ELECTRIC OSCILLATIONS GENERATED BY PLANT ROOTS AND A POSSIBLE FEEDBACK MECHANISM RESPONSIBLE FOR THEM

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Summary

An account is given of rhythmic variations which have been observed in the electric field generated by bean roots growing in water. These electric oscillations which have periods of about 5 min have been studied using apparatus which records automatically at frequent intervals the potential pattern near the root. A description is given of this apparatus and of a very sensitive instrument for recording the rate of elongation of the root.

The cause of these and similar oscillatory phenomena in biological systems is discussed and a possible feedback mechanism responsible for the observed electric oscillations is postulated.

I. INTRODUCTION

In an earlier paper (Scott, McAulay, and Jeyes 1955) a new method of measuring the bioelectric fields generated by plant roots was described. A root was grown vertically in a bath of water made weakly conducting with KCl. Potential differences were then observed between points in the water adjacent to the root due to electric currents generated by the root and flowing through the water. This method was claimed to be an improvement on those employed in previous investigations. Interference with the normal growth of the root by the measuring process was avoided, leading to results which appeared to be more consistent than those reported previously.

In the earlier paper the steady electric pattern generated by a normal, growing root was described. A more detailed study of this pattern has shown that under some circumstances large periodic fluctuations in the electric potentials are generated (McAulay and Scott 1954). These oscillations are superimposed on the steady or background pattern. They are sinusoidal in form and have periods of the order of 5 min, amplitudes of a few millivolts, and may persist for several hours. The observed oscillatory pattern and the conditions under which it is generated will be described in detail in Section III.

Study of these variations in electric pattern has been made practicable by the construction in this Laboratory of apparatus which automatically measures and records at frequent intervals electric potential differences between a number of points in the bath adjacent to the root. This apparatus will be described in Section II.

A new apparatus for measuring and recording the rate of elongation of a root simultaneously with the measurement of its electric potential pattern is also described in Section II. This apparatus was constructed in order to discover whether rhythmic oscillations of rate of growth accompanied the electric oscillations. Observations made with this equipment are described in Section III(d).

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The observation of rhythmic changes in the electric field of roots has raised the general question of the cause of these and similar oscillatory phenomena associated with biological material which do not appear to be related to any corresponding oscillatory changes in the environment. Possible mechanisms for the generation of such oscillations will be discussed in Section IV and in particular a possible source of the electric oscillations described in this paper will be suggested.

II. APPARATUS AND MATERIALS

(a) Automatic Apparatus for Measuring and Recording Potential Differences between a Number of Points near Plant Roots Grown in Water

The apparatus used for automatically recording bioelectric potential differences near bean roots growing in weakly-conducting water is shown in Figure 1. A schematic diagram is given in Figure 2. The basic recording instrument used was a Cambridge six-channel, quick-acting recorder with a maximum full-scale deflection of 1 mV. This recorder produced dots of different colours to distinguish the different channels. The time between successive dots was 5 sec so that each channel was recorded at \( \frac{1}{2} \)-min intervals. For most of the work described in this paper the chart was driven at 1.5 in./hr.

The recorder had to be modified so that it could be used with an electrometer stage input. This was necessary because the input resistance of the recorder was only 1000\( \Omega \), whereas an input resistance of the order of 10\( ^{11} \)\( \Omega \) was required for the bioelectric measurements to be described in order to prevent undue current drain.
and resulting polarization of the source. The electrometer used a pair of matched ME1400 valves in a balanced circuit and was designed to be as insensitive as possible to changes in H.T. or L.T. voltage. Currents flowing in the input circuit of this stage were never more than $10^{-12}$A under the conditions of measurement.

![Fig. 2.—Schematic diagram of the automatic apparatus for measuring plant potential differences.](image)

A photograph of the measuring bath is shown in Plate 1. It was constructed of "Perspex" and had the dimensions $11 \times 5 \times 3$ in. It was filled with 0-0001N KCl solution which was aerated, stirred, and temperature-controlled. For most of the measurements described in this paper the temperature was controlled at 25°C, although one or two experiments were conducted at temperatures as low as 17°C.

