# ELECTRICITY IN PLANTS

Electrical disturbances similar to the nerve impulse are associated with a number of plant life processes. It seems likely that these currents and fields somehow influence plant growth and development

by Bruce I. H. Scott

The processes of life have been found to generate electric fields in every organism that has been examined with suitable and sufficiently sensitive measuring techniques. In some organisms bioelectricity serves well-recognized functions. The electrical disturbance of the nerve impulse, for example, carries information down the length of the nerve fiber. The central nervous system as a whole can be compared with a telegraphic exchange with electrical pathways linking the nerve cells in networks of almost unimaginable complexity. When measuring techniques similar to those used by the nerve physiologist are applied to plants, it is found that they too generate electric fields and currents. Whether electricity plays any part in the growth or other metabolic activity of the plant, or is merely a by-product of these processes, is not yet known. Recent experiments have pointed, however, to possible ways in which the bioelectric fields and currents generated by a plant may serve in the coordination and control of its development. It has been found, for example, that large individual plant cells respond to electrical, chemical or even mechanical stimulation in just the same way as a nerve cell does: with an electrical impulse that sweeps along the surface of the cell.

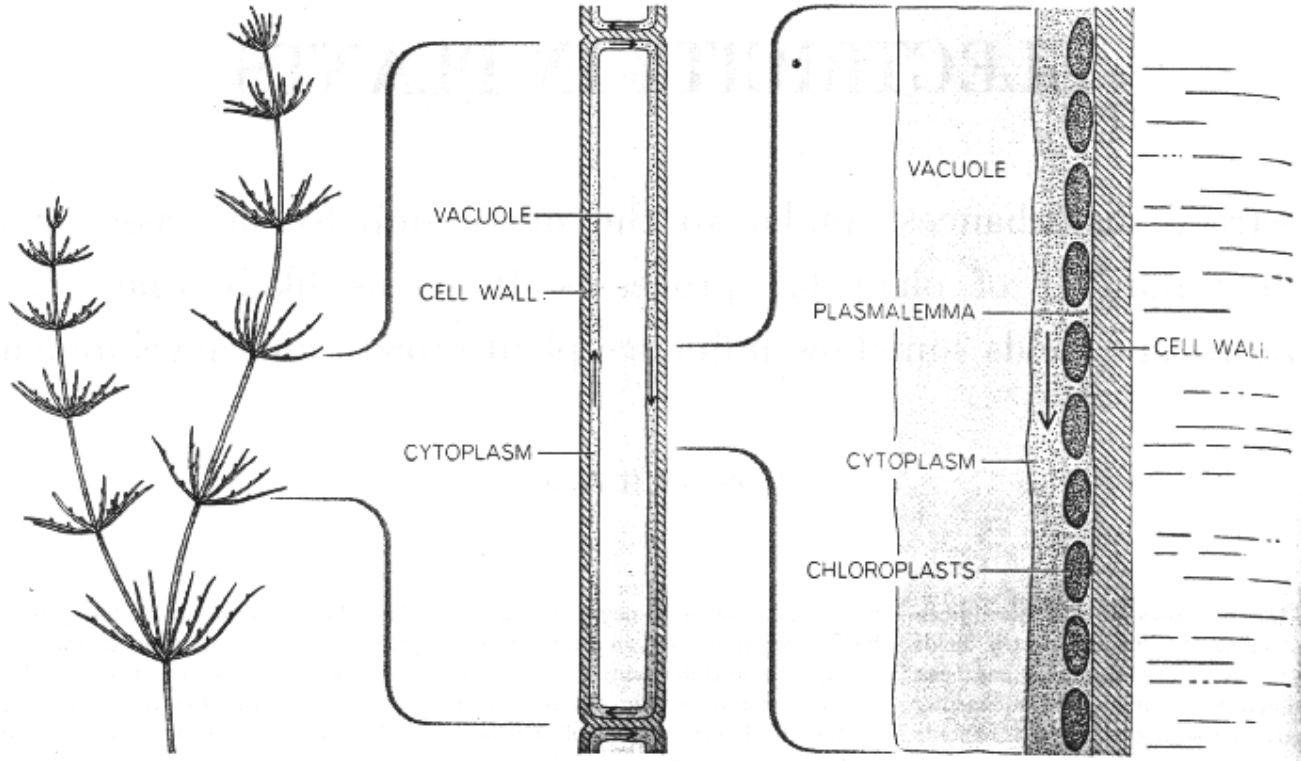
The delicately balanced distribution of inorganic salts in and around a living cell, whether plant or animal, accounts for its electrical properties. Living tissues are largely liquid; they consist of watery solutions of salts separated into compartments by membranes. In solution the salt molecules dissociate into electrically charged ions, some of which can pass more freely through the membranes than others. Where there are concentration differences across a membrane, positive and negative charges become separated and an electric field is set up. These differences in concentration are maintained by pumps, driven by the metabolism of the cell, that push ions through the membrane in one direction or the other [see "Pumps in the Living Cell," by Arthur K. Solomon; SCIENTIFIC AMERICAN, August]. In order to explain the potential difference in a given cell, therefore, one must take a complete inventory of the ions on each side of the membrane, determine how easily each ion can pass through the membrane and establish whether the ion is moving by diffusion or under an electric force across the membrane or is being pumped.

