ELECTRIC CORRELATION BETWEEN LIVING CELLS IN CORTEX AND WOOD IN THE DOUGLAS FIR

E. J. LUND

(WITH SEVEN FIGURES)

In presenting the results of the experiments which follow in this paper the writer will, for the sake of simplicity and proper evaluation of the observations, assume that the reader is familiar with the facts of electric polarity in the Douglas fir which have been presented in previous papers (Lund 1, 2, 3).

It will be recalled that when electrode contacts are made at the center of the wood and any point on the outer surface in the same cross-section of the tree, the center of the wood is always electropositive (in the external circuit) to the outer surface of the cortex. This is true for all regions of the tree stem below that of the first or second apical internode. Recent observations reported below indicate that the orientation of the radial polarity in the region of the most apical internode is reversed under conditions of absence of injury or stimulation.

Since all or at least the greater part of the radial P. D. is confined to the living parts of the wood-cortex system and since the cambium exhibits a bipolar structure which corresponds to the bipolar radial growth in wood and cortex, we might expect to find that the wood-cortex system including the cambium also exhibits a double electric polarity.

Up to the time of the present experiments and those to be presented in following papers on the effect of temperature, it had not been possible to demonstrate with certainty whether or not the cortex possessed an electric polarity of its own. The difficulty lay in the fact that any process of separation of the cortex from the wood axis involves more or less permanent injury, due to deformation of the cortex and therefore radical change in its electric polarity. This fact is also to be expected from the experiments reported in the preceding paper which pertain to the effect of mechanical stimulation on the electric polarity.

Various incidental observations seem to indicate that the radial E.M.F. per se in the wood is not affected to a noticeable degree by merely removing the cortex. This result might perhaps also be anticipated since no marked deformation of the wood occurs in such a process.

The preceding facts led the writer to devise a procedure by which the existence of the E.M.F. in the cortex could be made evident without injury or at least with a minimum of injury to the cortex.

The principle of summation of electric polarities of cells, which has been fully stated in previous papers, is obviously of fundamental impor-
tance. A proof of its validity and a demonstration of its rôle in electric correlation in the Douglas fir is one of the requirements, without which the writer's conception of the rôle of electric polarity of the cell in the process of correlation in tissues can not be considered established. The published evidence which appears to be conclusive is found in the experiments by Marsh (7, 8) on the onion root.

In the writer's first paper on the Douglas fir (Lund (1), pp. 10–11) and before we possessed any knowledge of the internal distribution of its correlation currents, it was assumed that the apparent algebraic summation of the external longitudinal E.M.F.'s along the stem was evidence for summation. This conclusion is of course correct provided it can be demonstrated that the origin of most or all of the observed external P.D. is not located at the surface of contact between the water leads of the electrodes and the external surface of the cortex. The experimental requirement was fully met in the experiments by Marsh on the onion root. In the following experiments it will now similarly be shown that the removal of the cortex between the contacts without involving any disturbance of the contacts themselves does produce characteristic and profound modifications of the E.M.F. similar to the results of the experiments by Marsh on the onion root. From these peculiar effects of the cortex on the E.M.F. we shall attempt to deduce in further detail the pattern of the correlation currents in the tree.

Experiments

The experiments reported here were carried out on the second and third internodes of the main axis of the tree. Each internode was isolated just before the beginning of the experiment. The lengths of the pieces varied from 50 to 70 cm. and the average diameters varied from 7 to 12 mm. The ratio of the length to the diameter was therefore actually about twice as great as that indicated in the diagrams of figure 1. Similarly in figure 6, the ratio of diameter to length of the internode is very much exaggerated for the purpose of illustration.

Procedure I

Figure 1.1, curves, figure 2

In this experiment the third internode from a tree fifteen feet high was isolated and clamped rigidly at each end to a heavy iron stand. Dry cotton pads were wrapped around the jaws of the clamps to prevent mechanical injury to the tissues.

At points 10 cm. from each one of the cut ends of the internode, a ring of cortex 4 cm. wide, was removed. Holes two mm. in diameter were drilled to the center of the wood axis, at points midway between the cut
surfaces of the cortex. Into these holes were inserted glass funnels X and Z. The inner openings of the funnels were placed exactly in the center of the wood axis. These funnels were filled with tap water and served as electrode contacts at the center of the wood axis. Cotton strips saturated with tap water were wrapped around the wood axis and dipped into the cups A', A and B, B'. These cups were filled with tap water and two movable Pb-PbCl₂ electrodes were hung over the edges of any pair of cups between which a measurement of P.D. was to be made.