![Fig. 3.—Section through the measuring bath to illustrate the liquid-switching arrangement. For simplicity only one of the liquid-conducting paths from the plant to the rear bath is shown.](image)

The plant under investigation $P$ was mounted in the tank with the root immersed vertically (Fig. 3). The ends of lengths of transparent "Nylex" tubing $N$ (3-mm bore) were brought close to the surface of the root at various points along its length. The other end of each tube dipped into an insulated plastic cup $C$, the cups and tubes being also filled with 0-0001N KCl. Tubes came from as many as
five points near the plant. A sixth tube came from a point in the bath some distance from the plant; this was used as a reference (see later).

Each of these cups was connected in turn to the measuring circuit by means of a liquid-switching arrangement. Associated with each cup was a glass bridging-tube B (also filled with the same KCl solution) which could dip into C and make a connection across to a small 0-0001N KCl bath R at the rear of the main bath and insulated from it. The bridging-tube made this connection when the solenoid S, on which it was mounted, was energized. The six solenoids were energized in succession, synchronizing with the recorder output channels (colour of trace on chart). One of the electrodes E (calomel half-cells) dipped into the rear bath, and the other into the main bath at a point some distance from the plant. These electrodes were connected to the electrometer. Thus it is seen that each point near the plant was connected in turn to the rear electrode via a path which was entirely of 0-0001N KCl.

Water was nowhere allowed to become stagnant. A fresh supply dripped into the rear bath and passed through the bridging and “Nylex” tubes to the main bath where the excess dripped out at an overflow.

It might appear that the rather complicated bath-switching arrangement described above and which required high insulation could have been avoided if, instead of using a single pair of electrodes and a single electrometer, separate electrometer stages and electrodes were used for each channel. Selection of the various channels for measurement could then be done by a relatively simple metallic selector switch in the recorder itself.

The former system was used, partly to avoid duplication, but more especially because electrometer circuits and half-cells are never absolutely stable, but show slow potential drifts over long periods of time. In order to determine whether an observed change in potential is a genuine plant effect or due merely to a drift in the measuring apparatus, it is necessary to “switch the plant out”, i.e. to measure the potential at a point in the bath remote from the plant and where the potential is presumably unaffected. To obtain a reference reading with an automatic recorder it is therefore necessary either to move the measuring probe away from the plant to a distant point at frequent intervals, or to use some sort of bath switch such as that described above, and for one channel to switch to a distant point.

In the present case the reference potential was recorded at 30-sec intervals. For convenience in reading the charts any drifts in the measuring apparatus were automatically compensated for, so that the reference trace always showed no deflection from zero on the chart. A phase-sensitive motor which drove the zeroing control in the electrometer was energized through contacts in the recorder whenever the reference potential differed from zero.

(b) Growth Meter which Automatically Records the Rate of Elongation of Plant Roots Growing in Water

It was desired to find a sensitive method of measuring the rate of elongation of a root in order to test whether rhythmic variations occurred in this rate and
if so whether they correlated with the electric rhythms detected with the recording apparatus (Section II(a)) and described in detail in Section III.

The rate of growth of a moderately active root is about 10 $\mu$/min. Consequently in order to observe small oscillatory variations in this rate, the periods of which might be only a few minutes, it was desirable that increases in length of about 1 $\mu$ should be detected. In addition to this requirement the method had to be suitable for use with roots growing in water, it should not interfere with the potential measuring apparatus, and it should lend itself readily to automatic recording of the growth rate.

![Diagram](image_url)

**Fig. 4.—Simplified diagram illustrating the principle of the rate-of-growth meter.**

None of the conventional methods appeared to be suitable. Optical methods could not easily be applied. Auxanometers of the type described by Koningsberger (1922) and recently modified by Ranson and Harrison (1955) could not be used because of electric interaction and the difficulty of keeping the switch contacts dry.

