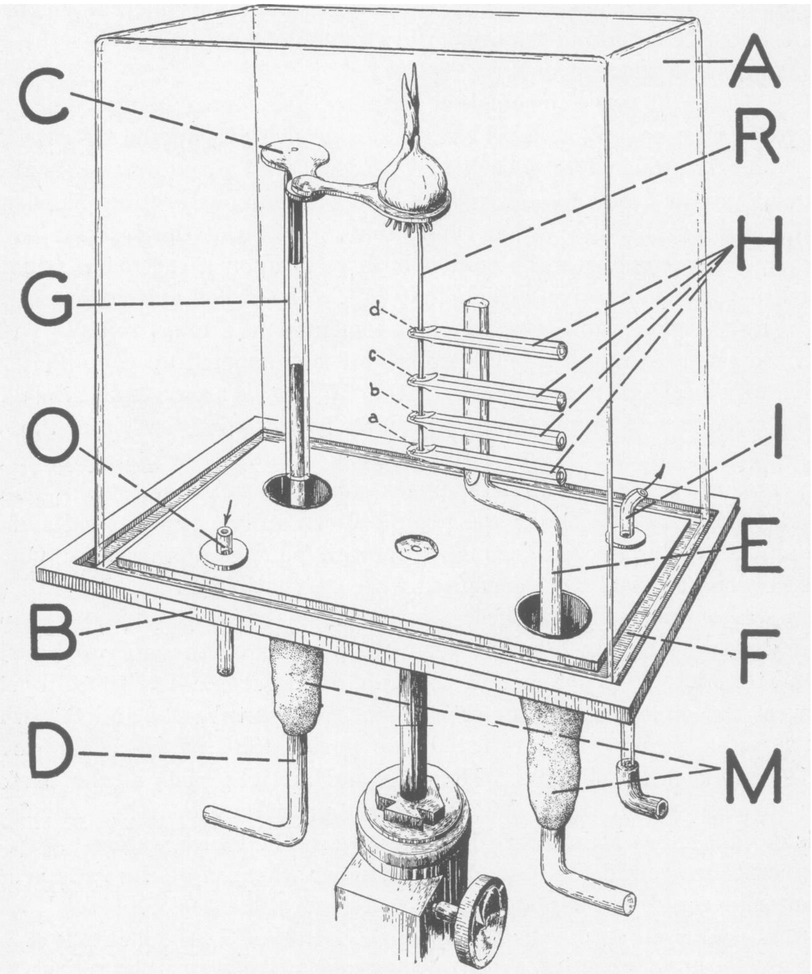


FIG. 1. Experimental chamber (description in text).

series of experiments to determine whether or not drying appeared. The root (R, fig. 1), was threaded through the openings (a, b, c, d) of the micropotometers by adjustments made with the micromanipulators on the outside, lowering the brass rod (D) and passing the root down through the openings; or by raising the glass rod (E) and passing the micropotometer tubes up over the root to the desired positions. All adjustments of the mechanical micromanipulators and all measurements were made with the aid of a horizontal microscope which was fitted with a micrometer ocular. By this means very delicate adjustments of the positions of the micropotometers could be made without mechanical injury. By raising the bulb support (D), or lowering the micropotometer support (E), at frequent intervals throughout an experiment it was possible to maintain the positions of the micropotometers at a given distance from the root tip as elongation took place. The quantity of water absorbed was determined by making consecutive minute measurements of the movement of the terminal meniscus in each tube. The height of the water column at each region was determined by measuring the distance between the upper and lower menisci around the root where it passed through the micropotometer. There was no flow of water down the root and after a period of an hour or more, depending upon the height of the water column at the beginning, the distance between the lower and upper menisci at each micropotometer contact reached a steady value which was maintained relatively constant. At the apex, where increase in diameter took place, there was a slight shift in the height of the water column. Determinations of the average diameter and height of the water column at each contact were made at frequent intervals, depending upon the nature of the experiment. No measurements were made during the first 5 to 10 hours after the onion had been placed in the chamber, in order to permit it to come into flux equilibrium with the conditions of the environment. Favorable conditions for growth were present in the experimental chamber, for the roots and leaves of the onions grew in a normal manner. New roots appeared and developed and these were sometimes used for observation. No root hairs were observed on any of the roots, whether grown in moist air, or in tap water.

Measurements were made in millimeters to the second decimal place. Although great precautions were taken when readings were made, and although the menisci at each contact appeared clear-cut and remained fairly steady after flux equilibrium conditions were reached, it might be that the absolute height of the water column was not observed. Variations of the diameters at the upper and lower menisci at a single contact did not exceed 0.02 millimeter. In all of the experiments during which the micropotometers were kept at relatively constant positions with respect to the root tip by lowering them at frequent intervals, the absolute distance from the apex varied from one reading to the next. When adjustments were made at intervals of fifteen minutes the variation did not exceed 0.11 mm., except in a very rapidly growing root, where it reached 0.2 mm. When the interval of adjustment was longer, the variation was, of course, greater.