In all the work care was taken to prevent excess wetting of the exposed wood axis by the cotton contacts. These contacts and the cups X and Z were rinsed occasionally to maintain symmetry. Flowing contacts gave the same results as contacts which were rinsed occasionally.

In the experiment illustrated by figure 1, the P.D. was measured between each pair of the contacts, X and A', X and A, Z and B, Z and B', X and B, Z and A, A' and B', A and B.

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**Fig. 1.** Diagrams I, II, III and IV of an internode show the position of the glass funnel contacts X, Y and Z and the cotton contacts A and B in procedures of experiments I, II, III, IV respectively, which are referred to in the text. The stippled part of the stem was killed in boiling water before the tests were made.
The duration of one set of measurements by means of the potentiometer was about four to five minutes. The readings were always taken in the same sequence. Successive sets of readings were taken at variable intervals as indicated by the points on the curves in figure 2.

The following convention for designating the orientation of the electric polarity between the contacts will be followed throughout this and the following papers. The designations XB, AB, etc., on the curves mean respectively that contact X is electropositive in the external circuit to contact B; contact A is electropositive in the external circuit to contact B, etc., whenever the reading of the P.D. is above zero on the ordinate. Whenever the readings of P.D. fall below zero the contact designated by the first letter is electronegative to the contact designated by the second letter.

It will be observed in figure 1, and in the curves of figure 2 that:

(1) XA', XA, and ZB, ZB' measure radial E.M.F.'s in the wood.
(2) XB measures what will be called the apical-basal diagonal E.M.F.
(3) ZA measures what will be called the basal-apical diagonal E.M.F.
(4) AB and A'B' measure what we shall call the longitudinal E.M.F.

The first fact to notice is that the sequence in the magnitude of the radial E.M.F.'s of the wood at the four pairs of contacts is ZB' > ZB > XA > XA'. This relation is maintained during the whole period of the experiment and is merely a confirmation of previous measurements on the radial E.M.F. in which it was found that the radial E.M.F. of the wood diminishes as we proceed toward the apex of the tree.

In accordance with these facts we have arbitrarily designated the E.M.F. in the wood at the basal end of the internode in diagram figure 6 by 8 (±) signs and that in the apical end by 6 (±) signs. The significance of these arbitrary numbers will be referred to later.

The main object of the experiments is to show what effect the removal of the cortex between the contacts A and B has on the E.M.F. between each one of the different pairs of contacts. With this object in view three successive sets of measurements were made during the first thirty minutes of the experiment previous to removal of the cortex. During such a preliminary period there usually occurs a marked relative stabilization of the E.M.F.'s.

At the time designated by the vertical arrows the cortex between the contacts was gently but quickly stripped from the wood. During this process which lasted about two minutes the electrode contacts were not disturbed because the ends of the stem were fixed in rigid clamps. After the cortex was removed a reading was taken of each pair of contacts as designated in the curves, and thereafter the readings were taken at irregular intervals as indicated by the points on the curves.
INTERPRETATION OF THE CURVES

Figure 2

Fig. 2. Upper curves XB, ZA, AB and A'B' show the relative magnitudes of the E.M.F.'s between the contacts X and B, Z and A, A and B, A' and B' respectively, as shown in figure 1.I. Lower curves ZB', ZB, XA, and XA' give the radial potentials of the wood between the correspondingly lettered contacts in figure 1.I. The upper and lower sets of curves are separated in order to avoid confusion. The magnitudes of the E.M.F.'s in the different curves should be compared.

The + or - sign of the potential on the ordinate axis always refers to the observed sign of the potential at the contact designated by the first letter. Thus in curve XB contact X is + to contact B in the external circuit. Similarly in curve A'B', contact A' is + to contact B' in the external circuit, except at one point on the curve where A' becomes - to B'. This method of designating the orientation of the E.M.F. is used in all the curves of the following figures. Position of arrows indicates the time when the living cortex was removed.
Curves ZB', ZB,XA and XA' show that under the conditions of this experiment, no marked effect is produced on the radial potentials of the wood when the cortex is removed. On the other hand curves AB and A'B' show that the removal of the cortex diminished the E.M.F. between contacts A and B, and A' and B', even though these contacts were not disturbed. If the origin of all the E.M.F. between the contacts A and B, and A' and B' was located at the contacts then certainly no change in E.M.F. would have been observed by removing the cortex. Since AB and A'B' are practically duplicates and therefore of the nature of controls for each other we can not regard the result as an accident. Furthermore all similar experiments on other internodes yielded the same kind of result. The drop in the curves AB and A'B' when the cortex was removed is in my experience only partially, if at all, ever recovered in such an experiment. The interpretation of this result must be that the origin of the E.M.F. in AB and A'B' is not merely due to a P.D. located at the electrode contacts, but that part of the total E.M.F. originates at loci along the stem between the electrodes. This constitutes important evidence for the validity of the principle of summation of E.M.F.'s in the stem. A permanent drop in the E.M.F. between A and B suggests the conclusion that the cortex is the seat of a permanent E.M.F. which, when the cortex is in position, in some peculiar manner augments (sums with) the longitudinal E.M.F. in the wood axis.