The method which was finally chosen was suggested by Dr. D. B. Idle of the University of Birmingham (personal communication). The apparatus is shown diagrammatically in Figure 4. KCl solution (0.0001N) from a constant head (about 120 cm of water) flowed along a tube in which there were two constrictions X and Y which restricted the flow of water by about the same amount. The constriction at Y was variable being covered by a flexible flap against which the root tip pressed lightly.

The method made use of the fact that a small increase in the resistance to the flow of water at Y caused a considerable increase in the water pressure between X and Y. This increase caused electric contacts in the mercury manometer to close, and the lift mechanism was activated. The plant was then raised through a small increment (1 $\mu$) thereby reducing the pressure on the flap and breaking the electric contact in the manometer. Thus the growing plant was raised up in 1 $\mu$
steps each time the manometer contacts were closed. During an active period of growth the plant was raised by 1 \( \mu \) increments at intervals of 2 or 3 sec.

The lift mechanism employed the screw and ratchet of a Cambridge rocking-arm microtome and this was operated by means of a solenoid. Power to energize the solenoid came from a relay circuit as an electric pulse each time the manometer contacts closed. In the event that a single upward step by the plant was insufficient to break the contacts (as would be the case, for example, if the root grew several microns suddenly) it was arranged that pulses from the relay should continue to energize the solenoid at 1- or 2-sec intervals until the contact broke. The number of increments was counted on a mechanical register.

In order to facilitate comparison of the electric pattern with the rate of growth, it was decided to record the number of growth increments each minute on the same chart as was used for the potential difference measurements. Each pulse from the relay turned the movable contact of a variable resistance through a small angle. Because a constant current was passed through this resistance the potential difference across it was proportional to the number of increments. This potential difference was registered by the recorder each minute, one of the channels being used for the purpose. The integrator was then automatically reset to zero to count the number of increments during the next minute.

(c) Material

The material used in the experiments described in this paper was the broad bean, \textit{Vicia faba} L., var. Johnson's Long Pod, which was grown in water-baths at 25°C. In most cases tap water was used, but in some the growth medium was 0.0001N KCl. The water was circulated and aerated. Plants 2-3 days old with roots about 30 cm long were used in most experiments.

III. Results

(a) Root as Source of Electric Oscillations

Whenever a new phenomenon is being studied it is especially important to check whether all possible artifacts have been accounted for and removed. In the present case careful tests were made to eliminate processes other than those due to the plant which could have given rise to the observed electric oscillations.

Such oscillations clearly could not have arisen in the electrodes, electrometer, or recorder, as the reference trace giving the potential at a point remote from the root in the bath showed no oscillations. Since the temperature of the measuring bath was thermostatically controlled it was necessary to check whether the electric oscillations correlated with the switching off and on of the heater. No such correlation was found; in fact, the electric oscillations still took place when the thermostat was disconnected. In a similar way it was shown that small fluctuations of height of the water in the bath were not responsible for electric fluctuations. Interaction with neighbouring electrical circuits was also ruled out.

That the root was itself the source of the electric oscillations could be seen most conclusively by moving the measuring probes in the vicinity of the root. The
amplitude of the oscillations became smaller as the probes were moved away from the root and varied with the position of the probes along and around the root. It is therefore concluded that the electric oscillations were generated by the plant itself.

(b) Description of the Oscillatory Pattern

The results obtained in 26 cases of bean roots which were observed to generate regular and persistent electric oscillations have been analysed. The general features of this oscillatory pattern will now be described.

When a plant was taken from the growth bath to the measuring bath and allowed to settle for some time (about 1 hr), the electric pattern in the water surrounding the root usually became steady, although slow changes occurred over long periods of time. This steady pattern agreed with that described previously (Scott et al. 1955); the region in the vicinity of the root tip being more negative than the root base. This indicated that an electric current flowed out from the plant at the root base, entering it again in the vicinity of the tip.

