PROOF OF THE PRINCIPLE OF SUMMATION OF CELL E.M.F.'S

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(WITH FIVE FIGURES)

The distribution of electric polarity in the unstimulated, uninjured root was first demonstrated by LUND and KENYON (**6**) in the roots of *Allium cepa, Eichhornia crassipes,* and *Narcissus.* Observations of the electric polarity of a number of other roots have been made by the writer and will be presented in detail in a separate paper. A distinctive feature of the electric polarity common to all the roots so far examined is the occurrence of a characteristic distribution of E.M.F. per unit length of root.

During the measurements of E.M.F. in the roots of different plants, it was observed that when a drop of water was placed around a region of the root between and not at the electrode contacts, the magnitude of total E.M.F. was altered. The water appeared to act as a shunt, changing the IR drop of the length of root over which the potential difference was being measured. This observation, and the fact that water is a necessary part of the environment in which roots can grow, led to the present study which was undertaken to determine the magnitude and direction of change in electric polarity produced by "liquid shunts" around the root.

Since more is known about the electric phenomena of the onion root (*A. cepa*) than about any other, it was selected as the experimental material. Observations made by LUND and KENYON (**6**), MARSH (**8**), and the writer on hundreds of different roots show that the electric polarity of the onion root changes from time to time. The root may manifest a stable potential difference for hours and then a steady increase or decrease in E.M.F. may appear, or it may exhibit rhythmic fluctuations of E.M.F. It has sometimes been observed that if, at a certain time of day, the roots of one bulb from a group of onions which were set at the same time exhibit rhythmic changes in electric polarity, the roots of most of the bulbs in this set will also manifest rhythm; at another time the roots of all the bulbs will exhibit a stable potential difference. From these facts it is obvious that in any analysis of the bioelectric potentials of the root tip the following must be taken into consideration: (*a*) the form of the curve of distribution of E.M.F. per unit length of root tip at a particular instant; (*b*) the variation of the characteristic form of the curve of distribution from instant to instant; (*c*) slow drifts of increase or decrease in potential difference between any two points which may occur; (*d*) occasional rhythmic fluctuations in E.M.F. which may vary in duration and magnitude from time to time. The changes mentioned in (*b*), (*c*), and (*d*) occur when all known external conditions are maintained constant. They are therefore conditioned by changes within the root itself. Hence in any experiment in which E.M.F. is modified by external conditions, it is necessary to distinguish between the spontaneous changes which are determined by causes of internal origin and the changes produced by altering the external conditions.

In order to determine whether the observed change in total E.M.F. of the root tip produced by surrounding a given region between the electrode contacts with tap water is uniquely characteristic of the system of maintained bioelectric potentials which is a distinguishing feature of electrically polar tissues, experiments were also made on the injury potential of nerve. It is a familiar fact that a potential difference between the cut end and the longitudinal surface of a nerve or muscle may be established and maintained for some time under suitable experimental conditions. It is also a familiar fact that the injury potential varies with the concentration of ions at the electrode contacts; but the writer knows of no work which shows that this E.M.F. may be modified by placing a conducting medium around an uninjured region between and not at the contacts, as will be shown to be the fact in the root.

Apparatus and method

The apparatus adapted for use in this investigation has been described in a previous paper (**13**). To surround a given region of the root with liquid, a glass cup (diagram M in figure 1) was used, which consisted of a piece of glass tubing, 5 mm. in outside diameter, with a small cover slip cemented on one end to form the bottom of the cup and a capillary tube cemented to a hole at one side at the base, to serve as a delivery tube. The cup was admitted into the moist electrode chamber through the opening *M*, shown in figure 2 of Rosene and Lund's paper (**13**). By means of a micromanipulator, the shunt cup (as it will be called) could be raised into position around the root which penetrated through a small hole in the cover glass that formed the bottom of the cup, or the holder with the bulb could be lowered by a different micromanipulator and the root passed through the cup. The liquid was admitted into and withdrawn from the shunt cup through the capillary tube which was connected to a reservoir. The water flow was controlled by the reservoir stopcock and by raising or lowering the rack and pinion stand supporting the reservoir. The apparatus permitted delicate control of all the manipulations and environmental conditions of the root.