The most striking effect of removal of the cortex is on the E.M.F. between X and B, and Z and A. Note that XB is diminished while ZA is increased. These effects are quite permanent. Since the only difference between XB and ZA is that of an opposite orientation with respect to the polarity of the stem axis, removal of the cortex must produce its opposite effects by virtue of the opposite orientation of the contacts with respect to the longitudinal axis of the stem. This apparently means that the E.M.F. in the cortex, when in situ, opposes the larger E.M.F. of the wood between the contacts ZA and augments (adds to) the E.M.F. of the wood, between the contacts XB.

The experiment reveals the peculiar fact that the cortex is a tissue which determines in part the magnitudes of E.M.F. measured between contacts on the wood. The cortex appears therefore to be the seat of an inherent E.M.F. apart from the inherent E.M.F. in the wood. This fact is what we suspected to be true in previous papers but were not able to prove at that time. The above indirect procedure appears now to yield the answer.

For the sake of clearness and unity of thought we shall present at this time a semi-theoretical formulation of the facts. The following experiments will be used as tests for the validity of our interpretation.
The relative magnitudes of the electric polarities and direction of the resulting internal correlation currents are illustrated in the diagram of figure 6. The facts upon which this diagram is based are:

1. A radial E.M.F. with the orientation indicated by the + and − signs exists between center and surface of the wood axis.
2. The magnitude of this radial E.M.F. is less as the apex of the tree is approached. This is arbitrarily indicated by the numbers 8 and 6, which correspond respectively to the numbers of the + and − signs. For the moment we shall limit discussion to only two regions whose location is given by 6, 5 and 8, 2.
3. It will be shown later that there is a radial E.M.F. in the cortex, which is oriented oppositely to that in the wood, that is, the outer surface of the cortex is electropositive in the external circuit to the inner cambial surface. Furthermore this radial E.M.F. increases toward the apex of the tree. This fact is indicated by the numbers 5 and 2 in the cortex.

Now suppose we apply contacts at a and b, a current would then flow from a to b in the external circuit. This agrees with all actual experimental observations. Under natural conditions this external “return” circuit we will assume to exist in the conducting outer layers of the cortex. The main seat of E.M.F. is assumed to be in the inner young active phloem and cambium layers similar to the observed location of the greater part of the E.M.F. in the outer layers of the wood (LUND 3). The arrows in the cortex indicate the direction of the internal “return” circuits.

Again suppose we lead off from b and d, the direction of the flow of the current in the internal part of the circuit would be inward in the direction of the vertical arrow. This again is in agreement with experiment. Suppose we make contact at points c and d in the central axis, then the diagram shows that we would expect the current to flow in the external circuit from d to c. But now we must remember that since the electrical resistance of the old wood at the center of the tree is very high and the greater part of the E.M.F. designated by the numbers 8 and 6, lies near the surface in the young actively growing wood we would expect to observe a small current, and a small E.M.F. between the central points c and d as measured by the potentiometer. This is just what the experiments in previous papers have shown. The observed magnitude and orientation of the longitudinal E.M.F. in the center of the wood axis depends upon the position of the leads (= inner ends of the glass funnels) in the wood axis. The direction of the arrows at the center indicate the general direction of flow of the correlation current chiefly in that part of the wood having a relatively low electrical resistance.

Suppose we lead off from c and a, experiment shows again that c is electropositive in the external circuit to a, at least in the regions of the
second internode and in all internodes below it (cf. later data). Therefore the current in the cortex-wood system in such an observation would flow from a to c just as was observed between b and d. However, if we include the E.M.F.'s in both of the polar regions between a and c, and between b and d in a complete system and connect them by conductors, the direction of the current will be determined by the basal region b–d and not by a–c, because the E.M.F. of b–d is $8-2=6$ units while the E.M.F. of a–c is $6-5=1$ unit. These two are opposed to one another and the resultant E.M.F. will be the difference or 5 units of E.M.F. in our simplified case. The actual direction of flow of electric current in the region between a and c will therefore be that which is indicated by the arrow and not the opposite (cf. Lund (3), p. 277).

Regions a–c and b–d we speak of as being electrically correlated. In the above very simple case we may say that the E.M.F. of the region b–d determines more or less the direction of flow of electrical energy in the region a–c. In this manner it now becomes obvious that mutual interaction of E.M.F.'s may result in mutual modification of electrochemical processes and therefore mutual modification of other linked metabolic processes in different regions.

