

COMPARISON OF RATES OF WATER INTAKE IN CONTIGUOUS REGIONS OF INTACT AND ISOLATED ROOTS

HILDA F. ROSENE

(WITH SEVEN FIGURES)

Introduction

Although extensive investigations dealing with the problem of water absorption in roots have been carried out for many years, practically no attempt has been made to obtain quantitative data on water absorption by root tissue *per se*. Most of the investigations in the past have been made on intact and topped plants. When, however, it is desirable to compare the activities of the root in the presence of shoot influences with those in its absence, it is imperative that all of the shoot tissue be removed; since it has been shown (16) that auxin applied to the topped stem influences translocation of water and solutes in the roots, it may be that substances produced by the stem will do the same.

It might be objected that roots removed from their "normal" connections by excision are in an "abnormal" state. Such roots nevertheless continue to grow and transport water and solutes for many hours after excision. As pointed out later, a given region in a single root under controlled conditions may even transport greater volumes of water *after* excision.

Experimental studies on isolated roots and pieces of roots under properly controlled conditions may yield results that are of fundamental significance to a basic understanding of the dynamics of water transport in all tissues. Indeed, many of the basic problems of solute absorption and accumulation have been effectively studied on excised roots by HOAGLAND (4), HOAGLAND and BROYER (5), PREVOT and STEWARD (11), and STEWARD (17). With respect to water transport in root tissue *per se*, WHITE (18) demonstrated that there was a continuous unidirectional flow through isolated tomato roots growing *in vitro* and that such roots manifest six atmospheres or more of root pressure.

Investigations on the direct determination of water absorption by various root regions are few in number. These have not been carried out under conditions or by techniques which make the results strictly comparable. Even the objectives of the investigators have been different. To obtain consistent results such variables as age and nutritional history of the roots, seasonal effects on the development of the root systems, and variability of material must be taken into consideration (HOAGLAND and BROYER, 5). ROSENE (13) demonstrated that the magnitude and distribution of rates of

water absorption in a single root change with aging of the tissues. Unless authors state the age of roots as well as the length, comparisons are not as significant as they might otherwise be. The structural differentiation of a 65-mm. onion root six days old, for example, is very different from that of a 65-mm. root which has grown slowly and is three weeks old; the first has no lateral branches, the second may be profusely branched. In the investigations of HÖHN (6), SIERP and BREWIG (15), and GREGORY and WOODFORD (3) water intake by different root regions was expressed in centimeter length of root. ROSENE (13) by means of a different technique determined simultaneously unit flow in unit time through unit surface area in the different root regions. Because of differences in diameter of a single root from apex to base and of different roots, significance of comparisons of the results of the different investigators mentioned above are limited.

HÖHN (6), working with roots of *Zea mays* and *Tradescantia fluminensis*, SIERP and BREWIG (15) with roots of *Vicia faba*, *Zea mays*, and *Ricinus communis*, and ROSENE (13) with roots of *Allium cepa* conclude that the entire surface of roots less than 10 cm. in length is capable of water absorption. Both HÖHN and ROSENE maintain that relatively little absorption occurs in the apical meristem, while SIERP and BREWIG conclude that this region frequently manifests water loss. HÖHN, SIERP and BREWIG, and ROSENE are in agreement that maximum rates of water absorption are exhibited by relatively more basal regions in roots less than 70 mm. in length.

Up to the present no study had been made to determine the rates of water absorption in different regions of an individual root both before and after excision. The present investigation was carried out with this purpose in mind. It serves as a foundation and departure for further studies of water transport by root tissue.

Experimentation

METHOD

The investigation was restricted to relatively young onion roots (*Allium cepa*) less than 65 mm. in length and not more than a week old. The onions were readily cultured in aerated solutions—TRELEASE culture solution or in nutrient tap water.¹ Ordinarily the roots develop no laterals in culture solutions until they are over 2 weeks old. Since the present study did not include effects of transpiration on water intake and since relatively long roots often developed before leaves, the roots were cultured in the dark. This appeared feasible because the bulb furnished a ready supply of carbohydrate. It also simplified experimental technique since the entire plant

¹ Analyses of tap water were kindly furnished at intervals by Prof. E. P. SCHOCH, Director of the Bureau of Industrial Chemistry.

could be transferred to a single experimental chamber in which it was not necessary to illuminate the leaves at the same time that the roots were protected from light. No analyses of roots were made; they were of unknown sugar and salt content.

Detailed description of the apparatus and technique employed are omitted since these have been published (13). It is, therefore, necessary to describe only those modifications in procedure which are pertinent to the present investigation. Having placed the plant in the moist chamber, the cover was not removed until the experiment was complete. This was possible because all manipulations were precisely controlled from the outside. When desired, fluid could be added to or withdrawn from the potometers, menisci adjusted, the root excised or cut into segments, and the potometers or the root raised and lowered without disturbing the interior atmosphere. Rates of elongation, the average diameter of the root, height of the water column at each root contact, and the movement of the terminal meniscus in each potometer were measured with an eyepiece micrometer. No water flow along the root from one potometer to that below was observed. Several methods, including the use of dyes, were used to check on this possibility. Probably the most convincing check that higher rates were observed at higher levels because of inherent characteristics of the root itself and not fortuitous circumstances was the fact that when the root was inverted the higher rates of basal levels produced greater withdrawal of water from the lower potometers. Clear cut water columns without merging of menisci were maintained when potometers were placed side by side and the distance between the menisci of the separate root contacts was 0.2 mm. There was no difficulty with the appearance of bubbles at either the potometer contact or within the potometer tube.