The roots were grown in tap water. Those which were selected varied from 50 to 80 mm. in length. All of the roots but one were removed from the onion bulb just before it was placed in the electrode chamber. The experiments were run at room temperature and measurements of electric potential were made by a Compton electrometer.

The general procedure was as follows: The root was placed in the electrode chamber and contacts were made by using the micromanipulators to move the glass claw projections of the electrode cups into position around the root (see fig. 4, 2A and 2B, ROSENE and LUND **13**). The preparation was allowed to rest for a short period and the distribution of potential was then determined by moving the positive electrode (to quadrants) at the tip toward the negative electrode (grounded) near the base, in steps of 1 or 2 mm., making a reading at each step. The positive electrode was then moved away from the root while the empty shunt cup was placed in position (as in diagram M, fig. 1). A horizontal microscope with ocular micrometer was used to determine the position of the contacts on the root and to make the measurements of length. With the shunt cup in position, observations of the electric behavior of the root under constant external conditions were made for a short period and then liquid (tap water or paraffin oil) was run into the shunt cup from the reservoir. The height of the liquid in the cup was determined by the horizontal microscope. With careful manipulation, no leakage of liquid from the cup occurred and mechanical stimulation was reduced to an insignificant minimum. The length of the period during which the liquid was retained in the cup surrounding the root was varied in different experiments, and sometimes in a single experiment. Throughout each experiment readings were made at 15-second or 1-minute intervals.

Experiments and results

PROCEDURE 1

ALTERNATE ADDITION AND REMOVAL OF WATER FROM SHUNT CUP

Figure 1, B, is the curve of distribution of potential along a root tip which does not exhibit a negative potential in the region 5–10 mm. from the tip. The diagram of the root below curve B is drawn to the same scale as the abscissa and shows the exact position of the shunt cup, *S.C.,* also drawn to scale, as well as the position of the electrodes which are indicated by arrows. In this experiment a shunt cup 2 mm. in height was employed. It surrounded that region of the root which exhibits the highest electropositivity. Curve A shows that each time the segment of the root surrounded by the cup was filled with water, an immediate and abrupt drop in E.M.F. occurred; and each time the water was withdrawn the E.M.F. of the root was abruptly increased. The magnitude of increase of E.M.F. did not quite equal the magnitude of decrease. This was evidently due to a film of water which remained on the root and acted as a partial shunt when the water was withdrawn from the cup.

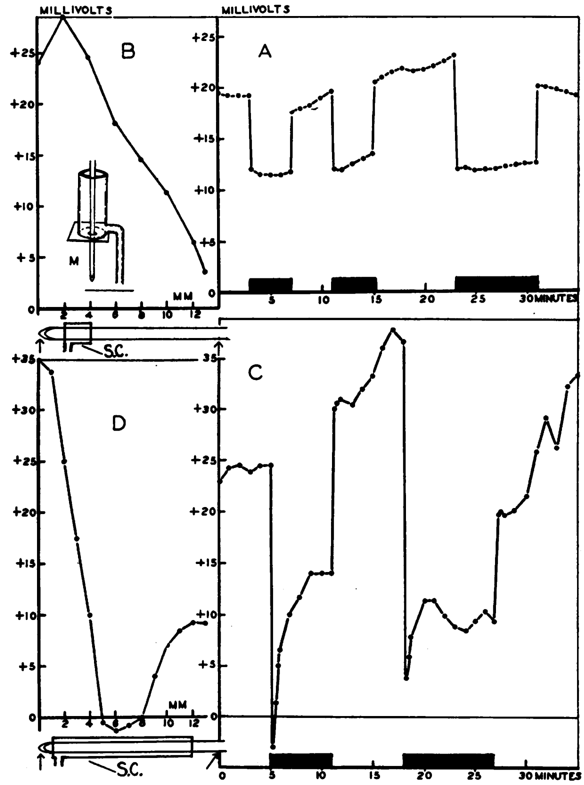

FIG. 1. Effect of liquid shunt around a segment of the root between the electrode contacts on the observed E.M.F. of the root. B and D are the curves of distribution of E.M.F. of two different roots obtained by moving in 2 mm. steps, the positive electrode from the tip toward the negative electrode which was stationary at 14 mm. from the tip. Abscissa gives the position of the positive electrode in mm. from the tip. The diagram below each curve, drawn to the same scale, shows the exact position of the shunt cup (*S.C.*) and electrode contacts (designated by arrows) during each experiment. Curves A and C show changes in E.M.F. when tap water is alternately added to and removed from the shunt cups in B and D respectively. Heavy portions on base lines A and C indicate duration of period when cup is full of water; intervals between when it is empty. Inset M, below curve B, shows shunt cup in position around the root. See text for description.