Such observations are at present out of the question on most individual plant cells. They are seldom more than a ten-thousandth of a cubic millimeter in volume. Fortunately, a few species offer cells that are much larger; these are the fresh-water algae *Nitella* and *Chara* and the marine alga *Halicystis*. Individual cells of *Chara* can be as much as 15 centimeters long and 1.5 millimeters in diameter. With respect to size, at least, these cells are freaks, and it may turn out that conclusions based on work with them are far from correct for the rest of the vegetable kingdom. Nevertheless, they have provided a starting point, much as the giant axon of the squid, a correspondingly outsized nerve fiber, facilitated early work on the electrochemistry of the nerve impulse [see "The Nerve Impulse and the Squid," by Richard D. Keynes; SCIENTIFIC AMERICAN, December, 1958].

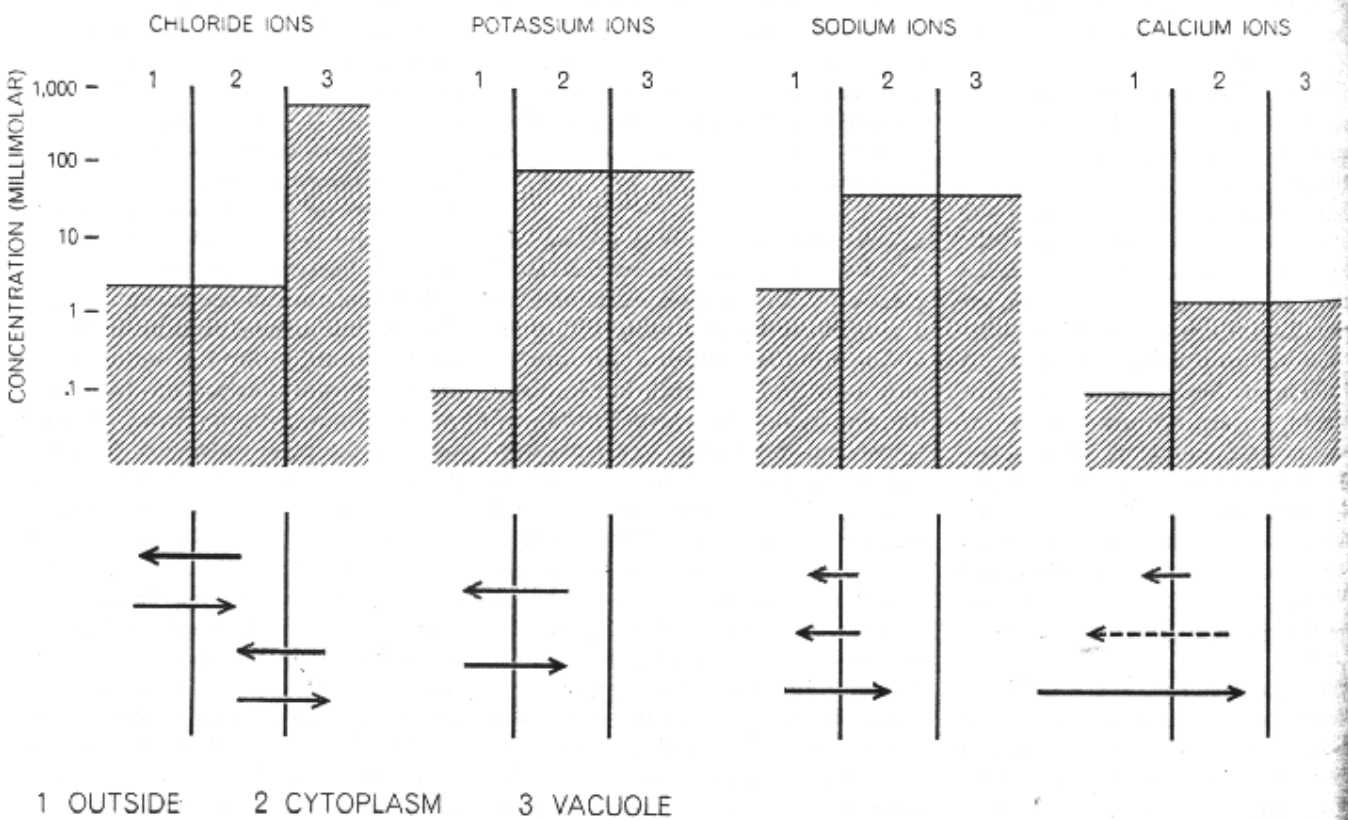
The *Chara* cell has a large central chamber, or vacuole, that contains salts (mainly potassium chloride and sodium chloride) in concentrations much higher than those that occur in the pond or river in which the plant grows. As a result a large osmotic pressure—which tends to equalize the concentration of salt by forcing water into the cell—puffs up the cell inside its tough cellulose wall. Lining the cell wall and separating it from the vacuole is a thin layer of living cytoplasm that streams continuously around the cell interior.