A duplicate potometer tube, separate from the root in the chamber and filled with the experimental solution was used as a control blank. Various methods were used to saturate the air within the experimental chamber with water vapor; in some experiments a continuous spray of water was maintained within the chamber without coming into contact with the plant itself; in others vapor-saturated air under a slight positive pressure was slowly passed through, or vessels of distilled water were placed on the chamber floor preceding the experiment and the interior was not disturbed during the experiment. Similar results were obtained by all three methods. Between readings, the fog on the thin glass window was removed by a special wiper manipulated from the outside. A relatively constant room temperature ($\pm 0.5^\circ$ C.) was maintained throughout an experimental period. Excised roots were maintained in position by attaching them to a fine glass rod with a minute quantity of vaseline; this rod was attached to the potometer support. Experiments were run in quadruplicate. Volume error in rates due to readings was less than 0.002 mm.^3 per mm.^2

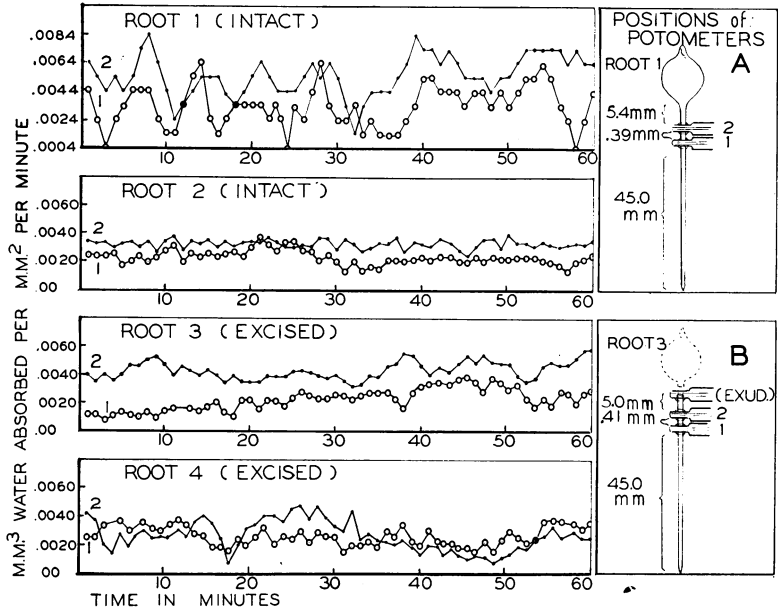


FIG. 1. Volume of distilled water absorbed per unit surface per unit time by two contiguous local zones of tissue in the basal regions of two intact and two excised roots in a vertical position. Diagrams A and B show positions of potometers 1 and 2 on roots 1 and 3. The potometers on roots 2 and 4 were in the same relative positions. Curves 1 and 2 for each root show the rates of intake at the corresponding potometer contacts. Roots were placed in the chambers 3 hours before observations were made. The roots were 4 days old. Room temperature, 26° C.

WATER INTAKE BY CONTIGUOUS REGIONS DURING SHORT INTERVALS OF TIME

Comparisons of the velocities of water absorption in two adjacent regions with relatively similar structural differentiation were made by placing two adjoining potometers at basal levels in both intact and excised roots of the same age and length. Diagrams A and B, figure 1, show the respective positions of adjoining potometers on two roots; curves of the rates of intake of distilled water at each of the potometer contacts in two intact and two excised roots are presented in figure 1. The curves are typical. Most roots, intact and excised, including many which absorbed nutrient solutions from adjoining potometers, manifested rhythmic variations in the rates of intake per minute; the magnitude of fluctuations varied from root to root, and sometimes a general drift in the velocity of absorption at each contact was observed. In most roots (less than 50 mm. in length and 3 or 4 days old), including those represented in figure 1, the rate at the proximal potometer contact was higher and the variations at the two contiguous contacts in each root appeared to occur quite independently of one another.

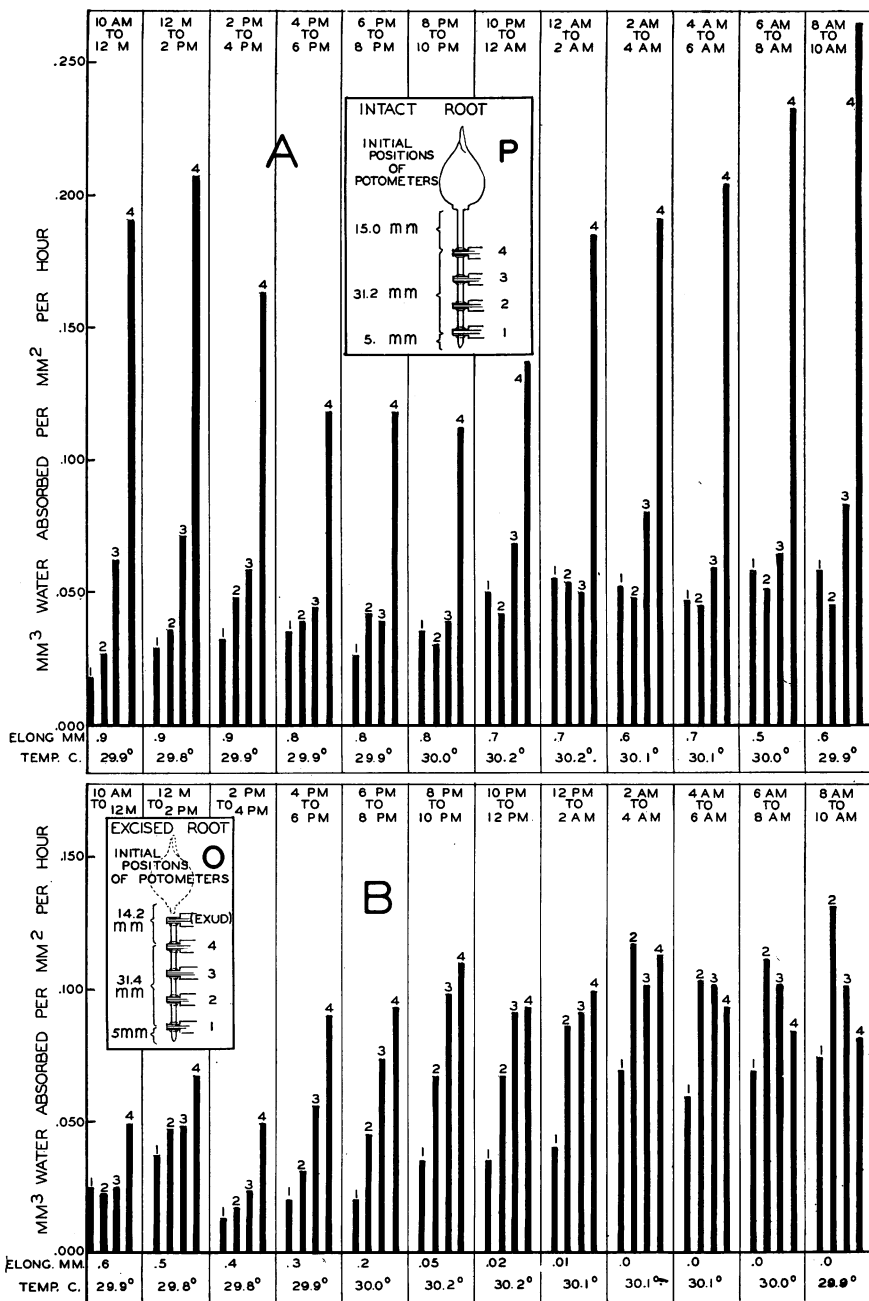
COMPARISON OF RATES OF WATER INTAKE IN DIFFERENT INTACT
AND EXCISED ROOTS DURING 24-HOUR PERIODS