The height of the larger cup, which was used in the next experiment, was 11 mm. Its exact position on the root is shown in the diagram below curve D, which gives the distribution of potential of that root. The shunt cup (*S.C.*) covered most of the region between the electrode contacts. As indicated by curve C, as soon as water rose upward from the bottom of the shunt cup, there was a sharp decrease in E.M.F. and the electric polarity of the root was suddenly inverted. During the period when the jacket was filled with water, the E.M.F. increased and normal orientation of the electric polarity was restored; but the potential difference was maintained at a low level. Removal of water produced a sharp rise in potential which reached a new high level. The potential difference continued to increase during the period that the cup was empty. Repeating the procedure produced a similar change in the magnitude of E.M.F., but the electric polarity of the root was not inverted. Similar slow fluctuations of E.M.F. occurred when the shunt cup was filled with water and when it was empty. The abrupt changes in E.M.F. produced by the addition and removal of water from the jacket are readily distinguished from the rhythmic fluctuations of E.M.F., which are associated with changes in the internal processes of the root, by the fact that the abrupt changes in the first case produce an immediate rise in the curve and in the latter case a definite slope is evident. A comparison of curves A and C shows that a greater magnitude of change in E.M.F. was produced in the second experiment. This is explained by the difference in the length of the "liquid shunt" in the two instances, which corresponds to the difference in the height of the water column of the different cups, and also in part by the fact that the total E.M.F. of the root region (14 mm. long) between the electrode contacts was greater in C.

Procedure 2

Addition and removal of water from the shunt cup in steps at definite intervals

When the distribution of E.M.F. was a single unidirectional gradient of fall of potential along the root, as indicated by figure 2, curve B, and water was added to the shunt cup at definite intervals, thus increasing the height of the water column around the root in steps, the E.M.F. of the root was correspondingly altered in steps. This fact is illustrated by curve A, figure 2. Each arrow which points downward indicates that the height of the water column in the cup was raised 1.5 mm., and each arrow which points upward indicates that the height of the water column was lowered 1.5 mm. The positions of electrode contacts and the shunt cup on the root are illustrated by the root diagram B′ below the curves of distribution, figure 2. As shown by curve A, the E.M.F. was diminished each time the water level in the cup was raised by adding more water and it was increased each time the water level of the cup was lowered by withdrawing water. In other words, as the length of the liquid shunt was increased or decreased, the E.M.F. was correspondingly increased and decreased. After the cup had been filled with water, the observed electric polarity of the root re-