Investigation

A. ABSORPTION OF WATER BY APICAL REGIONS

1. RATES OF ABSORPTION IN RELATIVELY YOUNG ROOTS 25 TO 35 MM. IN LENGTH

The quantity of tap water absorbed from 6 : 30 A.M. one day to 2 : 30 A.M. the day following, by four apical regions of the root exhibiting considerable diversity of morphological character, is shown in figure 2. The bulb with three leaves 4 to 6 cm. in length and a single remaining root had been placed in the chamber with the micropotometers in position the night before the determinations were made. At 6 : 30 A.M., by means of the mechanical micromanipulators on the outside, the micropotometers were lowered until the position of each was respectively 0.4, 5.0, 10.0, and 15.0 mm. from the apical point of the root. Every half hour or less, the micropotometers were lowered with respect to the growing root in order to maintain them in the

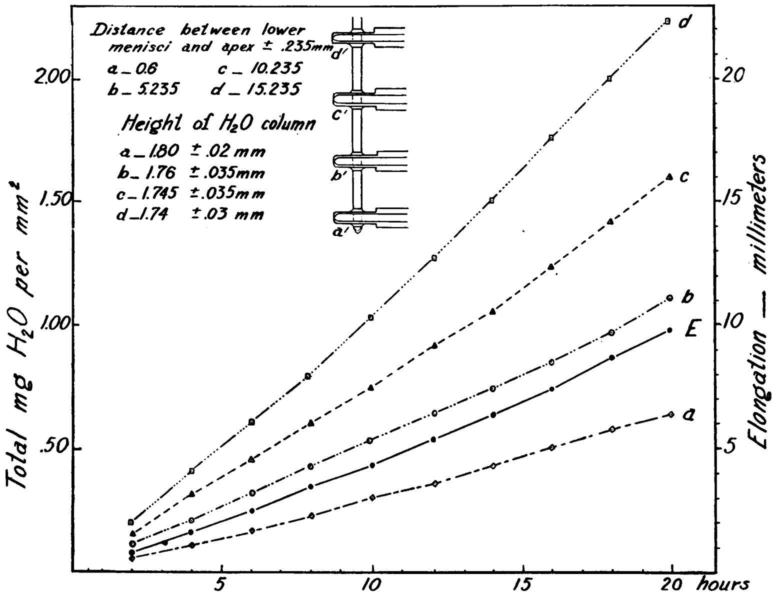


FIG. 2. Water absorbed by 4 apical regions of a single root with initial length of 25 mm. Curves *a, b, c,* and *d* show mg. of water absorbed per mm.[2] of absorbing surface at the micropotometer contacts *a′, b′, c′, d′* shown in the root diagram. Initial diameters at *a′, b′, c′* and *d′* are 0.710, 0.735, 0.740, and 0.752 mm. respectively. Curve *E* shows elongation in mm.

same relative positions. Measurements of the root diameters at each meniscus of the water columns, the height of the water column at each region, the movement of the terminal meniscus in the micropotometer, and elongation were recorded every four hours. The height of each water column with the maximum variations between readings, the distance between the lower meniscus at each micropotometer and the apex, and the average diameter of each contact are given in figure 2. Elongation is shown by curve *E*. The rate of elongation is fairly uniform, tending to increase during the night, especially after midnight. Curves *a, b, c,* and *d* (fig. 2), show the milligrams of water absorbed, calculated in terms of unit surface exposed to the water of each micropotometer.

Curve *a* represents the quantity of water absorbed by the surface in a region where active cell division is taking place, and tissue differentiation is at a minimum; curve *b* shows the milligrams of water absorbed by the surface in the fifth and sixth millimeters which is the zone just proximal to the region of elongation, and curves *c* and *d* give the quantity of water absorbed by regions relatively older where tissue differentiation has taken place and vacuolization tends to reach a maximum.

The curves clearly show that water was absorbed by the surface in all four of the regions mentioned above, and that the rates of absorption in the regions were very different. Greater quantities of water were absorbed by the relatively more basal regions. A comparison of the slopes of all of the curves shows that there was an increase in the rate of absorption in each region with time, the most rapid rates appearing toward the end of the experiment. In this experiment, which is typical, the greatest increase in the velocity of absorption of any one zone occurred in the region which is in the 15th and 16th millimeter from the apical point of the root.

When all of the roots are left intact, the quantity of water absorbed by any region of one of the roots is less than if all of the roots but one are cut off. This fact is shown by the curves in figure 3, which give typical results obtained when measurements were made on a given root with (1) all of the sister roots intact and (2) all of the sister roots removed. In this case, the observations were made on a bulb which had three leaves 3 to 5 cm. in length, and fourteen roots 10 to 30 mm. long. Three micropotometers were placed on a root which was 27.3 mm. in length in the positions designated as *x′, y′, z′* in diagram N (fig. 3). These positions corresponded to the regions (1) where active cell division was taking place; (2) where elongation was at a maximum; and (3) the zone proximal to the region of elongation. No observations were made until 8 hours after the bulb had been placed in the chamber. From then on, measurements were made every four hours, and adjustment for elongation was made at half-hour intervals except during the night. The two morning readings, therefore, showed