I wish to emphasize that the above formulation of the facts is to be thought of as a simplified description of the operation of the internal correlation mechanism. Without such simplification the presentation of the experimental facts becomes difficult and discouragingly indefinite.

Let us now return to the curves of figure 2. The fact that the longitudinal E.M.F.'s A'B' and AB are reduced by removal of the cortex, can now be understood from figure 6 in the following way. Since the inside surface of the cortex at b is more electropositive (=less electronegative) than the inside surface of the cortex at a, obviously this E.M.F. in the cortex when the latter is in its normal position, operates in series with the E.M.F. in the wood. That is, the E.M.F. between any two points in the longitudinal axis of the wood is increased by the presence of the cortex. Removal of the cortex would therefore be expected to result in a decrease in the longitudinal E.M.F. This agrees with the observed result.

The resultant E.M.F. of the cortex when in position, is oriented in the same way as the E.M.F. in the region d in the wood. Removal of the cortex should therefore cause a decrease in XB. The curve shows that it does.

On the other hand ZA is increased when the cortex is removed. This must mean that the E.M.F. in the wood in the region c is released from an opposing resultant E.M.F. residing in the cortex.

The opposite effects on XB and ZA caused by removal of the cortex, together with the fact that our diagram fulfills the requirements of observed
experimental facts, suggest very strongly that XB is, to a large extent, a
measure of the E.M.F. in the region d–b and that ZA is largely a measure
of the E.M.F. in the region a–c. The fact that the E.M.F. between c and d
is usually small also suggests the same interpretation.

It appears to be evident from curves ZB', ZB and XA, XA' that the
E.M.F. in the cortex does not affect these strictly radial potentials in the
wood. In our interpretation of the experimental facts we have attempted
to construct a diagram of the relations between the orientation and approxi-
mate relative magnitude of the internal correlation potentials in wood and
cortex, which will fit the facts. The success to which we have attained will
in part be indicated by the experiments which follow.

**Procedure II**

Figure 1.II, curves, figure 3

The arrangement of the experiment indicated by diagram II in figure 1
is essentially the same as that in procedure I, except that another contact
Y was added at the center of the wood and the contacts A' and B' were
dispensel with.

The curves in figure 3 show that most of the potentials underwent a
gradual decrease during the period of the experiment. When the drift
(shift in flux equilibrium, cf. LUND (6)) had become uniform the cortex
between A and B was removed. The time of removal is indicated by the
vertical arrows.

The curves ZB and XA show again that the radial potentials in the
exposed wood are affected little if any by removal of the cortex. Note also
that ZB > XA. This is to be expected since the position of ZB is more
basal than that of XA.

The E.M.F. of XB is decreased and that of ZA is increased by removal
of the cortex. This result and its interpretation is again the same as that
in procedure I above. It will be noted that this increase and decrease of
E.M.F. resulting from removal of the cortex occurs in spite of the continual
drift of the E.M.F.'s.

The longitudinal E.M.F. AB also drops to a very low value and remains
low or absent during the remainder of the experiment. This result is the
same as in procedure I.

The curves for the two measurements YB and YA are interesting for
two reasons: First, because YB > YA. This indicates that YB measures
largely the radial oblique E.M.F. located toward the basal region near the
contact B, while YA measures the corresponding radial oblique E.M.F. in
the apical region near the contact A. (cf. about p. 638). The second fact
of interest is that after removal of the cortex, YB and YA approach each
other in magnitude: Why? The answer is apparently given by our dia-
Fig. 3. Upper curves ZB, XB, ZA, and XA refer to E.M.F.'s between corresponding contacts in figure 1.II, and are strictly comparable to the curves in figure 2 designated by the same letters. The middle curve AB is strictly comparable to curve AB in figure 2. Curves YB and YA measure the E.M.F.'s between the corresponding contacts. Their relative magnitudes should be noted.
gram figure 6. Namely, the E.M.F. of the cortex when in contact with the wood, is applied so as to augment the difference in E.M.F. between the regions d and c, namely 8–6 = 2. In order to augment this apparent difference (=difference between YB and YA) the E.M.F. at d(=8) is increased, while that at c (=6) is decreased. Or stated in other words the resultant E.M.F. of the cortex sums with the local and relatively basal radial E.M.F.’s in the wood since they are oriented in the same direction and are therefore in series, while relatively apical and local radial E.M.F.’s in the wood are decreased because the resultant E.M.F. of the cortex opposes the inherent apical radial E.M.F. in, for example, the region c. A second experiment of this kind gave the same results. Our diagram in figure 6 appears to be in striking agreement with the facts.