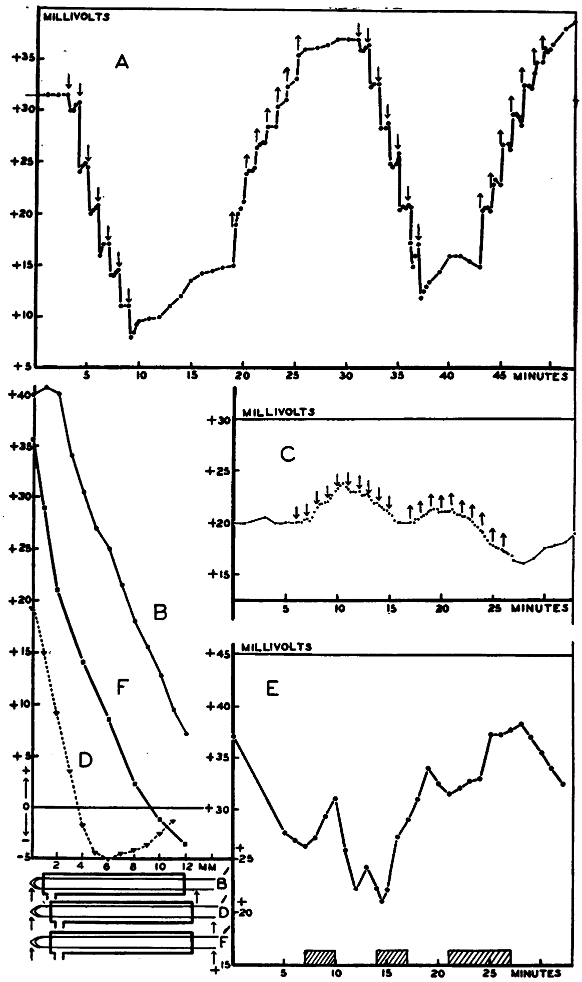

FIG. 2. (*a*) Effect on E.M.F. of root when the liquid shunt is increased and decreased by increments, at successive intervals, and (*b*) absence of effect when paraffin oil is added to and removed from shunt cup. The curves are from three different experiments on three different roots. Arrows pointing downward in curve A show when height of water column in shunt cup was increased by 1.5 mm. increments; arrows pointing upward, when it was decreased in a corresponding manner. Arrows pointing downward in curve C show when height of oil column in shunt cup was increased in steps of 1 mm., arrows pointing upward, when it was correspondingly decreased. Shaded intervals on base line in E indicate when shunt cup was filled with paraffin oil; intervals between, when it was empty. B, D, F are curves of distribution of electric potential for each root and correspond to A, C, and E respectively. Diagrams of the roots B′, D′, F′, below the curves of distribution, show exact respective positions of shunt cup and electrode contacts (arrows) in each experiment.

mained at a relatively lower level; and after the cup had been drained it remained at a higher level. The curves which are represented by figures 1, C, and 2, A, were obtained under conditions in which the height of the water column in the full cup was the same in each case, and the length of the region of the root over which the E.M.F. was measured was also the same.

Procedure 3

Addition and removal of paraffin oil from the shunt cup

In order to determine whether the observed change in E.M.F. of the root produced by adding tap water to the shunt cup could also be produced by adding a non-conducting liquid, paraffin oil was substituted for water.[1] Figure 2, C, shows the results obtained when procedure 2 was followed. The arrows pointing downward indicate the time at which the level of paraffin oil in the cup (which was empty at the beginning of the experiment) was raised in steps of 1 mm. The arrows pointing upward indicate the times at which the oil was removed in a corresponding manner. The curve illustrates the fact that the root exhibited rhythmic fluctuations in E.M.F. but did not show the striking change in E.M.F. which was produced when water was added and removed from the cup around the root under similar conditions, as shown by curve A, figure 2. The corresponding curve of distribution of electric potential for this root is given by figure 2, D, and the position of the jacket by diagram D′, below the curve.

Figure 2, E, was obtained when the shunt cup was at alternate intervals filled and drained with paraffin oil. Throughout the experiment, the root manifested a distinct rhythm in electric behavior, but it shows no quick change as a result of adding and withdrawing oil from the cup. This is clearly evident when the curve is compared to curve C in figure 1, which was obtained by a similar experimental procedure using water instead of oil. The perpendicular changes in curve C, figure 1, which express the alteration of E.M.F. when water was added to or removed from the cup, are entirely absent in curve E, figure 2, when tap water is replaced by the non-conducting oil.

Procedure 4

Addition and removal of water from the shunt cup when position of cup around the root is changed

Figure 3, B, shows the distribution of potential over 25 mm. of a root tip which exhibits two regions with opposed electric polarities. Figure 3, A, shows the curve obtained when the cup was placed, in turn, in two dif-

[1] The paraffin oil was non-toxic, since, when the roots were replaced in water, they grew in a normal manner.

ferent positions corresponding to the regions of opposed polarities and was alternately filled and drained at intervals while in each position. The first part (below the bracket (*a*) of curve A, figure 3) was obtained when the cup was near the apical contact, as illustrated in the upper root diagram B′ below the curves of distribution, and the second part of the curve (below the bracket *b*) was obtained when the jacket was in a position near the basal