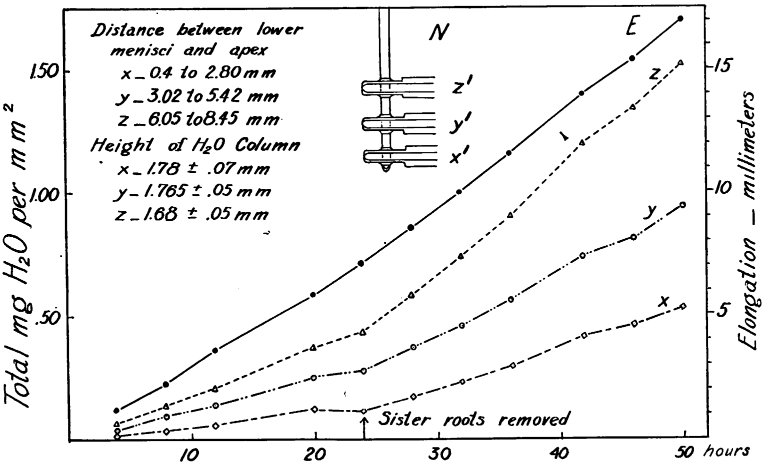


FIG. 3. Absorption of water by 3 apical regions of a single root when (a) all the roots were intact and (b) the sister roots were removed. Curves x, y and z show the mg. of water absorbed at the contacts of the micropotometers x', y' and z' illustrated in diagram N. Diameters at contacts of the micropotometers x', y', z' were 0.77, 0.787 and 0.80 mm. respectively. Curve E shows elongation. The arrow on the base line indicates time at which the sister roots were removed.

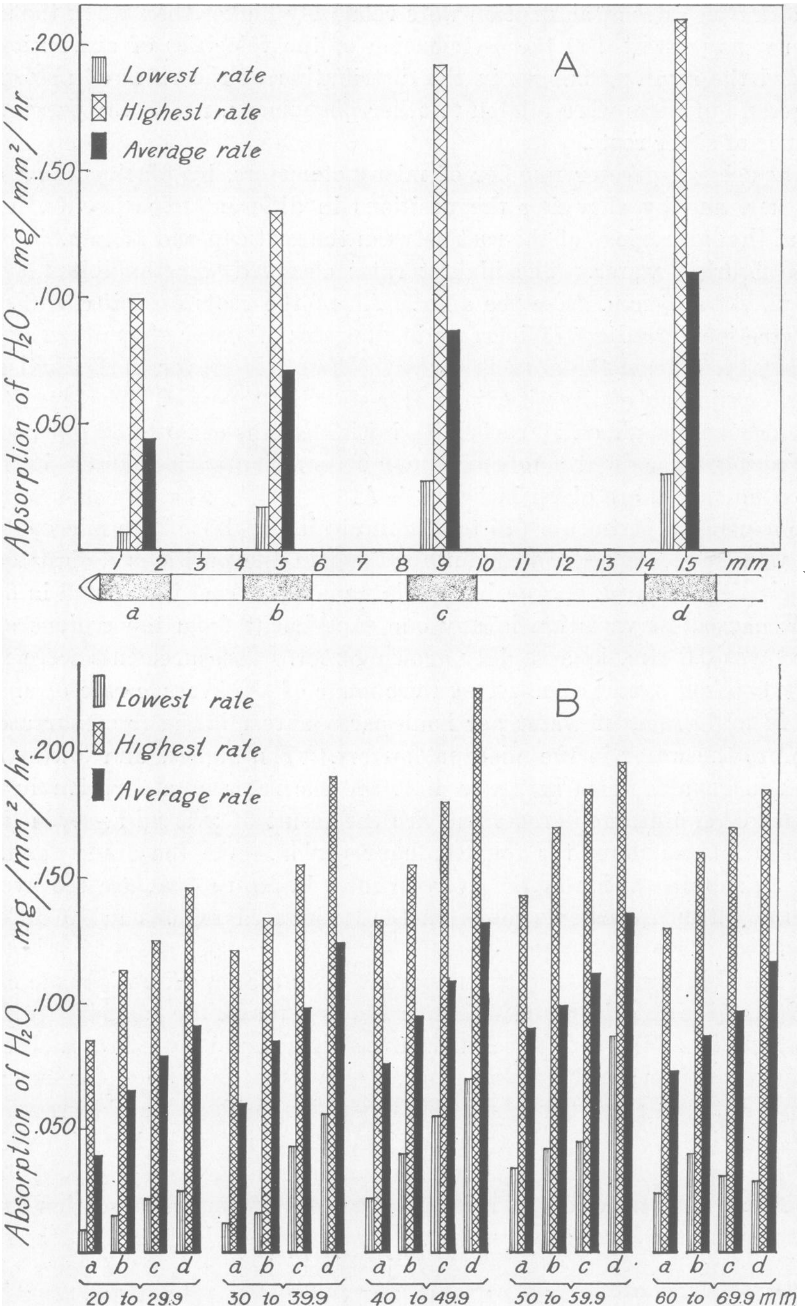
higher values since these represented the absorption of water during an interval when the positions of the micropotometers relative to the base varied from 2 to 2.5 mm. After 24 hours, as designated by the arrow on the base line in figure 3, all of the roots but the one which was in contact with the water in the micropotometers, were quickly cut off with sharp scissors without changing the positions or the terminal menisci of the micropotometers in any way. The heights of the water columns are tabulated in figure 3. Maximum variation during any one interval was 0.07 mm. which occurred at the apical micropotometer the second night. The limits of variation in the positions of the micropotometers relative to the apex of the root, and the average diameter at each contact, are also tabulated in figure 3. As shown by curves *x*, *y*, and *z* (fig. 3) tap water was absorbed by the surfaces in all three of the regions mentioned above. Pronounced change in the slopes of the latter half of each curve demonstrates that after the sister roots had been removed, greater quantities of water were absorbed by all of the surfaces exposed to tap water in the micropotometers. Ten other experiments similar to the above, with the micropotometers in various positions, showed essentially the same results. In each case, the rate of absorption in the single intact root was greater after removal of the sister roots, and the greatest quantity of water was absorbed by the region nearest the base. In all of the experiments in which measurements of the absorption of water were made on a single intact root with the sister roots removed, the observed rates of absorption were relatively higher than when the sister roots were present, but the distribution of the velocities of absorption remained the same. Changes in the distribution of the rates of absorption occurred but these were related to other phenomena, not to the presence or absence of sister roots.