In order to compare variations in the axial distribution of the velocity of absorption of intact and excised roots, readings were made at two-hour intervals throughout a 24-hour period. A two-hour time interval was selected in part because apical regions manifest comparatively slow rates; volume intake per unit surface area per hour was calculated for each interval.

The onion bulbs with attached roots were placed in the experimental chambers the evening preceding each experiment. They were supplied with abundant water and aeration. At 8 A.M. the following morning, without removing the glass chamber covers, the potometers were refilled and their positions adjusted and the roots in two of the chambers were excised. Each root was maintained in a vertical position and threaded through potometers 10 m. apart. (See diagrams P and O, figs. 2 and 3). Exudate was collected in the top potometer in two chambers which contained excised roots. No readings were made until 10 A.M.

Sixteen experiments were run. Since uniform results were obtained throughout, data from only four roots present the facts adequately; data showing the axial distribution of rates in two roots (one intact, the other excised) from an experiment run at a temperature of $30 \pm 0.2^\circ$ C. are presented in graphic form in figure 2, A and B, and from another experiment at $23.5 \pm 0.2^\circ$ C. in figure 3.

A comparison of the heights of the vertical bars during the first interval (10 A.M. to 12 M.) show that all four roots exhibited the highest rate of intake at a relatively basal level when the experiment began. With the exception of the excised root shown in figure 2, B, this region continued to maintain the highest velocity of intake throughout the 24-hour period; the maximum in root B, figure 2, appeared at a lower level after 2 A.M. The maintenance of a strict unidirectional gradient of distribution of velocities from interval to interval was not exhibited by any of the four roots considered above; this was also true in the other roots observed but not included in the figures. In both intact and excised roots the gradient varied from interval to interval, sometimes showing one or more minor peaks with a maximum at 30 mm. (from the apex) or above; the pattern of axial distribution thus exhibited a state of flux which was determined by the fluctuations that appeared in each region. These fluctuations in a given root are evident when the heights of the bars with a given number are compared. Comparison of the rates at neighboring regions show that they sometimes exhibited fluctuations opposite in direction, one manifesting an increase and the other a decrease during the same interval of time. The magnitude of



change during consecutive intervals was not uniform in the different regions of a single root.

The roots absorbed water at higher rates during the latter half of each experiment. Elongation in the excised roots ceased during the latter half of the 24-hour period but continued in the intact roots as indicated by the rates given below the vertical bars in each figure. Since the potometers were not moved throughout the experiments, the position of each relative to the tip "migrated" towards the base. The same tissue remained at each contact all the time, but since elongation occurred at the apex, the regions became more basal relative to the apex. "Migration" of the tip away from the potometers was greater in the intact root and therefore this may account for the steeper gradient sometimes observed in intact roots (*cf.* gradients of roots A and B, fig. 2). Since high rates at basal levels occur in young roots as a rule (13), this increase is to be expected in intact roots at this stage of development. The change in rate with time was not synchronous in the different root regions of intact and excised roots; different regions of the same root manifested maxima at different intervals. Although elongation had ceased in excised roots, they continued to absorb water at rates higher than those manifested during the first 10 hours after excision. In one or two cases not represented by figures, maximum rates were observed during the first half of the 24-hour period in both intact and excised roots. Whether or not excised roots exhibit periodicity was not determined.

The range of variation in rates from minima to maxima in intact and excised roots throughout the 24-hour period was greater in excised roots in most cases. Minimal and maximal rates at each region in 12 roots observed during the 24-hour period are shown in figure 4. The ratio $\frac{\text{maximum}}{\text{minimum}}$ given below each set of two vertical bars shows the magnitude of increase at the regions designated by the numbers above the bars. Diagrams of the exact positions of the potometers on each of the 12 roots are not given owing to lack of space.

The greatest magnitude of increase exhibited by an intact root is repre-

FIG. 2. Comparison of the axial distribution of rates of water intake in four different regions of an intact and excised root during two-hour intervals throughout a 24-hour period. Roots 5 days old; grown in tap water; same medium in potometers. A. Velocity of absorption in *intact* root; B. Velocity of absorption in *excised* root. Initial positions of potometers in each case are shown by the inset diagrams P and O. Height of each vertical bar gives average rate of absorption in a given region during a two-hour interval; each region is indicated by the number above each bar which corresponds to the number of the potometer in that region in the diagrams P and O. In each case the bar which represents the rate at the potometer in the most distal position (nearest the apex) is at the left, the others follow in order. Elongation in millimeters and the average temperature during each interval are given below the bars.