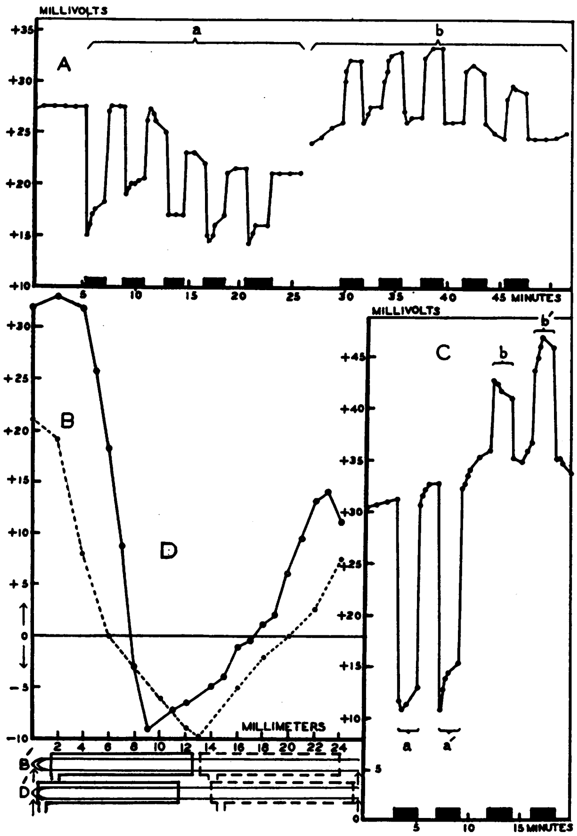

FIG. 3. Effect of placing a liquid shunt on different regions of opposed electric polarities. Curves B and D show distribution of potential in two different roots. Upper root (diagram B′) below the distribution curves shows exact positions of electrode contacts (arrows) and two successive positions of shunt cup in experiments from which curves (*a*) and (*b*) in A were obtained. Lower root (diagram D′) is corresponding diagram for curves in C. In A and C the portions of the curves indicated by the brackets (*a*, *a*′) were obtained when the shunt cup was in the position indicated by the continuous heavy outline of the cup on each root diagram; those portions indicated by brackets (*b*, *b*′) when it was in the position indicated by the interrupted outline of the cup. Heavy portions of the base line of A and C show when the cup was filled with water; intervals between, when it was empty.

contact, as indicated by the dotted outline on the same root diagram. In each position the shunt cup was alternately filled and drained at 2-minute intervals. That portion of the curve under bracket (*a*) shows a *decrease* of the total E.M.F. of the root each time water was added to the cup, and an increase when it was removed. On the other hand, that portion of the curve under bracket (*b*) shows an *increase* in E.M.F. each time water was added to the cup and a decrease when it was removed. *The opposite effects on the electric polarity of the root with the cup in the positions corresponding to the regions of opposed polarities, show that the direction of change of E.M.F. produced by adding a liquid shunt is determined by the orientation of the electric polarity in the cells of the shunted region and also demonstrates that the two systems of opposed E.M.F.'s summate in an algebraic manner.*

In another root, following a similar procedure, the shunt cup was placed first at the apical contact and second at the basal contact, so that when it was filled, the entire length of root covered by the cup and the specific electrode contact near it were surrounded by water. In each case therefore a relatively extensive region at the electrode contact was shunted. The results are shown by figure 3, C; the curve of distribution of E.M.F. per unit length of root is shown by figure 3, D; and the positions of the cup and electrode contacts are indicated in the lower diagram of the root D′ below the distribution curves. In each position the cup was filled and drained at 2-minute intervals. As shown by the brackets (*a, a′* and *b, b′*) in curve C, opposite changes in the electric polarity are observed in apical and basal ends of the root. The greater magnitude of the change shown by the positions of the curves (*a, a′*) occurred in the region of the root which exhibited the higher difference in potential.

In a third root, which also manifested the characteristic distribution of E.M.F. with a "valley" of negativity at 8–30 mm. from the apex, as indicated in figure 4, B, the cup was at successive intervals placed in three different positions on the root. It was then filled and drained once while in each position. The successive positions of the cup on the root are indicated below the curve of distribution of E.M.F. by diagrams a, a′, and b. Those portions of curve A, figure 4, which are indicated by the brackets (*a, a′*, and *b*), show the corresponding changes in electric polarity of the root when the cup was filled in each of the three positions. The greatest change in E.M.F. occurred when the region with the highest potential was surrounded by water. As in the preceding two experiments, the direction of change of E.M.F. was determined by the orientation of the electric polarity in the region upon which the shunt was applied.