Procedure III

Figure 1.III, curves, figure 4

Effect of killing the basal half of the internode by heat.—The second internode from a tree twenty feet high was used. The total length of the internode was 50 cm. The apical and basal diameters of the wood at A and B were 8.5 and 12 mm. respectively. The lengths of the cortex between Y and A, and between Y and B, were 14.5 and 14.0 cm. respectively. The length of each ring of cortex which was removed at A and B was 4 cm. The set up in procedure III was identical with that in procedure II except that the basal half of the internode (stippled) was immersed in boiling tap water for two minutes. The heated cortex assumed a brown color.

During exposure of the basal half of the internode to the boiling water, the apical half was protected from injury by wrapping it in cloths soaked with cool water. The heated half of the internode was now cooled in running tap water, wiped dry and fixed in position with the contacts. The preparation was left for over an hour, during which several readings of P.D. were taken. Toward the end of this period the P.D.’s became relatively constant.

When this had occurred, the dead cortex on the basal half of the internode was quickly removed. The time of removal is indicated by arrows in figure 4. A set of measurements was taken and immediately after these readings, the living cortex on the apical half of the internode was also removed. Readings of E.M.F. were taken thereafter at intervals as indicated on the curves.

The effects produced by removal of the cortex in this type of experiment appear somewhat bewildering at first sight. A study of each curve by itself is however quite illuminating and reveals a number of interesting facts. The first fact which is apparently indicated in the curves is that
removal of the living apical half of the cortex produces quicker and greater change in certain E.M.F.'s than the removal of the dead cortex.

Curve ZB which represents the radial E.M.F. in the dead wood is constant and has the same orientation as the E.M.F. in the living tissue. Similarly YB has the same orientation but not a greater magnitude relative to YA in the living apical half, as would have been found if the region YB
were living. Curve XA of the radial E.M.F. of the living wood shows a drift in the E.M.F. but is apparently not affected by removal of the cortex. This result agrees with those of all other experiments.

Comparing YA and YB we see that YA which is living is increased by removal of the living cortex just like ZA was increased in procedures I and II above. On the other hand YB, which is dead, is not at all affected by removal of its dead cortex. Evidently ZA is comparable to YA since both include the living region and are increased by an equal amount. We may perhaps infer from this that YA and ZA measure the E.M.F. of approximately the same region, namely that near A. On the other hand the contacts X and Y with respect to B are not the same, because XB includes the living wood end and is therefore affected by removal of the living cortex, while YB does not include any living wood and is not affected by removal of either living or dead cortex. This is the reason why removal of the cortex does affect XB but does not affect YB. The E.M.F. of XB is decreased in a similar way to that in procedures I and II. However its polarity is finally inverted so that X becomes electronegative to B.

Removal of the living cortex decreases very much (= inverts) the longitudinal wood E.M.F., AB. This is fundamentally the same result as that obtained in all experiments of procedures I and II above. With reference to figure 6, the interpretations of the effects of removal of the living cortex in procedure III are identical with the interpretations given above for procedures I and II, and therefore we shall not repeat them.

Procedure IV

Effect of Killing the Apical Half of the Internode by Heat.—The experimental procedure was the same as that in the previous experiment except that the third internode of the same tree was used, and the apical half of the internode was killed by immersion in boiling water for four minutes. The times of removal of the dead and living cortex are indicated by the vertical arrows on the curves.

1 Any partial critic of the oxidation-reduction theory of the origin of continuous bioelectric currents might obviously consider these facts as support for the common theories of bioelectric currents, according to which bioelectric E.M.F.'s are due to differences in concentration of inorganic ions. In this connection the writer merely wishes to repeat that several types of electric potentials in all probability enter into various bioelectric phenomena. The problem which concerns us is the identification of the particular kinds of E.M.F. which occur in different electrical phenomena inherent in the living cell. In any case the existence of a P.D. in a dead system is obviously no secure basis for inferences regarding the nature of the E.M.F.'s in the previous living state of that system.
Fig. 5. Upper curves show the changes in E.M.F. produced by removal of apical (dead) and basal (living) cortex between the different pairs of contacts in figure 1. IV. The corresponding curves in figures 4 and 5 should be compared. For interpretation see text.
Again the radial E.M.F.'s, ZB and XA do not show any appreciable affect of removal of the cortex. The longitudinal wood E.M.F., AB, now shows a distinct increase in E.M.F. as compared to a decrease in all the previous types of experiment when the living cortex was removed. The question is, why do we obtain opposite effects on AB in the two procedures III and IV when the living cortex is removed?