By using a greater number of micropotometers, by placing them close together, and by changing the positions in different experiments, it was found that all regions of the root between the root cap and 16 mm. from the apex absorbed water. The highest rates observed were exhibited by the region 14 to 16 mm. from the apex. All of the roots exhibited a distinct unidirectional gradient of increase in the rates of water absorption by unit surface areas from the apex towards the base. However, individual roots show considerable diversity in water-absorbing power. The results of measurements made on 10 roots with initial lengths of 25 to 32 millimeters, continuing throughout a fourteen-hour observation period, and using four micropotometers are given in figure 4, A.

Frequent adjustments (15 to 30 minute intervals) of the micropotometers were made in order to maintain them in the positions designated by the stippled areas (*a, b, c, d*) in the diagram of the root illustrated in figure 4. The greatest variation in any one experiment from the regions designated was 0.5 mm. in a rapidly growing root. Measurements were made every two hours, and calculations were made of the average rate of absorption in milligrams of water per hour per square millimeter of surface exposed to the water in the micropotometers. The highest and lowest rates given in graphic form in figure 4 A, are the rates of absorption in four regions of two different roots and are the result of averaging seven determinations throughout the fourteen-hour period. On the other hand, the graphic representation of the average rates in figure 4 A, are the average rates of all measurements made on the designated regions in 10 different roots.

Several interesting facts are apparent when a comparison is made of the heights of the bars in figure 4 A. In the first place, the comparison shows that there is a wide variation between the highest and lowest rates observed in any one region; in the second place, it shows that in spite of the large difference between these two roots which exhibit the highest and lowest rates, each individual root manifests a distinct functional polarity with respect to the distribution of the rates of absorption in these regions; and in the third place, the polar distribution of the rates of water absorption is also shown by comparing the average rates of all of the regions in all of the roots.

A comparison of the percentage differences in the average rates of absorption of the four regions in all of the roots shows that the region between 14 and 16 millimeters from the apex absorbed water at a rate which


A
Lowest rate
Highest rate
Average rate
Absorption of H_2O mg/mm²/hr
.200
.150
.100
.050
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 mm
a
b
c
d
B
Lowest rate
Highest rate
Average rate
Absorption of H_2O mg/mm²/hr
.200
.150
.100
.050
a b c d
20 to 29.9
a b c d
30 to 39.9
a b c d
40 to 49.9
a b c d
50 to 59.9
a b c d
60 to 69.9 mm

was 26.4 per cent. greater than the region between 8 and 10 millimeters, 54.9 per cent. greater than the region between 4 and 6 millimeters, and 150 per cent. greater than the region 0.5 to 2.5 millimeters from the apex. The region between 8 and 10 millimeters absorbed water at a rate which was 22.5 per cent. greater than the rate in the region between 4 and 6 millimeters, and 17.7 per cent. greater than the region at the extreme apex; and the zone between 4 and 5 millimeters absorbed water at a rate 61.3 per cent. greater than the most apical region designated as *a* in the diagram of the root in figure 4 A. These four regions were selected for special study because they are the regions which determine the characteristic distribution of bioelectric potential in the onion root.