These experiments indicate that if observations are made of the E.M.F. of a given length of root which manifests oppositely oriented polarity poten-

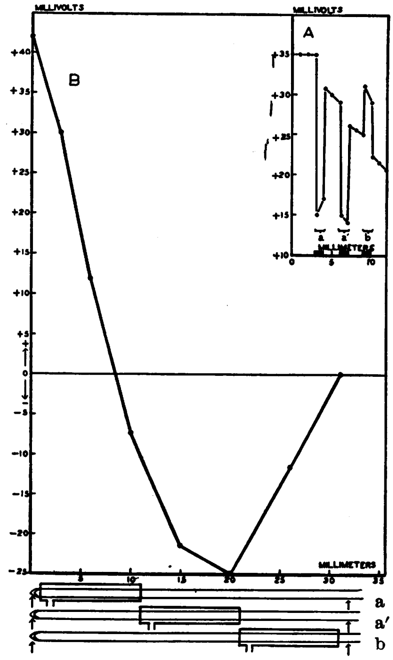

FIG. 4. Effect on electric potential, of addition and removal of a liquid shunt at three different positions on the root with a curve of distribution of E.M.F. as shown in B. Diagrams a, a′, and b below base line show successive and exact positions of shunt cup on same root. Arrows indicate positions of electrode contacts. The parts of the curve above the brackets (*a*) and (*a′*) and (*b*) in A indicate the change in E.M.F. produced by adding and removing water from the shunt cup in the positions corresponding to a, a′, and b of the root diagrams below.

tials, during an interval when the shunt cup filled with water is moved up or down the root, increase or decrease in E.M.F. would appear when the cup passed over a ''hill'' or ''valley'' of potential difference. In this way the orientation as well as the relative magnitude of E.M.F.'s per unit length could be determined.

Many such determinations on different roots were made, and the orientation and relative magnitude of E.M.F.'s per unit length was ascertained in this manner. In each case results were checked by comparison with the curve of distribution of E.M.F. per unit length obtained by moving the positive electrode toward the negative electrode as described above. When the empty cup or the cup filled with paraffin oil was similarly moved, no changes in E.M.F. were observed.

These experiments show further that we are dealing with a system or systems of E.M.F.'s, some of which at least have their origin in polar cells arranged in series. This point will be clear if the reader will refer to the discussion and diagrams of cells in series and in parallel in LUND's paper (**4**) on the theory of cell correlation. In diagram I of figure 2, pages 285, LUND gives a simple hypothetical system of four cells, A, B, C, and D, arranged in series in which A is from the region of highest positive potential, B from a region just proximal to A, C from an isoelectric region, and D from a region of oppositely oriented polarity. When connected in series as illustrated, the total E.M.F. of the system would be equal to the algebraic sum of the E.M.F.'s of the cells between the contacts as represented by circuit 4 in the diagram (fig. 2, I, LUND **4**). If, in such a system, a decrease is produced in the IR drop of cells A or B or both, the total E.M.F. of the system would necessarily fall; and if such a decrease is sufficiently great in magnitude the polarity of the system would be reversed since it would then be determined by the polarity of cell D. This is the explanation for the drop in potential shown in curves A and C, figure 3, and curve A in figure 4 when the conducting medium was placed around a region of high positive potential. If, on the other hand, a decrease is produced in the IR drop of cell D, the E.M.F. of which is opposing the P.D.'s of cells A and B, an increase in the total E.M.F. of the system will appear, as shown by the rise in potential in curves A and C, figure 3, and curve A, figure 4, which occurred when the conducting medium was placed around a region that exhibited a negative polarity potential.

PROCEDURE 5

SHUNT CUP OUTSIDE OF THE ELECTRODE JACKET

Very little or no change in E.M.F. of the root is observed when water is added to or removed from the shunt cup when placed outside of the electrode circuit. Figure 5, X and Y, shows the positions of the electrode contacts in two such experiments. The shunt cup in one experiment was filled with water during the first half of the experiment and with paraffin oil during the latter half. At 1-minute intervals the cup was alternately raised and lowered, thus surrounding 1.5 mm. of the extreme tip with water when raised. The position of the cup when over the tip is indicated by the interrupted outline in figure 5, X. The results are represented by curve A. The stippled portions of the curve show the intervals during which the apex dipped into the water-filled cup and the portions indicated by diagonal lines give the intervals during which the apex dipped into the oil-filled cup. Each time the water-filled cup was raised over the root, a small but definite drop in E.M.F. occurred, and each time it was lowered a small increase in E.M.F. was observed. No such change in E.M.F. was noticed when the oil-filled cup was similarly raised and lowered. In both experiments the effect was very small.