Referring to figure 6 we recall that the resultant of the E.M.F.'s in the cortex is oriented in such a manner that it augments (= increases) the radial E.M.F. of the wood in the region d, but opposes the radial E.M.F. of the wood in the region c. After the removal of the living cortex in procedure III, A is electronegative to B (inverted polarity). In this case the resultant E.M.F. of the cortex is evidently opposed to the inherent longitudinal E.M.F. of the wood when the cortex is in situ. The result is that the inherent (inverted) longitudinal E.M.F. in the wood between A and B in curve AB of figure 4 is diminished by presence of the cortex and increased by its removal.

The opposite explanation evidently applies to curve AB in procedure IV because the curve shows that after removal of the living cortex, A is electropositive to B. In this case the orientation of the resultant E.M.F. in the cortex was again opposite to that in the wood, since removal of the living cortex in procedure IV resulted in an increase in the longitudinal E.M.F. of the wood. Since contacts Z and A of procedure III are comparable respectively to contacts X and B of procedure IV, in their relation to dead and living parts of the stem, we should expect that removal of the living cortex would affect both of these E.M.F.'s in the same manner. The same statement applies to curve ZA of figure 5 and curve XB of figure 4. Both of these expectations are fulfilled as shown by the curves.

Again since the contacts Y and A in procedure III are comparable respectively to contacts Y and B in procedure IV in their relation to dead and living parts, we should perhaps expect that removal of the living cortex would effect both of these E.M.F.'s alike. The curves show that both of these E.M.F.'s are increased. Finally curve YA shows that the E.M.F. of this dead segment is not affected by removal of the dead cortex. This result is the same as that in curve YB of figure 4, procedure III.

Discussion

Increase in the Radial E.M.F. in the Cortex Toward the Apex

The preceding experiments, especially those of procedures I and II, have shown that the effects of removal of the cortex² lead to the conclusion

²By cortex is of course meant the living parts without specifying which particular cells are primarily concerned in the electric phenomena. Identification of the particular cells concerned is of course a problem for the future.
that the resultant E.M.F. of the cortex augments the resultant longitudinal E.M.F. of the wood. This leads to the inference that the radial E.M.F. in an apical part of the cortex is relatively greater than that in a more basal part of the cortex, at least under conditions of absence of injury and stimulation. The arbitrary numbers 5 and 2 in figure 6 are intended to indicate this fact.

![Diagram](image)

**Fig. 6.** Diagram of an internode having the same contacts as that shown in fig. 1, procedure II. The numbers 2 and 5 represent arbitrarily chosen values of the radial E.M.F.'s in the cortex at this level, and correspond to the numbers of + and - signs. Similarly the numbers 8 and 6 represent arbitrarily chosen values of the radial E.M.F. in the wood. The indicated orientation and relative magnitudes of the radial E.M.F.'s in cortex and wood are those which would fulfill all the requirements of the observed experimental facts. The direction of flow of the resulting current produced by the two systems of E.M.F.'s in cortex and wood is indicated by the direction of the arrows. Note that the resultant E.M.F. in the cortex is in series with that in the wood. At the bottom of the figure is shown two layers of cells in section; these represent diagrammatically the bipolar cambium and other living cells in cortex and wood in which the E.M.F.'s originate. The direction of the arrows indicate the general direction of the flow of electric current. For fuller description see text.

Now if the reader will refer to the diagram E in figure 7, page 271, and table 4, page 275 in the article by LUND (3), it will be found that the magnitude of the basal-apical oblique E.M.F.'s have always the following relation $E_3 > E_2 > E_1$. A specific illustration is given in table 4 where $E_3 = 67.5$ m.v., $E_2 = 52.0$ m.v., and $E_1 = 31.5$ m.v. As the external contact in such a series of measurements is moved farther toward the apex the E.M.F.'s decrease until they finally become zero. Above this zero point the E.M.F.'s
Fig. 7. This diagram attempts to show the approximate distribution and usual orientation of the E.M.F.'s in the wood and cortex of the Douglas fir together with the resulting orientation of the externally observed polarities in the main axis and branches. The relative magnitude of the E.M.F.'s in wood and cortex of the main axis are indicated by the groups of + and − signs on the right hand side of the diagram. Each branch is the seat of a similar distribution of E.M.F.'s.

The system of arrows in the wood and cortex on the left hand side indicates the direction of the resultant E.M.F. in the wood-cortex system in the tree under conditions of absence of stimulation. Experiments show that the E.M.F.'s in the apical regions are especially subject to large fluctuations in magnitude and direction. The diagram is of course not to be taken too literally, although it fits all the observed experimental facts which are known at present.
increase again but the outside apical contact now becomes electropositive (in the external circuit) instead of electronegative to the lower contact in the center of the wood axis.