2. EFFECT OF AGE ON THE RATES OF ABSORPTION IN APICAL REGIONS

In order to determine the effect of age, measurements of the rate of absorption were made throughout a growth period when the roots elongated from an initial length of 20 mm. to 90 mm. or more. The micropotometers were maintained in the relative positions designated as *a*, *b*, *c*, and *d* in the diagram of the root (fig. 4 A) by moving them at intervals of an hour during the day and 6 hours at night. The values obtained at the first morning determinations were therefore a little high. The greatest shift in the position of the micropotometers in a single root was 4 millimeters, the average for all roots, 2.4 millimeters. The micropotometers had to be refilled during the course of the experiments but this was done very quickly with a pipette and no apparent drying of the root occurred.[2] Measurements were made every 4 to 6 hours. In order to compare the change in the rate of absorption of each region with age, the average rates of each region in each root during a growth interval in which the root increased in length from 9 to 9.9 mm. (to be designated as a 10-mm. growth period) were determined. Measure-

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[2] Recent modifications of the apparatus permit refilling of the micropotometers, and removing any collected fog on the glass wall facing the microscope, without changing the humidity of the interior of the chamber.

FIG. 4. Comparative rates of absorption in different roots. A. Rates of water absorbed by 4 apical regions of 10 different roots during a 14-hour observation period. Initial lengths of roots were 25 to 32 mm. The positions of the micropotometers are indicated by the stippled areas *a*, *b*, *c*, and *d*, in the diagram of the root while the vertical bars above represent rates of absorption in the corresponding region. Bars with vertical lines give rates of absorption in the root which manifested the lowest rate, bars with crossed lines give rates of absorption in the root which manifested the highest rate (each bar is average of 7 observations). Solid black bars give average rates in the designated regions during the 14-hour period for all roots. B. Change in rate of water absorption with age. Vertical bars represent the rates of absorption during 5 growth intervals by each region corresponding to *a*, *b*, *c*, and *d* in the diagram of the root. Bars with vertical lines and crossed lines give lowest and highest rates respectively, solid black bars give average rates of 11 different roots. Growth intervals are designated in mm. below the vertical bars.

ments were made on many roots. The exact time at which the 9 to 9.9 mm. increase in length was reached was not observed in all cases, since on certain nights the time interval from one reading to the next was 6 hours. Only the results obtained from eleven roots, in which the transitional changes from one growth interval to the next were observed, are included in the graphic representation in figure 4 B. Tables of detailed measurements are omitted in order to save space.

The highest and lowest average rates observed in individual roots during the 10-millimeter growth period are represented graphically in figure 4 B by the vertical bars with the crossed lines, and with the vertical lines, respectively. A comparison of the heights of the bars with vertical lines shows that in the corresponding root the increase in rate of absorption of each region for each 10-mm. growth period was not uniform. Regions *a* and *b* in this instance reached a maximum rate during the 50 to 59.9-mm. growth period, region *c* in the 40 to 49.9-mm. growth interval, and region *d* in the 50 to 59.9-mm. interval. A comparison of the heights of the crossed bars show that in another individual root region *d,* which was 14 to 16 mm. from the apex, reached a maximum earliest (40 to 49.9-mm. interval), and regions *c, b,* and *a* followed in the next interval (50 to 59.9-mm.). The results obtained from measurements on these two roots demonstrate that individual variations exist and that a given region does not necessarily exhibit a maximum rate of absorption when another region (or regions) of the same root reaches a maximum rate. However, characteristic changes are the rule. The majority of roots tend to manifest maximum absorption rates when they reach lengths between 40 and 60 mm. as shown by a comparison of the heights of the solid black bars in figure 3 B. These represent the average rates of absorption in the designated regions for all of the roots during five growth intervals. Since during the night there was a relatively greater increase in the distance of each water column from the apex, this would tend to make the average rates of absorption somewhat higher at each region than if the positions of the micropotometers relative to the apical point did not change. Exceptions were found, especially in relatively short roots (less than 40 mm.) which developed late and grew slowly, and in relatively long roots (over 60 mm.) which developed early and grew rapidly. Calculations of the percentage difference in the average rates of absorption in each region for all the growth periods are tabulated below.

1. Region *d* which was 14 to 16 millimeters from the apex.

Growth intervals in mm.	Percentage differences
20 to 29.9 and 30 to 39.9	36.0 per cent. increase
30 to 39.9 and 40 to 49.9	6.4 per cent. increase
40 to 49.9 and 50 to 59.9	3.0 per cent. increase
50 to 59.9 and 60 to 69.9	16.2 per cent. decrease

2. Region *c* which was 8 to 10 millimeters from the apex.

Growth intervals in mm.	Percentage differences
20 to 29.9 and 30 to 39.9	24.1 per cent. increase
30 to 39.9 and 40 to 49.9	11.2 per cent. increase
40 to 49.9 and 50 to 59.9	2.75 per cent. increase
50 to 59.9 and 60 to 69.9	15.4 per cent. decrease

3. Region *b* which was 4 to 6 millimeters from the apex.

Growth intervals in mm.	Percentage differences
20 to 29.9 and 30 to 39.9	30.7 per cent. increase
30 to 39.9 and 40 to 49.9	11.7 per cent. increase
40 to 49.9 and 50 to 59.9	4.2 per cent. increase
50 to 59.9 and 60 to 69.9	13.7 per cent. decrease