![Graph](image-url)

Fig. 5.—(a) Electric oscillations generated by a bean root. Each graph shows the time variation of the potential V (measured relative to a distant point in the bath) at a point close to the root a distance d mm from the tip. (b) Corresponding graph of V against d. The two curves are the extreme forms of the standing-wave pattern a half cycle apart. Note the phase reversal about the node 9 mm from the tip.

In the case of the group of plants now under consideration, oscillatory variations were observed to be superimposed on this normal steady potential pattern. These oscillations commenced from 1 to 10 hr (with an average of 4.7 hr) after setting the root up for measurement, and continued for an average of 5.8 hr. The average number of oscillations generated by the plant during this time was 55.8.

It was noticeable that the oscillations were very nearly sinusoidal in form. Certainly they never resembled relaxation oscillations. For a particular plant the period of oscillation at all points in its vicinity was the same and remained remarkably constant while the plant was in the oscillatory state. For a typical root, the average period for 42 cycles was 5.68 min with a standard deviation of 0.60 min. For the majority of plants studied the period was of this order, although in four cases it was longer, ranging from 12 to 32 min. If these slowly oscillating cases are excluded, the mean period for the main group was 5.75 min with a standard deviation of 1.02 min.
The amplitude of oscillation varied with position along the root. The most active region was nearly always within 8 mm of the tip. The average over a number of plants for the maximum peak-to-peak amplitude of the oscillation in the most active region was 1.7 mV although in two cases amplitudes as large as 5 mV were recorded. Although the amplitude of oscillation at a particular point usually remained approximately constant over many cycles, it was observed in five cases that the amplitude slowly built up to a maximum value, then fell away to zero, the process being repeated several times. The period of these "beats" was about 2 hr.

A study of the phase relationships of the oscillations taking place at several points along the root has revealed some interesting data. In most cases the oscillatory pattern was in the form of a standing wave, the oscillations taking place above and below a particular point (node) along the root being reversed in phase (Fig. 5). In some cases two nodes were observed, the oscillations near the tip and the root base being in phase, but opposite in phase to those of a region in between (Fig. 6).

![Figure 6](image)

**Fig. 6.**—As for Figure 5, except in this case the standing-wave pattern has two nodes.

Such phase reversals are to be expected, since a rise in potential of the water near one part of the root must be accompanied by a fall somewhere else along the root, if the electric current leaving the root is always to balance exactly the current entering it. As large oscillations were often observed near only a relatively small part of the root it appeared that the active source of the electric oscillations in these cases was confined to this region. Other parts of the root were inactive, small oscillations being observed there merely because of the return path of the oscillatory current through them.

In a few cases (Fig. 7) the phase relationship was considerably more complicated suggesting that a wave of activity was moving along the plant. It is seen that the oscillations were in phase near the root base, but closer than 15 mm to the tip the phase changed with position and was not related in a simple manner to that at the root base.

A pattern of this type might be produced by a root having more than one active source. If this were so, some mechanism would be required to synchronize the sources to oscillate at very nearly the same period, as the phase differences were found to remain almost constant for more than 30 cycles. As suggested above a more plausable explanation is that a disturbance generated by a source moved in
the form of a wave along the root thus causing electric oscillations which lag more and more in phase as the distance from the source is increased. In the present example, the observed phase relationship would be consistent with that caused by a wave travelling up the root from the tip with velocity 3.0 mm/min or alternatively down the root with velocity 1.4 mm/min. The phase relationships warrant further study, particularly to test whether the phase changes continuously along the root in the active region.

![Diagram](image)

**Fig. 7.**—Illustration of the complex phase relationship sometimes observed. (a) The time variation of the potential $V$ at points along the root $d$ mm from the tip. For simplicity only the oscillatory component of $V$ is shown. (b) A vector diagram illustrating the amplitude and phase relationship of the oscillations taking place for various values of $d$.