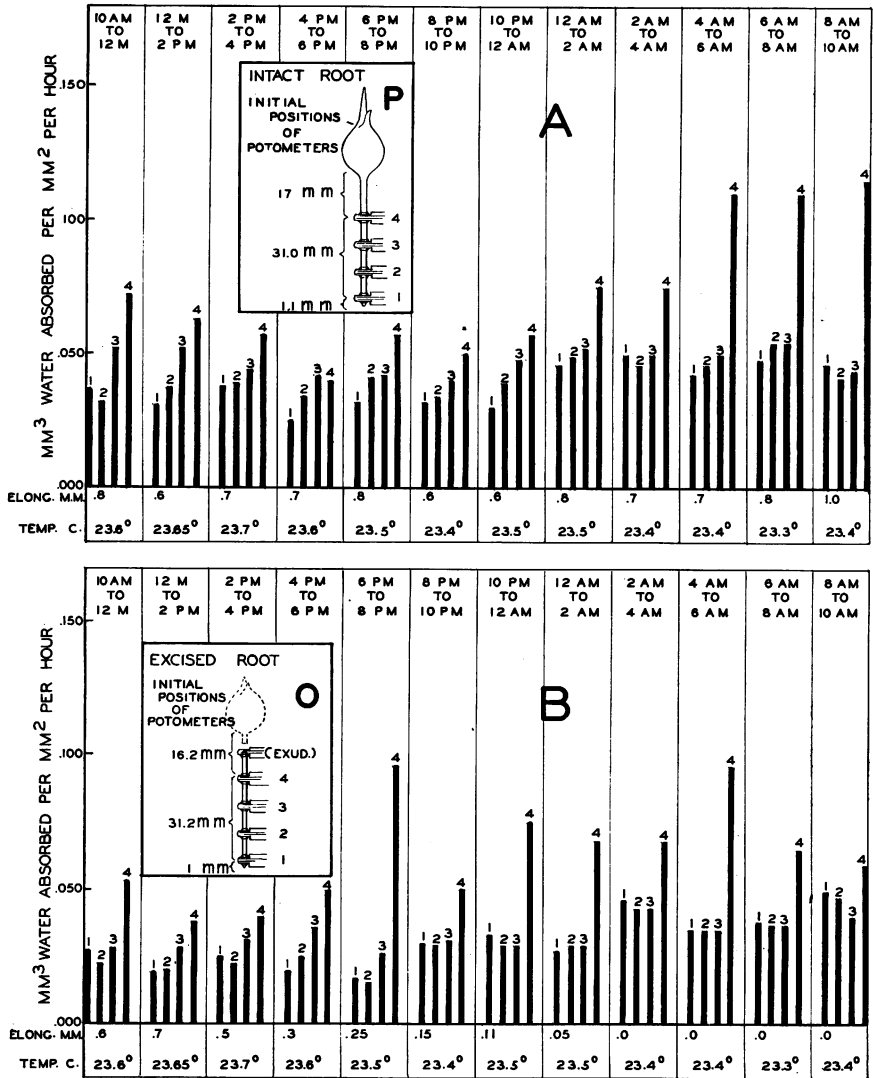


FIG. 3. Legend as for fig. 2.

sented by the ratio of 5.97 (change in rate of 600 per cent. which occurred in root II, figure 4, at potometer 3, at approximately 25 mm. from the apex²), a 5-fold increase occurred in two other intact roots (fig. 4, roots I and VI). The minimum increase exhibited by intact roots of this group is

² Rate of elongation and the consequent "migration" of each potometer from its initial position was not the same in all roots.

represented by the ratio of 1.35 in the case of root IV, potometer 3 (approximately 25 mm. from the apex).

On the other hand, the excised roots show ratios ranging from maxima of 11.5 and 10.5 (25- and 35-mm. levels of root VIII, fig. 4) to a minimum of 1.65 (at approximately 25-mm. regions of roots IX and X, fig. 4). Although a 3-fold increase at any one level was observed in only one of the 6 intact roots (root III), increases of this magnitude occurred at one or more levels in five of the excised roots.

In general the magnitude of increase in volume flow with time was greater in excised roots; but the absolute velocity of absorption in the different root regions was usually greater in intact roots, especially in the relatively more basal regions. Exceptions occurred in which excised roots manifested higher rates than intact roots of the same experiment.

These experiments show that the polar axial gradient of distribution of velocities of intake of water exhibited by intact roots is an inherent characteristic of the isolated root removed from all bulb influence; the experiments also demonstrate the occurrence of oscillating rates in volume flow at different root regions in both intact and isolated roots but a general increase in volume flow in each region with time. With respect to water absorption marked differences in the behavior of different intact and isolated roots appear to be absent.

The data indicate that local regions of any one root exhibit characteristic rates of absorption which depend upon the nature of the local tissue in question. This is true both when attached to the bulb and after isolation from the bulb by cutting as substantiated in the following section.

EFFECT OF PRESENCE AND ABSENCE OF BULB ON WATER INTAKE BY THE SAME ROOT

The above experiments on different intact and isolated roots did not show whether or not absorption in one or more local regions of the same root is visibly affected when the root is cut from the bulb. Consequently, experiments were run in which measurements of the rates of intake were made at given levels of the same root both preceding and following excision.

Uniform results were obtained in all the experiments; typical data from experiments with potometers in relatively (1) apical and (2) basal positions are shown in figures 5 and 6 respectively. The initial positions of the potometers relative to the apex are shown in the corresponding diagrams A and B. Five or six potometers were used on each root; exudate collected in the top potometer (no. 6, fig. 5, and no. 5, fig. 6) after excision. Clean cut excision of each root without disturbing the menisci of the lower potometers was made by placing an excess of culture solution around the root region at the top potometer and deftly cutting the root with a sharp piece

of thin razor blade attached to a long glass rod manipulated from the outside.