4. Region *a* which was 0.5 to 2.5 millimeters from the apex.

Growth intervals in mm.	Percentage differences
20 to 29.9 and 30 to 39.9	53.8 per cent. increase
30 to 39.9 and 40 to 49.9	25.0 per cent. increase
40 to 49.9 and 50 to 59.9	18.4 per cent. increase
50 to 59.9 and 60 to 69.9	23.2 per cent decrease

B. ABSORPTION OF WATER BY RELATIVELY MORE BASAL REGIONS

By placing a large number of micropotometers on a given root, and by shifting the positions of the micropotometers when desired, determinations of the rates of absorption in all the root regions between the root cap and the bulb were made. It was found that all the root regions from the root cap to the base absorbed water, but at different rates, and that the distribution of the rates of absorption was not the same for all roots. The determinations demonstrated that in roots less than 50 mm. in length, there was in general an increase in the rate of absorption per unit surface from apex to base, and the highest rates occurred in the regions nearest the bulb; whereas in roots over 70 mm. in length, the regions of maximum absorption were relatively more apical. In the majority of roots over 80 mm. in length, maximum rates were observed in regions within the first 40 mm. from the apex. Although experiments have been made on many roots of different lengths and age, it was found that all of the root regions between the root cap and the base absorbed water. The longest root studied was 220 mm. in length. Most roots tend to develop lateral roots at the age of 2 to 3 weeks. It was observed that there was a definite shift of the region of maximum absorption rate towards the apex, with the development of lateral roots. It is entirely possible and highly probable that the regions of the

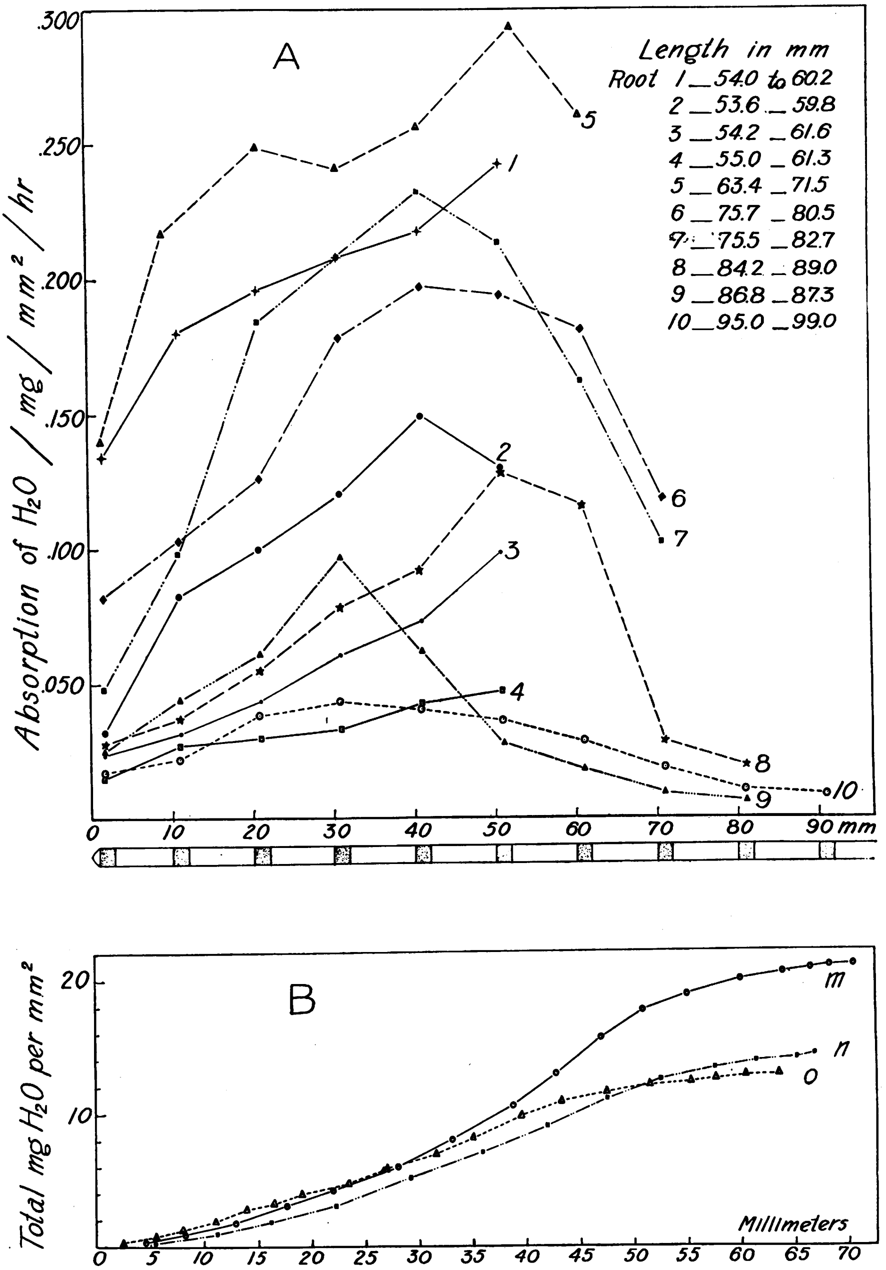

FIG. 5. A. Rates of water absorption in 10 selected regions of 10 different roots during a 12-hour observation period. Curves 1 to 10 represent the average rates of water absorption by 10 different regions in ten different roots corresponding to the numbers on

root not exposed to the water of the micropotometers also absorbed water since they were in a saturated atmosphere.