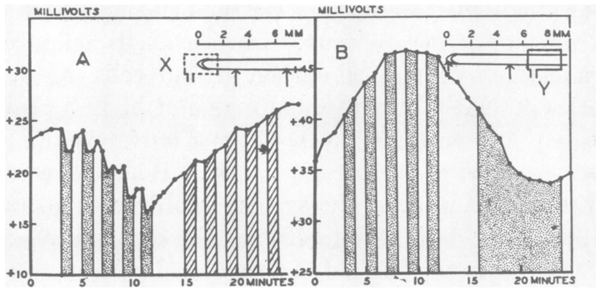

FIG. 5. Effect of tap-water shunt on E.M.F. of a given region when it is applied to a region of the root outside of the electrode circuit. Insets X and Y are diagrams of two different roots which show exact position of the segments of the root covered by the shunt cup, as indicated by the interrupted outline in X and the solid outline of the cup in Y. Stippled areas on the base line of A and B show when the shunt cup is filled with water, diagonal portions when it is filled with paraffin oil, and intervals between when the cup is empty.

In the other experiment the cup was placed in position around a region of the root relatively basal, as illustrated by figure 5, Y. It was filled with water during the intervals represented by the stippled portions of curve B, figure 5. Curve B indicates that no change in E.M.F. is produced by adding and removing water from the cup under these conditions.

Both experiments showed that the electric polarity of the root was in a fluctuating state manifesting rhythm. The small change in E.M.F. observed when the water-filled cup was raised and lowered indicates that part of the electric field at the apical electrode contact was included in the region covered by the cup when it was raised.

Experiments on frog nerve

The frog's sciatic nerve was carefully isolated and a thread tied around the proximal end by means of which the nerve was gently threaded through the openings of (*a*) the glass projection (contact) of the electrode connection to the quadrants, (*b*) the bottom of the empty shunt cup, (*c*) the glass projection (contact) of the grounded electrode cup, and finally fastened in a glass clamp which thus suspended the nerve in the moist electrode chamber. The electrode cups and glass projections were filled with frog Ringer solution. When both electrode contacts surrounded the uninjured surface of the nerve no potential was exhibited, but when the nerve was cut at the electrode contact (to quadrant) on the distal portion below the cup, an injury E.M.F. appeared. This E.M.F. was not subject to change by adding and removing Ringer solution around the region surrounded by the cup, nor did any effect appear when paraffin oil replaced the Ringer solution. Although the procedures described above in the experiments on the onion root were repeated with different nerves, the presence of a liquid conductor around the uninjured surface of the nerve between the electrode contacts failed to produce an effect on the injury potential in any way comparable to that which was observed on the maintained E.M.F. of the polar cells in the root tissue. Evidently the systems of E.M.F. are fundamentally different in one or more respects; in the root tissue there is a system of cellular E.M.F.'s arranged in series (and probably in parallel also) such that the addition of a liquid conductor around cells between and not at the contacts will alter the total E.M.F. of that system, whereas in the injured nerve the system is closed and the addition of a liquid conductor between the contacts does not alter the E.M.F. In the latter case, the origins of the P.D.'s are probably limited to the electrode contacts. In the root electrically polar tissue is present, the cells of which are the seats of individual E.M.F.'s that summate algebraically to give the E.M.F. of that system.

Conclusions

The preceding experiments show that when tap water is placed around a region of the onion root between the electrode contacts the E.M.F. of the root is altered, but when paraffin oil is similarly placed around a region of the root no change in E.M.F. is observed. This fact indicates that when a liquid which contains electrolytes surrounds a region of the root the output of electric energy by the root is altered. The effect on individual cell E.M.F.'s is summated and expressed in the change of the electric polarity of the whole. A liquid shunt around the region of the root which exhibits a positively oriented unidirectional polarity diminishes the electric polarity of the whole, while a liquid shunt around the region which exhibits an oppositely oriented unidirectional polarity increases the electric polarity of the whole. This fact furnishes conclusive evidence that the total observed E.M.F. of the onion root is the algebraic sum of the definitely oriented E.M.F.'s of individual cells.