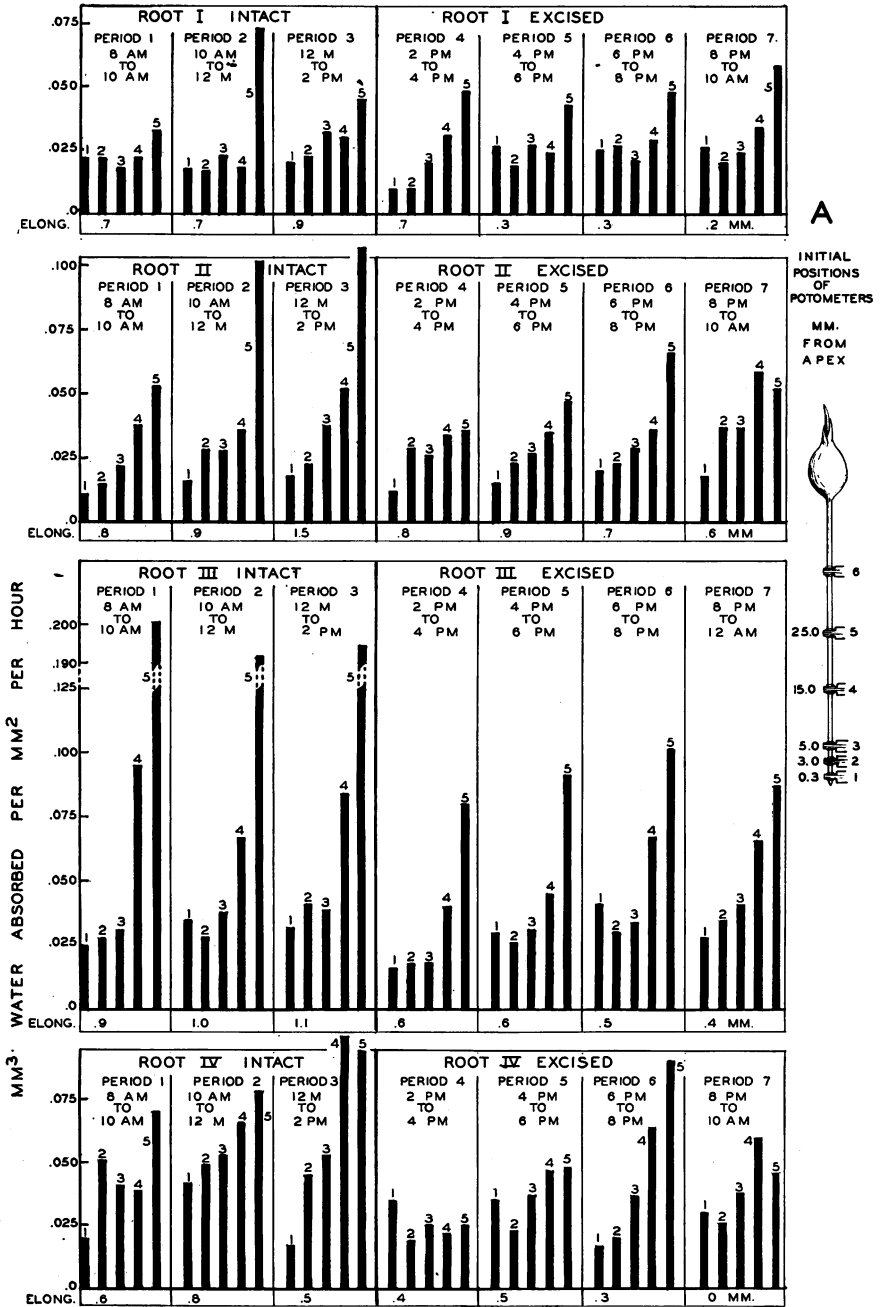
The data represented by figure 5 were obtained from experiments with readings at 2-hour intervals for 6 hours preceding and 6 hours following excision. The average rates during a subsequent overnight period of 14 hours were also determined.

A comparison of the axial gradients of distribution in figure 5 shows that the polar apical-basal differences exhibited when the bulb was present *were maintained in its absence*; the magnitude of the apical-basal difference, however, was less in three of the roots after excision. When the rates manifested in period 3 immediately preceding excision are compared with those of period 4 immediately following, both an increase and decrease in rates at different regions are noted. The decrease in rates was conspicuous at potometers 3, 4, and 5 but root I showed a slight increase in volume flow at potometer 4; an increase in rates was also manifested at potometer 1 in root IV, and at potometer 2 in root II.

It is interesting to note that these changes in rates at local regions between periods 3 and 4 were not necessarily any greater in magnitude nor different in direction from the fluctuations which appeared between two other consecutive intervals, either in the presence or absence of the bulb; compare, for example, the magnitude and direction of change at potometer 5 root I, and at potometer 1 root IV, during periods 1, 2, and 3 when the bulb was present. Furthermore, increase in volume flow during subsequent periods (periods 5, 6, 7, fig. 5) was exhibited by one or more regions in the absence of the bulb; measurements of rates of intake made immediately following excision are not necessarily representative of the rate of intake in the excised state as shown in the previous section.

At all levels in root V (fig. 6) the average rate for 6 hours preceding was greater than that for 6 hours following excision, and an immediate drop occurred at each potometer contact except one (number 4 at 46.4 mm. from the apex). Decreased volume flow at all potometer contacts was also exhibited by root VI immediately after cutting from the bulb. On the other hand, the total volume intake in root VII (fig. 6) increased after the root had been isolated, although the region at potometer 3 maintained a higher

FIG. 4. Comparison of the minimal and maximal rates of water intake exhibited in different regions of 12 different roots during a 24-hour period. Vertical bars indicated by number 1 represent rates within the first 5 mm. (from the apex); bars designated by the numbers 2, 3, and 4 represent the rates at regions respectively 10, 20, and 30 mm. more proximal than the position of potometer 1. Solid black bars show minimal rates at each region; bars with crossed lines, the maximal rates, in the same regions. The magnitude of increase in each region is given by the ratio $\frac{\text{maximum}}{\text{minimum}}$ directly below the corresponding bars.



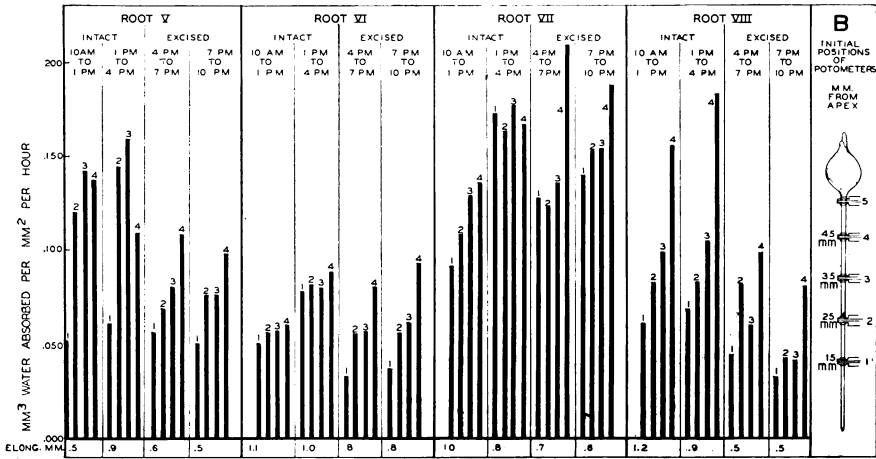


FIG. 6. Comparison of the rates of water absorption at 4 local regions during 6 hours preceding and 6 hours following excision. Initial positions of potometers indicated by diagram B. Initial lengths of roots numbered V, VI, VII, and VIII were 52, 57.6, 59, and 57.5 mm. respectively; age 6 days; grown in TRELEASE culture solution. Placed in chambers night preceding the experiment. Height of each vertical bar represents the rate of water intake at the potometer contact with the corresponding number in diagram B. Room temperature, $25^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$.

intake before excision; in this root the axial gradient of distribution, exhibited during a three-hour interval immediately following isolation of the root, was steeper than that exhibited in the 3-hour period immediately preceding, when the bulb was present. There was considerable slowing down of the velocity of absorption in root VIII (fig. 6) with a consequent flattening of the longitudinal gradient of distribution of rates.