Figure 5 A shows the rates of water absorption in selected regions of ten roots, the initial lengths of which varied from 54 to 95 mm. The positions of the micropotometers were maintained relatively constant with respect to the apex of each root by moving them at intervals of one-half hour or less. Measurements were made every two hours during a 12-hour period, and the average rate of absorption for each 12-hour period was calculated and plotted on a graph as shown in figure 5 A. The initial and final lengths of each root are given in figure 5 A, after the first column of numbers, which correspond to those of the curves of distribution. The stippled areas in the diagram of the root below the curves represent the positions of the micropotometers which were placed 10 mm. apart. A comparison of all of the curves shows that the highest rates of absorption are exhibited by relatively more basal regions, and that the region where maximum rates occur varies in individual roots, but is closely linked with the lengths of the root. The initial lengths of the 4 roots which exhibited the rates given by curves 1, 2, 3, and 4 (fig. 5), were less than 60 millimeters. A comparison of the slopes of these curves demonstrates considerable individual differences in the rates of absorption of different roots, but all manifest an increase in the rate per unit surface from apex to base. Note that in curve 5 (fig. 4 A) there are variations in the distribution of the rates of water absorption, although the highest rates relative to the apex are observed in the basal regions. As shown by curves 1, 2, 3 and 4, maximum rates of absorption are found at or very near the base in roots of this length. These roots were 10 to 15 days old. Curves 5, 6, 7 (fig. 5 A), which represent measurements on roots 63 to 75 mm. in length, show that comparatively rapid rates of absorption are exhibited in all regions and that the maximum rate appears in regions nearer the apex. The experiments show that, with increasing age, the regions of maximum absorption shift toward the apex. This fact is further emphasized by comparing curves 1 to 8 with curves 8, 9, and 10, obtained from experiments on roots over 80 mm. long.

The above results and those depicted in figure 4 B indicate that each root region exhibits an increase in the rate of absorption, which goes through a maximum with age. Experiments to prove this were made, and the results are given by curves *m, n,* and *o* (fig. 5 B). Each curve represents the

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the right of the figure. The corresponding initial (first column) and final lengths (second column) of each root are given after the root numbers. Stippled areas of the root in the diagram below the curves show the positions of the micropotometers. B. Change in quantity of H_2O absorbed by a given region with age. Curves m, n, and o obtained from 3 different roots show the mg. of water absorbed by a single region during an observation period when the distance between the fixed micropotometer and the apex increased with growth.

rates of absorption in one region of a single root. The initial lengths of the roots which correspond to curves *m, n,* and *o,* were respectively 20.3, 27.0, and 32.6 millimeters. In each experiment, after the onion bulb had been in the chamber 8 hours, the position of the single micropotometer used was adjusted so that the lower meniscus was within 0.5 mm. of the root tip. Measurements were made at 10-hour intervals. Since the position of the micropotometer on each root was not changed, the distance between it and the growing root tip increased with increase in root length as the root grew, but remained the same distance relative to the base of the root, after fifteen hours or less, depending upon the rate of elongation. The slopes of the curves *m, n,* and *o,* all show a typical sigmoid curve. It is obvious that at each region there was an increase in the rate of absorption with age, and that each region passed through a maximum when it was from 40 to 60 mm. from the apex. These experiments corroborate the conclusions given above that the distribution of the velocities of absorption depends upon the age of the root.

Discussion

The experimental evidence which has been presented heretofore regarding the absorption of water by the apical meristem is not in agreement. PRIESTLEY and TUPPER-CAREY (5) showed that the apex was relatively impermeable, HÖHN (1) that comparatively little absorption occurred, while SIERP and BREWIG (8) maintained that the first 5 mm. of the apex not only showed an absence of absorption, but that it actually gave off water. A large number of investigators, including POPESCO (4), URSPRUNG and BLUM (9), KELLER (2), and HÖHN (1), claim that the chief absorbing zone is the region just proximal to the zone of elongation. KELLER (2) maintains that the distribution of the rates of water absorption in the root corresponds to the distribution of bioelectric potentials. Most of the work on absorption rates has been carried out on roots other than those of the onion. Just as individual roots exhibit variations in the velocities of absorption and their distribution, it is to be expected that differences will be found in the roots of different plant species. However, such differences would not account for the pronounced lack of agreement found among the investigators mentioned above.