The fact that the E.M.F. between the cut end and the longitudinal surface of the frog sciatic nerve was not altered by following the procedure used in the experiments on the root shows that the observed effect produced by adding a liquid shunt to the root is uniquely characteristic of the system of continuously maintained bioelectric potentials, distinctive of the root cells.

The fact that the potential difference of the root may be increased or decreased by a liquid shunt indicates that the electric circuit system of the root is not a closed system. In its natural environment the root is exposed to soil or other solutions which contain electrolytes. Bioelectric currents flow outward into the surrounding medium from regions of high electric positivity in the root and currents flow inward from the surroundings to regions which exhibit relatively low positivity or negativity. Accordingly, the observed phenomena are obviously significant in relation to the problems of (1) transport of ions, (2) absorption of water and solutes by the root, (3) transpiration, and (4) growth.

Energy changes are involved in the process of absorption, and many investigators have shown that permeability and osmotic relations alone are inadequate to explain the phenomena of absorption in the root (**1, 3, 9, 14**). The electric energy produced by the oxidative metabolism of the cells (**5, 13**) is continuously available for work and may be utilized by the root in the processes of absorption and transport. It has been shown that absorption of water and ions by the root is directly correlated with oxidation (**10, 2, 7**), and it has been demonstrated for the first time that the electric potentials of the root and oxygen tension are quantitatively interdependent (**6, 13**). A consideration of the fact that the electric circuit of the root is not a closed system, and the above mentioned relations (*i.e.*, (*a*) of bioelectric currents to oxidation and (*b*) of absorption to oxidation) indicates that these are linked phenomena.

The fact that electric energy is available for the transport of ions, and the additional fact that the E.M.F. of the root is modified only when an electrolytic solution comes in contact with the root, indicate that the available output of electric energy by the root is related to the conductivity of the solutions in which the roots grow. Root growth is dependent upon ion transport and upon the absorption of water and solutes. It may possibly differ in solutions of low and high electric conductivity.

A detailed discussion of the experimental results in relation to the phenomena mentioned above will be omitted, since the purpose of this report is to show that the magnitude and orientation of cellular E.M.F.'s is modified by an electrolytic solution around the root and that the electric circuit of the root is not a closed system, but attention is called to the fact that the study of electric behavior of the root establishes a precise and intelligible approach to the problems of (1) transport of ions, (2) absorption of water and solutes, (3) transpiration, and (4) growth.

Summary

1. The electric polarity of a given region of the root tip (*Allium cepa*) is decreased or increased when an electrolytic solution such as tap water (liquid shunt) surrounds a segment of that region.

2. The magnitude of change in electric polarity is directly related to the length of the liquid shunt, and the direction of change is determined by the orientation of the polarity potential in the segment to which the shunt is applied.

3. The level of E.M.F. manifested before the liquid shunt is applied is reestablished when the shunt is removed.

4. The observed changes in E.M.F. produced by the addition of a liquid shunt to the root are distinguished from the rhythmic fluctuations in E.M.F., produced by causes of internal origin, by the abrupt change in E.M.F. which occurs when the shunt is added.

5. The observed changes in E.M.F. are determined by the presence of ions in the applied solution. No change in E.M.F. of a given region of the root is observed when a non-conducting liquid is applied to a segment at that region.

6. The results indicate that the system of continuously maintained E.M.F.'s present in the root involves cells arranged in series so that their polar axes coincide.

7. When the liquid shunt is applied to a region outside of the electrode circuit no change in E.M.F. is produced.

8. There is an absence of effect on the injury E.M.F. of frog sciatic nerve following the same procedure used in the experiments on the root. The observed change in E.M.F. of the root, produced by the addition of a liquid shunt, is uniquely characteristic of the system of maintained cellular E.M.F.'s present in the root.

9. The observations furnish direct evidence that the principle of algebraic summation of E.M.F.'s in polar cell systems applies to the electric polarity of the onion root.

The writer wishes to express gratitude to Prof. E. J. LUND for valuable suggestions and criticisms. The investigation was aided by a grant from the research fund of the Department of Zoology, University of Texas.

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