(c) Transient Oscillations Resulting from Stimulation

The electric pattern of a bean root was very sensitive to stimulation and changes in environment, large changes in the electric potential along the root being produced immediately. When the cause of the disturbance was removed, the pattern again became practically steady after a time which might range from a few minutes to an hour, depending on the degree of stimulation.

During this transitory time before the steady pattern is restored, the potential changes were frequently in the form of damped oscillations (Fig. 8). Such oscillations almost always occurred when a plant was taken from the tank in which it was grown and set up for measurement. Overshoot processes followed by damped oscillations were also observed to result from such treatments as mechanical stimulation of part of the root, sudden changes in the salt content of the water in the bath, addition of indoleacetic acid to the bath, and exposure of the root to air for a short time.

In a preliminary study of these patterns it was found that the period of the transient oscillations was of the same order as the maintained oscillations described in Section III(b) although the variability was greater, both during the oscillation of one plant; and from plant to plant. Further study of these transient electric changes is planned.

(d) Observations of the Rate of Elongation of the Root

Since an earlier paper (Scott et al. 1955) had shown some correlation between the steady electric pattern and the mean rate of elongation of the root, it was
considered possible that the observed oscillatory electric changes might be accom-
panied by corresponding oscillations in the rate of elongation.

The rate of elongation of the root was measured and recorded simultaneously 
with the electric potential measurements, using the apparatus described in Section II. 
No special tests were made of the accuracy and reliability of the growth meter, but 
this was considered to be good judging by the small amount of scatter (less than 
10 per cent.) which was observed in the rate-of-growth record of some roots. Other 
roots showed more random scatter than this, and this was considered to be due 
to a genuine variability in the rate of growth, although no exhaustive tests have 
yet been made of other possible sources of scatter.

![Graph of damped oscillations](image)

**Fig. 8.—Damped oscillations in the potential pattern following 
stimulation. The symbols have the same meanings as in previous 
graphs.**

On a few occasions, variations which were approximately periodic were observed 
(Fig. 9) but these did not occur while electric oscillations were being generated 
and there appeared to be no correlation between the two. It is, of course, possible 
that growth oscillations too small to be detected were taking place during the time 
of electric oscillation. If this were so, the amplitude of the oscillations must have 
been less than about 15 per cent. of the mean growth rate in order to escape detection.

The lateral movements of bean roots have been studied using time-lapse 
photography. It has been found that the growing root usually spirals around a 
vertical axis with a period of about 2 hr. So far there is no indication of a 5-min 
rhythm superimposed on this.
(e) Correlation with Pressure Applied to the Root Tip

A large number of treatments have been applied to a root producing its normal steady electric pattern with a view to causing it to start generating electric oscillations. None of these treatments has been entirely satisfactory. Nevertheless there is some evidence that pressure applied to the root tip tending to prevent elongation is one important factor required for the oscillatory state.

![Graphs showing growth rate over time](image)

Fig. 9.—Tracings from four charts showing the rate of growth of bean roots as measured and recorded by the apparatus described in Section II. Note the presence of oscillations in the rate of growth in the two lower graphs. These were not found while electric oscillations were being generated by the root. The period of the growth oscillations is rather longer than most of the electric oscillations.

On only two occasions were roots which were not experiencing tip pressure observed to be generating electric oscillations. On 18 other occasions, oscillations were in each case found to be associated with the presence of an upward force on the root tip. In some cases oscillations were produced when the root grew against a fixed obstacle, while in others they were produced when the root tip experienced a constant upward force of about 100 dyne. These oscillations usually commenced soon after pressure was applied to the tip, and lasted for some time after it was removed, although in one or two cases oscillations ceased while the root was still experiencing pressure. Permanent bending of the root frequently resulted from these tip pressures.
Although the above results suggest that tip pressure is an important contributing factor for the oscillatory state it is not true to say that oscillations always arise if tip pressure is applied. On a large number of occasions roots were subjected to tip pressure and no electric oscillations were observed.