The experiments discussed above represent typical results obtained from measurements on 32 roots. When comparisons were obtained between the average rate of water intake during the 6-hour period preceding, and the 6-hour period following excision, seven of the roots displayed an increase in volume flow during the second 6-hour period when the bulb was absent. The experiments show that the longitudinal gradient of velocity of absorption in a saturated atmosphere is usually flattened by excision owing to greater decrease in rates at relatively more basal levels after isolation; but

FIG. 5. Comparison of the rates of water absorption at 5 local regions during 3 intervals preceding and four following excision. Initial positions of potometers relative to the apex indicated in diagram A. Initial lengths of roots numbered I, II, III, and IV were 51, 48.3, 49, and 47 millimeters respectively; age 4 days; grown in TRELEASE solution; same medium in potometers. Placed in chambers night preceding the experiment. Height of each vertical bar represents the rate of intake at the potometer contact with the corresponding number in diagram A. Room temperature, 25°C .

they also demonstrate that volume flow at a single local region and even at all regions may increase immediately after the root has been isolated.

ABSORPTION OF WATER BY ROOTS IN AN INVERTED POSITION
WITH RESPECT TO GRAVITY

In order to determine whether or not higher rates were observed at higher levels because of vertical orientation of the root, experiments were run on both intact and excised roots when inverted.

The bulbs, including short leaves if present, were fitted in an inverted position into perforated corks placed on the floor of each chamber and the inverted roots carefully threaded through the potometers without injury. The length of the root, the positions of the potometers, and duration of the experiments were varied. Consistent results were obtained in all the experiments; typical data are given in figure 7. Rates were first determined in the intact roots for a short period of 3.5 hours and a subsequent period of 10 hours; each root was then cut from the bulb without removing the chamber covers and rates again determined during two periods of different duration.

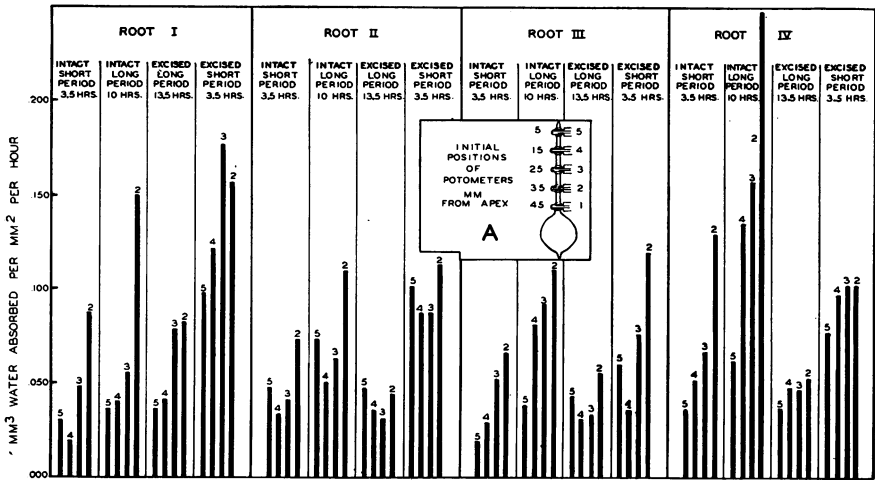


FIG. 7. Comparison of distribution of rates of intake before and after excision in 4 roots, oriented in an inverted position with respect to gravity. Initial positions of potometers shown by inset diagram A. Vertical bars represent rates; numbers above correspond to potometers in diagram A. Rates during four consecutive periods are shown; first reading 8 A.M. Age of roots, 5 days; initial lengths 51 to 54 mm.; grown in tap water; same medium in potometers. Room temperature, 24.5° C.

Comparisons of the data show that in both the intact and excised state, lowest velocities of intake appeared at the apical regions which in this case withdrew water from the highest potometers. A strict unidirectional gradi-

ent of distribution of rates was maintained by roots III and IV during the two periods preceding excision; following excision the steepness of the gradient was less and a minor peak appeared at potometer 5 (near the apex) in root III. Minor peaks in the gradient also appeared in roots I and II both before and after excision (at potometer 5 during the first 3.5-hour period in the intact root and at potometer 3 in the excised root). An increase in rates with time was manifested by the different levels both in the presence and absence of the bulb; in roots I and II the average rates observed during the second period (short period of 3.5 hours) in the absence of the bulb were greater than that observed at corresponding levels during the two periods in the presence of the bulb.

These experiments furnish further evidence that local regions along the root axis manifest independent characteristics whether or not the root is attached to the shoot in a saturated atmosphere.

WATER INTAKE AT CONTIGUOUS REGIONS IN DEAD ROOTS

Intact and excised roots which had been killed showed both liquid loss from, and liquid intake by, a local region at a single potometer contact but during different intervals. Table I shows typical results obtained from experiments during which the roots were quickly killed by dipping them into boiling water or applying a jet of steam. The roots were sectioned and examined after the experiments.

Although liquid loss appeared at different levels in the dead intact root A and the dead excised root B, both roots showed greater water uptake than liquid loss during the 10-hour experimental period; the uptake by the excised root was much less than that of the intact root. Comparisons of rates at the same levels in the same root in the presence and absence of the bulb show that root C manifested a marked increase in water uptake at 3 levels and liquid loss at one level after it had been killed, root D exhibited a decrease in water uptake at basal levels, but no liquid loss; after excision water uptake practically ceased.

No water uptake occurred in dead intact roots when the period of exposure to heat was longer than two seconds; in such cases pronounced liquid loss from the root occurred at each level and the root flattened into a thin ribbon.

The experiments showed that dead root tissues in either the intact or excised root are leaky systems with respect to water uptake; in both cases a given level may manifest water influx simultaneous with liquid loss in an adjacent region.