A series of measurements was carried out on the apical ends of lateral branches. The contacts were those designated by GA, GC, GB, GD, GE and GF in figure 1 of the preceding paper (Lund 5). All of these measurements showed that the apical contacts were electropositive to G except F, and GF exhibited only a small E.M.F. This is interpreted to mean that the total radial E.M.F. of the wood plus cortex diminishes toward the apex. This decrease is due to the decrease in diameter of the wood axis toward the apex, because it has been shown that the radial E.M.F. is proportional to the thickness of the peripheral living active part of the wood axis.

The basal-apical oblique E.M.F.’s in apexes are relatively large. The greater part of this E.M.F. must have its origin in the cortex since the orientation of the E.M.F. between these contacts is reversed in the extreme apical regions. In other words the radial and therefore the resultant longitudinal E.M.F. in the cortex of the growing apical segment is greater than that in the thin tubular wood axis. It is evident that in the apex it is the E.M.F. of the cortex which dominates the electromotive phenomena.

In figure 7 this basal-apical increase in radial E.M.F. in the cortex is indicated by the larger number of + and − signs. We conclude from the preceding facts that there must exist a point at some distance below the apex where the radial E.M.F. of the wood plus cortex equals zero.3 The facts taken as a whole show that the radial E.M.F. of the apex is subject to unusually large fluctuations in magnitude when compared to other regions of the tree. The person who likes to contemplate the adaptive features of biological mechanisms will find interesting material in the operation of the mechanism of electric correlation.

General Consideration of the Results and their Bearing on Energy Transformation in the Plant

The experiments have revealed a group of new phenomena, the consequences of which are of special interest for cell correlation and related processes. In the first place they show in an unequivocal manner that the E.M.F. which is observed when we measure the external electric polarity of the stem and branches of the tree is the algebraic result of a system of internal E.M.F.’s, the elements of which are located in two main regions, namely the cortex and wood. The experiments show that the resultants of these systems of E.M.F.’s augment one another, that is to say they operate

3 This point corresponds to that on the main axis of the stem at which the extrapolated curves of E.M.F. in Lund ((3) figure 4, page 265) cuts the horizontal axis.
in series like two complex systems of batteries. In general they show that an electric current flows downward in the outer cortex and upward in the wood axis. The results therefore confirm previous observations but in addition show that the cortex is the seat of a separate E.M.F. Figure 7 is presented as an approximate summary of the facts to date. To help visualize a little more accurately the direction of flow of the transverse and longitudinal components of the currents, the bipolar cambium and other bipolar origins of the E.M.F. are represented diagrammatically in figure 6 by two layers of cells with a system of arrows to indicate the general direction of the correlation currents. Future experimental analysis of the distribution of correlation currents will of course be toward a description of the patterns in microscopic dimensions. In all probability these patterns will be found to correspond more or less to the complex cellular architecture of the wood and cortex in which they originate and in which their energy is being transformed and dissipated.

One fact of extreme interest which must be clearly recognized is that when we measure the E.M.F. between any two contacts the magnitude of this E.M.F. is in general not necessarily directly proportional to the total electric current which flows in the local circuits in the tissues between the electrode contacts. In other words the system operates more like a complex network of conductors with a relatively fixed pattern of local origins of E.M.F.’s. It appears certain from this consideration that relatively large amounts of electrical energy are being transformed into electrical work and heat, which would not be indicated by single measurements of E.M.F.’s or electric currents led off from a single pair of contacts as we do in actual practice.

It is not improbable that a considerable part of the total heat energy output by the plant is derived from continuous electric currents, the energy of which appears only secondarily as heat. If this is true then it is obvious that the experiments have opened to us a new vista of the phenomena of energy transformations in the plant. We shall discuss briefly some of the possibilities in what follows.

CONTINUOUS CORRELATION CURRENTS AS THE POSSIBLE SOURCE OF ENERGY FOR ELECTROENDOSMOTIC TRANSPORT IN THE PLANT

The writer can not forego the opportunity at this time of presenting what appears to him a distinct possibility, namely that one of the functions of the continuous electric current which is directed upward in the wood is to supply electrical energy for electroendosmotic flow of sap in an upward direction in the conducting vessels of the wood. This suggestion may also apply to a downward flow in the cortex as well as transport across the stem.
If this is the case we would expect that the well known equation for velocity of flow in a system of capillaries caused by the application of an E.M.F. would apply, namely,