These preliminary investigations suggest that the plant must comply with certain other conditions, as yet not ascertained, before it has the capacity to generate electric oscillations. Only then will it oscillate when pressure is applied to the tip.

(f) Effect of Auxin

In one series of experiments indoleacetic acid (IAA) was added to the measuring bath in which a root was generating electric oscillations. The concentration of IAA
was usually made 2 mg/l. At this strength the auxin inhibits elongation of the root (Scott et al. 1955).

In each case it was observed that IAA had a marked effect on the electric oscillations. A typical example is shown in Figure 10. It will be seen that the electric potentials were immediately altered (stimulation effect) after which the oscillation was rapidly damped. At the same time the rate of growth fell until the root had practically stopped elongating about 1 hr after the addition of auxin. After several hours the plant was sometimes observed to generate an oscillation again and at about the same time the root in some cases resumed elongating slowly. As the experiment was performed in daylight it was thought possible that the auxin effect was reduced due to destruction of the auxin by light.

IV. Discussion

Rhythmic oscillatory processes are frequently observed in living systems. Most of these rhythms are clearly related to rhythmic changes in the environment such as diurnal, annual, or tidal changes or periodic variations in light or temperature (Kleitman 1949).

In addition to these, rhythms are sometimes found in systems living in an apparently unchanging environment as is the case for the oscillations described in this paper. Other examples are the autonomic to-and-fro or circular movements of elongating shoots, roots, tendrils, and rhizomes (Darwin 1880; Bennet-Clark and Ball 1951) and the periodic changes in colour and oxygen consumption of the fiddler crab in a controlled environment (Brown, Bennett, and Webb 1954). These endogenous rhythms have recently been reviewed by Bünning (1956). In the examples quoted above and in the case of the electric oscillations described in this paper the periods of the rhythms are of the order of minutes or hours.

Cases of overshoot and sometimes damped oscillation in biological systems following stimulation or a change in environment have also been described previously in the literature (Burton 1939; Idle 1955).

Little serious attempt appears to have been made to explain the mechanism of the internal processes which give rise to spontaneous rhythms which have periods of more than a few seconds. Bünning (1956) has described the rhythms as analogous to the movement of a pendulum. A comparison of this type is quite misleading. Consider a simple inertial system subject only to restoring forces (such as the
PENDULUM) which has a natural period of the order of minutes or hours. The amount
of energy associated with this system would be so small that it would be dissipated
in a small fraction of a period. For example, the energy of a 1-g body oscillating
with an amplitude of 1 cm and period 5 min is only $2 \times 10^{-4}$ ergs. In order to maintain
a sinusoidal oscillation in such a system, energy losses would have to be replenished
at exactly the correct rate.

The most likely source of slow sinusoidal oscillations is a negative feedback
system. It is not proposed to consider here in any detail the behaviour of these
systems as they have been studied fully in connection with servomechanisms and
automatic control processes (Porter 1950). The following simple example (Fig. 11(a))
serves to illustrate the basic principles.

$A$, $B$, and $C$ are three variable quantities which are interrelated in such a
manner that a change in $A$ causes a change in $B$ which in turn causes a change
in $C$. If now the change in $C$ causes $A$ to alter in such a manner as to oppose its original
change, the system is said to be a closed-loop control system or a negative feedback
system. In order to gain adequate control the signal fed back is usually amplified
(by a factor known as the "feedback loop gain") and some external energy source
is necessary. It will be seen that negative feedback tends to stabilize the system
against disturbing influences and because of this is widely used in automatic control
systems. A familiar example is the thermostat which is controlled by the temperature
of the room, and which in turn governs the rate of flow of fuel to the furnace which
heats the room.

Control by negative feedback can never be instantaneous as some time delay
in the various processes in the feedback loop cannot be avoided. If either the time
delays or the feedback loop gain is too large the system may become unstable and
start to oscillate spontaneously. These oscillations are sinusoidal provided the
quantities involved in the feedback loop are related linearly to one another. They
may be of any period depending on the time delays occurring in the loop.