Discussion

In onion roots (*Allium cepa*) water intake is a continuous flux process but with changing velocity. The different rates of intake are sharply local-

TABLE I

EFFECT OF KILLING ROOTS ON WATER INTAKE BY DIFFERENT LOCAL REGIONS
 RATES (mm.³/mm.²/hr.) OF WATER INFLUX DESIGNATED BY “+”
 AND OF LIQUID LOSS DESIGNATED BY “-” SIGNS

Root A	Data from <i>intact</i> root killed with hot water					
	Positions of potometers; mm. from apex					
	Interval	5	15	25	35	
	8-10 A.M.	-0.201	-0.086	+0.030	-0.014	
	10 A.M.-12 M.	+0.073	+0.034	0.000	+0.187	
	12-2 P.M.	-0.091	-0.033	+0.046	+0.045	
	2-4 P.M.	+0.146	+0.069	+0.029	+0.072	
	4-6 P.M.	-0.009	+0.051	+0.006	+0.004	
Root B	Data from <i>excised</i> root; killed with hot water before excision					
	Positions of potometers; mm. from apex					
	Interval	3	10	20	30	
	8-10 A.M.	0.000	+0.025	-0.114	+0.026	
	10 A.M.-12 M.	0.000	+0.003	+0.204	-0.019	
	12-2 P.M.	0.000	-0.011	+0.110	0.000	
	2-4 P.M.	-0.008	0.000	-0.022	+0.049	
	4-6 P.M.	-0.010	+0.020	0.000	+0.005	
Root C	Data from single root <i>before</i> and <i>after</i> killing; steam applied to root only					
	Positions of potometers; mm. from apex					
	Interval	4	14	24	34	44
Intact living	8-9:30 A.M.	+0.025	+0.021	+0.023	+0.036	+0.040
	9:30-11 A.M.	+0.029	+0.036	+0.027	+0.049	+0.067
Intact dead	12-1:30 P.M.	+0.083	+0.120	+0.149	+0.148	-0.162
	1:30-3:00 P.M.	+0.082	+0.089	+0.094	-0.398	-0.410
Excised dead	3:00-4:30 P.M.	+0.022	+0.002	+0.013	-0.049	no exudation
	4:30-6:30 P.M.	-0.012	0.000	-0.027	+0.018	no exudation
Root D	Data from single root <i>before</i> and <i>after</i> killing; steam applied to root only					
	Positions of potometers; mm. from apex					
	Interval	6.5	16.5	26.5	36.5	46.5
Intact living	9-11 A.M.	+0.033	+0.047	+0.116	+0.119	+0.110
	11 A.M.-1 P.M.	+0.030	+0.037	+0.102	+0.125	+0.106
Intact dead	2-4 P.M.	+0.053	+0.040	+0.55	+0.075	+0.72
	4-6 P.M.	+0.050	+0.066	+0.79	+0.075	+0.70
Excised	6-8 P.M.	+0.025	+0.032	-0.270	+0.015	no exudation
	8-10 P.M.	+0.021	+0.001	0.000	+0.021	no exudation

ized at different levels at any one instant. With respect to time and space, water absorption involves a shifting pattern of rates along the longitudinal axis. More knowledge of cell dynamics is necessary to explain what factors

alter the flux equilibria of contiguous cells similar in structure, and further experimentation is necessary to reveal how adjacent regions in the root often manifest simultaneous positive and negative accelerations in water influx under constant external conditions in both intact and excised states. Are such oscillations characteristic of adjacent "spots" on the surface of a single cell—does the spacial pattern of dynamic forces in the cell vary from instant to instant causing simultaneous restriction of intake at one "spot" and acceleration at another (*cf.* LUND, 9)? Studies in the electrophysiology of onion roots show that spontaneous variations of electric potentials occur in adjacent regions under constant external conditions (1, 9, 10, 12, 14). From his experiments on Douglas fir (8) LUND concluded that the inherent electric energy output might function in electroendosmotic flow. Whether or not there is any interrelation between spontaneous variations of bioelectric potentials of the root and water intake or transport is not known at present. Fluctuations of ion uptake by single plant and animal cells have been reported by BROOKS (2).

The fact that the basal regions of roots less than 65 mm. in length and less than a week old continue to absorb greater quantities of water per unit surface, even after excision in a saturated atmosphere, indicates that the same inherent difference in machinery operating to maintain this apical-basal difference before excision continues to exist after excision, and in this respect is fundamentally independent of the shoot-root relationship. This does not imply that the shoot-root relationship does not also enter in as a condition because the absolute rates of intake in the basal regions are in *most* cases immediately lowered by excision. It may be that the difference (before and after excision) in basal regions represents a "pull" by the shoot which in this instance acts as a "suction pump." *In some roots, however, the basal regions may absorb even greater quantities of water after excision*—in that case the difference may represent a "push" or the action of a "force pump" in the root tissue; but we have no critical evidence which isolates the "push" and "pull" forces that might be operating in the root tissue *per se*. It may be that the demands of the bulb and growing leaves are greater at some times than at others, and differ in different roots, so that a greater water deficit actually exists in some roots before excision, and, furthermore, it may be that some roots contain greater amounts of nutritional reserve. Water deficits in excised roots would hardly be expected to exist after the roots manifested vigorous exudation; yet the rates of intake were greater when possible deficits were supposedly satisfied. The quantity of water absorbed immediately after excision does not represent the maximum absorbing capacity of the root tissue because the rates increase with time after excision under the given conditions. Removal of the bulb and growing leaves in a saturated atmosphere may remove an accessory suction

force but the data show that the unit *volume of transport through a given level in an excised root may be just as large or larger than when it had the added force of the bulb to supplant its own in the transport of water.*

PREVOT and STEWARD (11) demonstrated that the entire surface between the apex and emergence of secondary roots of 12-day-old barley plants represented a potential absorbing surface for salts. They also showed a pronounced longitudinal gradation in the capacity of salt accumulation, and that segments near the apex attain higher concentrations than those more remote. Since the roots were not only a different type, but were also slightly older than the roots discussed in the present paper, strict comparison of results cannot be made; but it is interesting to note that opposite gradients occur; in the excised barley root the peak of salt intake for a given interval is within the first 15 mm.; in the excised onion root the peak of water intake is beyond this region and near the base. If the gradient of ion intake in the onion root is similar to that of barley this would mean greater dilution of surrounding solution at the apex during a given interval since ion intake would be relatively greater and water intake relatively less than in basal regions. Experiments are under way to determine whether or not this occurs.