$$v = \frac{q\varepsilon H \zeta}{4\pi\eta l}$$

In this equation $v =$ volume flow, $q =$ area of cross-section of the capillary system, $H =$ the applied E.M.F., $\varepsilon =$ the dielectric constant of the liquid, $\eta =$ the viscosity, and $l =$ length of the capillary system, $\zeta =$ the electrokinetic potential between the liquid and wall of the capillary. Suppose we consider a certain bundle of conducting vessels or a single conducting vessel in the water conducting region of the wood (Overton 9). The orientation of the radial and resultant longitudinal E.M.F.'s is that represented in the diagram figure 6. It is evident that $q$, $\varepsilon$, $\eta$ and $l$ are determinable quantities. $H$ is supplied by the inherent E.M.F., leaving the electrokinetic potential $\zeta$ to be considered. Now it has been shown by Stamm (10) that the orientation of the electrokinetic potential of the walls of wood vessels against water is such that the liquid in all the types of wood which he examined namely, Sitka spruce, Alaska cedar, western red cedar, western hemlock, Douglas fir and yellow poplar, moved from anode to cathode, showing definitely that water with respect to the capillary vessel wall carries a positive charge.

Stamm's experiments therefore demonstrate first, that an electrokinetic potential exists between the water and the wall of the conducting vessel. The presence of the electrokinetic potential as the equation shows, is a sine qua non for the occurrence of electrokinetic flow, for if $\zeta$ is 0 then $v =$ 0. The second significant fact about Stamm's experiments is that the electrokinetic potential is oriented in the right direction, that is, water is electropositive to the wall of the vessel and therefore the observed inherent E.M.F. in the wood, figure 6, which now takes the place of $H$ in the equation will of necessity tend to transport the water upward and not downward in the vessels of the wood.

With these facts in mind a few preliminary experiments were carried out on the apexes of lateral branches of the Douglas fir. The procedure was as follows. The apical part of a lateral branch was cut off about one inch below the origin of the two most distal symmetrically placed lateral shoots. Care was taken to select tips of branches in which these two lateral shoots were placed exactly opposite one another at the base of the main axis shoot. The cut basal end was dipped into a solution of eosin in water. Tap water electrode contacts were attached to the tips of the two lateral shoots. A constant electric current of a few microamperes was sent into the apex of one of the symmetrical lateral shoots and out through
that of the other. The applied current therefore passed downward in one and upward in the other shoot. The current was left on usually for eight to twelve hours. During this period the solution usually ascended several cm. in the wood axis.

Removal of the cortex showed that in most cases the distance to which the dye had risen in the two lateral shoots was unequal. In all the experiments showing distinct inequality the solution had penetrated to the greatest distance in that lateral shoot in which the electric current flowed from base to apex in the wood. In some of these preliminary experiments the difference was very marked while in others the result remained uncertain.

The results of these preliminary experiments are merely to be considered as suggestive. However, the results indicate agreement with the interpretation which we have presented above.

At present the phenomena are being investigated with a fuller consideration of the many factors which are involved. It is obvious that such phenomena as guttation and bleeding pressures may be the expression of the same type of mechanism.

The possible application of correlation potentials in roots (Lund and Kenyon, 6) to the problem of differential absorption of ions will be considered in later papers.

Summary

1. The results of the experiments constitute direct and conclusive evidence that the principle of summation of E.M.F.'s applies to phenomena of electric correlation between living cells in the Douglas fir.

2. The cortex of the Douglas fir is the origin of a characteristic E.M.F. The orientation of the radial E.M.F. in the cortex is opposite to that in the wood.

3. Several lines of evidence show that this radial E.M.F. in the cortex increases toward the apex, while that in the wood decreases.

4. It is shown that the resultants of each one of the two systems of E.M.F.'s in the cortex and wood operate as if they are placed in series.

5. Removal of a ring of living cortex which lies between two contacts placed on or in the wood axis results in a permanent change in the previously observed E.M.F. between these contacts. The direction of change depends upon the position of the contacts.

6. Removal of similar rings of cortex from stems which had been killed by heat did not produce any such marked effects.

7. Electromotive forces are present in stems killed by heat, but the behavior of such E.M.F.'s is radically different from those in the living cortex.
8. Attention is called to the possible rôle under certain conditions of electric correlation currents in the wood as a source of energy for electro-endosmotic transport of water upward in the conducting vessels of the wood. It is shown that all present known facts agree with this possibility.

9. The observed small quantities of electric energy which may be led off from two contacts on the tree are not to be considered as indicative of the actual amounts of electrical energy which are transformed into work and heat in the plant. There is every reason to believe that the quantity of electrical energy which is transformed is much larger than has heretofore been suspected.

UNIVERSITY OF TEXAS, AND
PUGET SOUND BIOLOGICAL STATION,
FRIDAY HARBOR, WASHINGTON.

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