Thus it is seen that a system which under normal circumstances is kept stable
and resistant to external disturbing factors by negative feedback may lose control
and start to oscillate if one or more of the relationships in the feedback loop is
altered. If the equilibrium of a system on the verge of instability is disturbed, it
executes a damped oscillation before finally returning to the equilibrium state.
The rather delicate balance which exists between stability and instability is familiar
to those who handle feedback-controlled systems.

It will be noted that the root which generates electric oscillations has many
properties in common with the systems discussed above. The electric field of the
root may be almost steady for several hours when suddenly quite large oscillations
which are approximately sinusoidal commence. If a plant producing a steady
electric field is stimulated, damped electric oscillations often result.

It is therefore attractive to suggest that some automatically controlled process
involving negative feedback is associated with the growing root. Under normal
circumstances the system is stable but only just so, since transient changes are in
the form of damped oscillations. Occasionally some change in the properties of
the system causes it to become unstable thereby upsetting the control process.
Many self-regulating processes employing negative feedback are now recognized in the higher animals (Wiener 1948, Walter 1953). These include the homeostatic controls of such factors as temperature, balance, and blood pressure, as well as many others requiring conscious effort. So far very few similar controls have been found in the forms of life without nervous systems such as plants.

It is noteworthy that despite the frequent use of feedback processes in complex living systems, oscillatory behavior is seldom observed. Evidently the method of stabilizing these systems is effective over a considerable range of operating conditions.

In the present case not enough is known to say what aspects of the growth of the root are being controlled and what processes are involved in the feedback loop assuming that one is present. It seems unlikely that these processes are entirely electric. It is known that the electric impedance of cellular membranes has relatively large resistive and capacitative components (0·25 MΩ and 1 μF for 1 cm² in the case of Nitella (Blinks 1930, 1936)). These might conceivably be associated to form a long-period RC oscillator, say of the Wien bridge type, but it is difficult to see how this could be achieved. An amplifier of the correct gain would have to be available and the outputs of the individual cellular oscillators would have to be synchronized so as to give an observable oscillation in the external medium.

So far no other oscillatory variations in the bean root’s behaviour have been found to be associated with the electric variations. It is of course possible that the electric field itself is not an active element in the loop but is merely coupled to some other process which is directly involved. If this is the case, the electric field is acting as a very convenient and sensitive indicator of the stability or otherwise of the control system.

To conclude this discussion some tentative suggestions as to the sequence of processes involved in the proposed feedback loop will be made. Suppose the auxin concentration in the elongating region of the root controls the permeability of the cell walls to salts (Thimann 1949). This would undoubtedly affect the electric resistance of the plant tissue and hence the magnitude of the electric currents flowing in the plant root and returning via a path in the external medium. If it is now supposed that the electric field modifies the rate of supply of auxin within individual cells or groups of cells to sites at which it affects permeability a feedback loop is thereby completed (Fig. 11(b)). Under some conditions the feedback system might become unstable and give rise to the observed oscillations. Sufficient feedback loop gain should be available because of the sensitivity of auxin action.

The possibility that the bioelectric field plays a part in the movement of auxin in plants was suggested many years ago (cf. Went 1932; Kögl 1933). Although the relationship is certainly not as simple as it first appeared, recent experiments by Schrank and Backus (1951) have suggested that the diffusible fraction of auxin may well be moved electrophoretically. The fact that swamping the water around the root with indoleacetic acid quenches the electric oscillation suggests that auxin plays some part in the feedback process.

Further search for other changes in the root while electric oscillations are being generated is necessary before the feedback system can be specified with any
Photograph of measuring bath showing a bean root set up for measurement.
electric oscillations generated by plant roots

certainty. Some estimate of the time delays in the processes would then have to be made in order to see whether they are compatible with 5-min electric oscillations.

V. Acknowledgments

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