In seeking clues to the working of this cell, investigators have adopted various stratagems. They have extruded the vacuolar sap from the cell and compared its chemical content with that of the pond water. Thanks to ingenious techniques developed by Nobuo Kamiya of Osaka University, even the cytoplasm that envelops the vacuole can be extracted and analyzed, although the results are uncertain because there is so little cytoplasm and one cannot be sure that its ionic content remains unaltered during extraction. By the use of radioactive isotopes information has been gained about the movement of ions between the pond water and the cytoplasm and between the cytoplasm and the vacuolar sap. Finally, investigators have inserted glass micropipettes, filled with conducting salt solutions, into the cell and used them for measuring membrane potential differences and resistances. Essentially the same methods and tools were employed by the nerve physiologists in their work on the giant axon.

The present picture of the electrochemistry of the *Chara* cell is most notably the product of investigations by J. Dainty at the University of Edinburgh and by A. B. Hope and N. A. Walker of the Commonwealth Scientific and Industrial Research Organisation in Australia. It appears that the high salt concentration in the fluids of the cell is principally maintained by a chloride pump




CHARA CELL used in experiments on plant electricity is from *Chara australis*, a large fresh-water alga. The plant, illustrated at left, has a long stem composed of a succession of single giant cells, one of which is indicated by the bracket and is enlarged in the drawing at center. A small segment of the cell wall is in turn enlarged in the drawing at the right. The cytoplasm is the living tissue of the cell and chloroplasts are the organs of photosynthesis. Plasmalemma is the controlling membrane. Vacuole is filled with sap.