It is doubtful if much value can be placed on the recent experiments carried out by SIERP and BREWIG (8) since the roots were stimulated by inverting the normal orientation with respect to gravity and by wrapping the roots at intervals with cotton thread. It does not seem likely that the apical meristem gave off (excreted?) water unless disintegration of the tip occurred. The authors state (8, p. 107) that the increase in the micropotometer volume was at least 149 mm.^{3} whereas the increase in the volume of the root apex resulted in a maximum of 3 mm.^{3} but they do not state how they determined the increase in root volume. Measurements have been made by the author on the roots of onions maintained in the inverted position but no such unique phenomenon has been observed. On the contrary, the regions between the root cap and base all absorbed water and the polar distribution of the rates of absorption was maintained. However, in these experiments, transpiration was at a minimum. SIERP and BREWIG on the other hand, enclosed the inverted stems of their plants in a chamber and varied the humidity.

SIERP and BREWIG also state that, with increase in transpiration rates, there is a migration of the region of maximum absorption toward the apex. They do not, however, show whether this shift is dependent on age, as it is in the onion root. Owing to the fact that the onion bulb provides a reservoir of water, the onion does not furnish good material to determine the relations between water absorption and transpiration. Nevertheless the writer found that in the onion root there was an increase in absorption at all of the root regions under certain conditions when transpiration was increased; but the polar distribution of the rates of water absorption was always maintained.

HÖHN (**1**) claims that the entire root surface of the roots he studied (*Zea mays, Triticum vulgare, Tradescantia fluminensis*) absorbed water. As mentioned above, he failed to make simultaneous measurements of water absorption in a single root, and his tabulated data do not support the conclusions he has made. HÖHN maintains that the hourly water absorption of an old root, calculated on the basis of unit length, is greater than that of a younger root in most of his experiments; but his tables do not warrant such an interpretation. Table 8 (**1**, p. 550) shows, for example, that a root 65 mm. in length absorbed 0.43 mg. of water per hour per mm. length of the root, whereas a root less than half this length (26 mm.) absorbed 0.89 mg. of water per hour per unit root length. It may be that the shorter root had grown slowly and was actually the older root, but HÖHN presents no evidence in favor of this suggestion. Table 9 (**1**, p. 551) shows that a root 58 mm. in length absorbed 0.62 mg. of water per unit length in unit time, while another root 25 mm. in length absorbed 1.16 mg. of water. The longer root, which was over twice the length of the shorter, absorbed water at half the rate. HÖHN's tables merely establish the fact that individual differences exist with respect to the rates at which different roots absorb water. Although HÖHN states that he used "similar" roots, his data furnish no evidence in support of his statements, since no measurements of root diameter were made.

KELLER (**2**) used dyes to determine the rates of water absorption in the root, and reached conclusions similar to those of POPESCO (**4**). In favor of his hypothesis that electro-osmotic forces are involved in water absorption and transport, KELLER calls attention to the correspondence of their results—which maintain that the main absorbing region of the root is the region of elongation—with those of LUND (3) on bioelectric potentials in the onion root, which show that the region of elongation is electronegative to other regions of the root.

The results presented in this paper of direct quantitative determination of the rates of water absorption in the onion root itself show that there is no correspondence between the unidirectional gradient of distribution of the velocities of water absorption in roots less than 50 millimeters in length, and the distribution of electric potentials in roots of similar length as shown by LUND and co-workers (3, 7). The region of relatively low electronegativity from 4.5 mm. to between 7.5 to 14 mm. is not the region which exhibits either a maximum or minimum rate of absorption except in very old roots (over 3 weeks) and then rarely. The fact that the gradient of the distribution of electric potentials in the onion root does not correspond to the gradient of the distribution of velocities of water absorption does not necessarily indicate that electric energy is not utilized in the processes of absorption and transport. Experiments to determine possible linkage between the production of electric energy and the absorption of water in the onion root are being carried out at the present time.

The most striking facts brought out in this paper are that in the onion root, all root regions between the root cap and the base absorb water at different rates, that the rates of absorption per unit area change with time, going through a maximum. The precise measurements show definitely that the distance from the apex to the exact region which exhibits the highest rate of absorption differs in individual roots and changes with age.

The present paper makes no attempt to consider the mechanism or mechanisms involved in the absorption of water; but it furnishes for the first time precise quantitative data concerning the distribution of the velocities of water absorption in a single intact root under carefully controlled conditions.

Summary

1. A technique is described by means of which precise quantitative data on the velocities of absorption of tap water by different root regions of the same intact root may be simultaneously determined under carefully controlled conditions.

2. All root regions of the onion root between the root cap (on which no measurements were made) and the bulb absorb tap water but at unequal rates.

3. In relatively young roots (less than 50 mm.) there is a unidirectional gradient of the distribution of velocities of water absorption, the region of maximum absorption appearing at the base.

4. In relatively older roots (more than 70 mm.) there exist two pronounced unidirectional gradients with maximum absorption velocities appearing in regions 40 to 60 mm. from the apex.

5. The velocities of absorption of water are less in all root regions between the root cap and base in any one root when all of the sister roots are present. Removal of sister roots increases the rates of absorption in all root regions of the remaining root.

6. Each root region goes through a maximum with respect to age, exhibiting highest velocity rates when the root is from 40 to 60 mm. in length.

7. With increase in age there is a shift of the region exhibiting maximum rates toward the apex.

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