Death of the tissues destroys the mechanism *regulating* water intake in both intact and excised roots; water uptake in a dead root occurs by an entirely different mechanism. The dead excised root which no longer manifests exudation at the basal end exhibits siphon action and leaks at one or more levels; the dead intact root which may serve as a wick to a greater or less extent also leaks at one or more levels; the wick action immediately after death may involve greater or less uptake than in the living state; some dead roots in both the intact and excised state manifest no water uptake whatsoever. It is not known whether or not liquid loss occurred in the dead roots of KRAMER's experiments (7) because he was interested in transpiration rates and did not measure water intake. KRAMER maintains (7, p. 484) that "in experiments with sunflower, tomato, and tomato plants it was found that in most cases during the first twenty-four hours after the roots were killed the plants with dead roots transpired only about one-half as much water per unit of leaf area as the plants with living roots."

The living root is not merely a piece of machinery which interposes resistance to water, neither is it merely a sieve or a wick with regard to transpiration and the transport of water. The living root in position can deliver more water than that same root when dead. In a saturated atmosphere it manifests a characteristic flux gradient of water intake which is maintained by that root when it is upright or inverted, intact or excised, but which disappears when it is killed, liquid loss appearing at one or more levels. There is no cessation of water influx in the healthy living intact and

excised root; although changes in flux rates occur in contiguous regions, there appears to be a continuous overall drive of water through the root tissues. Before operative details of the working machinery of water absorption can be forthcoming we need further accurate accounts of the rates of volume transport in different types of roots, old and young, under carefully controlled conditions.

Attention should be called to the point that the objective has been to isolate the mechanism of transport of water into the root and reduce the problem to characteristics of absorption at a small element of root surface. This cellular mechanism has a large but variable volume capacity for transport of water across it and in this respect the problem is fundamentally the same as that of the uriniferous tubule in the animal.

Summary

1. By means of a technique previously described (13) simultaneous measurements of the rates of water absorption by contiguous regions were made in a saturated atmosphere on single intact and excised onion roots (*Allium cepa*) 65 mm. or less in length and less than a week old.

2. The experiments on intact and excised roots of corresponding age, length, and history carried out under comparable conditions of humidity, temperature, and light showed similar characteristics of behavior in water absorption with respect to (a) localization of the highest rates in relatively more basal regions; (b) an over-all increase of rates at each level with time throughout 12 two-hour intervals (24-hour period); and (c) fluctuations of rates in contiguous regions and in the axial gradient of distribution under constant external conditions.

3. The rates of water influx at contiguous levels of the same root after excision were equal to, greater, or less than before excision.

4. Both intact and excised roots which had been killed showed pronounced irregularities of water intake in contiguous regions; both liquid loss and uptake occurred at different levels during the same interval. The living root in position can deliver more water than that same root when dead.

Acknowledgment is made to A. A. HORAK for technical assistance.

THE UNIVERSITY OF TEXAS
AUSTIN, TEXAS

LITERATURE CITED

1. BERRY, L. J., JR. Spontaneous variations in the electrical potentials of the root of *Allium cepa*. Dissertation. Univ. of Texas, 1939.
2. BROOKS, S. C. Ion exchanges in accumulation and loss of certain ions by the living protoplasm of *Nitella*. Jour. Cell. Comp. Physiol. **14**: 383-401. 1939.

3. GREGORY, F. G., and WOODFORD, H. K. An apparatus for the study of the oxygen, salt, and water uptake of various zones of the roots, with some preliminary results with *Vicia faba*. *Ann. Bot. N. S.* III: 147-154. 1939.
4. HOAGLAND, D. R. The plant as a metabolic unit in the soil-plant system. *Essays in geobotany*. Univ. of California Press. 1936.
5. —————, and BROYER, T. C. General nature of the process of salt accumulation by roots with description of experimental methods. *Plant Physiol.* 11: 471-507. 1936.
6. HÖHN, K. Die Bedeutung der Wurzelhaare für die Wasseraufnahme der Pflanzen. *Zeitschr. Bot.* 27: 529-564. 1934.
7. KRAMER, PAUL J. The intake of water through dead root systems and its relation to the problem of absorption by transpiring plants. *Amer. Jour. Bot.* 20: 481-492. 1932.
8. LUND, E. J. Electric correlation between living cells in cortex and wood in the Douglas fir. *Plant Physiol.* 6: 631-652. 1931.
9. —————. The distribution of electric potential on the external surface of single cells. *Science n. s.* 87: 429. 1938.
10. MARSH, GORDON. Relation between continuous bioelectric currents and cell respiration. IV. The origin of electric polarity in the onion root. *Jour. Exp. Zool.* 51: 309-325. 1928.
11. PREVOT, P., and STEWARD, F. C. Salient features of the root system relative to the problem of salt absorption. *Plant Physiol.* 11: 509-534. 1936.
12. ROSENE, H. F. Proof of the principle of summation of cell E. M. F.'s. *Plant Physiol.* 10: 209-224. 1935.
13. —————. Distribution of the velocities of absorption of water in the onion root. *Plant Physiol.* 12: 1-19. 1937.
14. —————, and LUND, E. J. Linkage between output of electric energy by polar tissues and cell oxidation. *Plant Physiol.* 10: 27-47. 1935.
15. SIERP, H., and BREWIG, A. Quantitative Untersuchungen über die Wasserabsorptionzone der Wurzeln. *Jahrb. wiss. Bot.* 82: 99-122. 1935.
16. SKOOG, F., BROYER, T. C., and GROSSENBACHER, K. A. Effects of auxin on rates, periodicity, and osmotic relations in exudation. *Amer. Jour. Bot.* 25: 749-759. 1938.
17. STEWARD, F. C. Salt accumulation by plants. The rôle of growth and metabolism. *Trans. Faraday Soc.* 33: 1006-1016. 1937.
18. WHITE, P. R. "Root pressure"—an unappreciated force in sap movement. *Amer. Jour. Bot.* 25: 223-227. 1938.