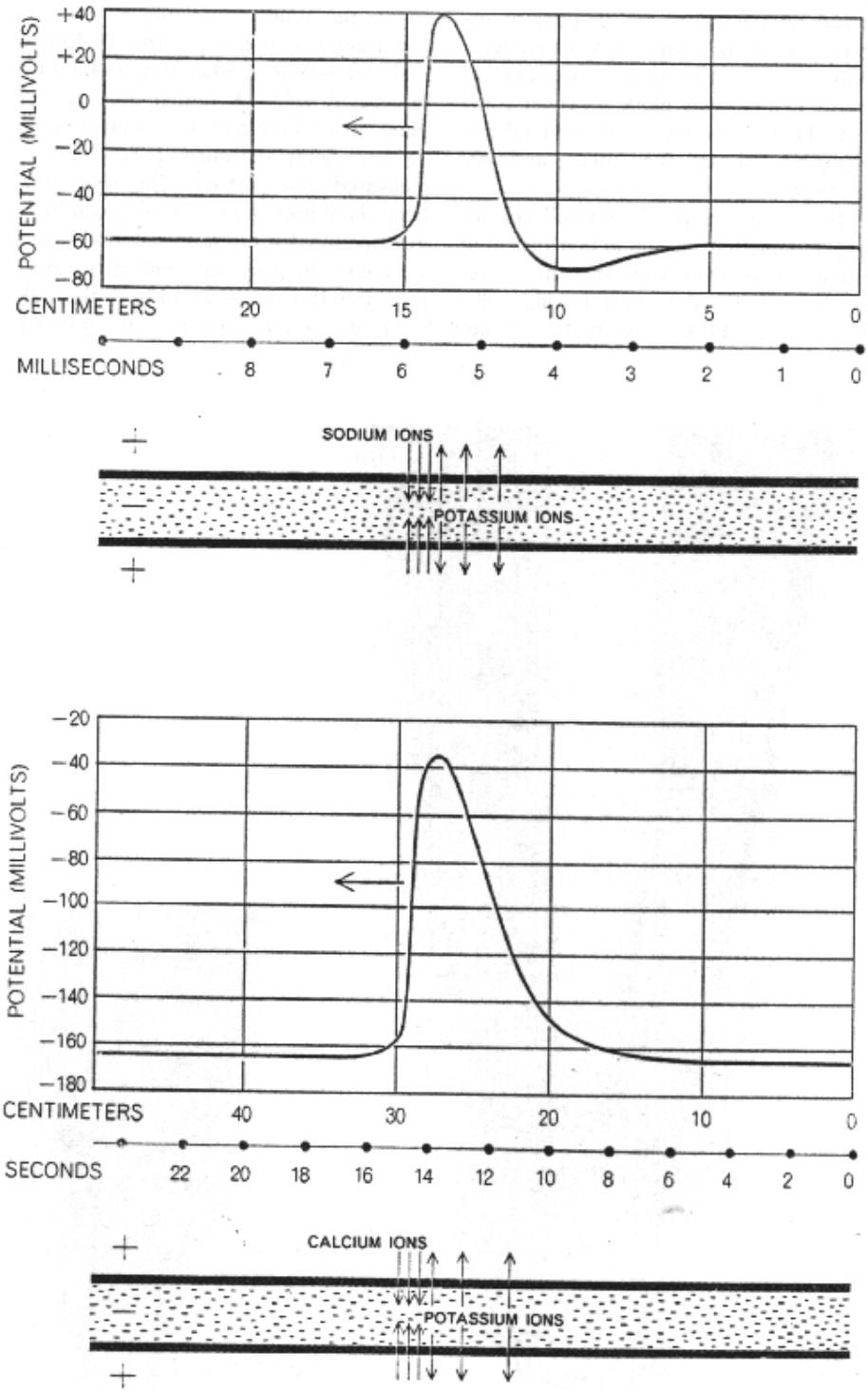

CONCENTRATIONS of four ions inside *Chara* cells and in the pond water are maintained by three processes. The bars show the concentrations of each ion outside the cell (*1*), in the cytoplasm (*2*) and in the vacuole (*3*). Cytoplasmic concentrations are not well established. The gray arrows represent movement of ions due to concentration differences. The potential difference across the plasmalemma causes positive ions to move in and negative ions to move out (*black arrows*). Except in the case of potassium, an active pump (*colored arrows*) is required to balance ion movements. The arrow for pumping is broken in the case of calcium, since these ions may never reach equilibrium across the membrane. The high chloride concentration makes inside of the cell negative.

that pushes the negative chloride ion into the vacuole from the external medium. This makes the inside of the cell negative. As a result the positive ions of potassium, sodium and calcium are pulled in passively. All of these ions tend to leak back into the external medium. The cell's books are balanced in the case of each ion only when the net gain due to the electric force and the active pump, if there is one, offsets the loss through leakage. A weak outward pumping of sodium and calcium thus seems to supplement the inward chloride pump in maintaining the interior negative charge. Because potassium can most easily pass in and out of the cell, it is this ion that has most control over the steady-state, or resting, potential. On the other hand, the resting membrane appears to be relatively impermeable to calcium. The main barrier to leakage of the ions from the cell is apparently the plasmalemma, on the outer surface of the cytoplasm inside the cellulose wall.

This understanding of how the cell behaves when it is undisturbed sets the stage for consideration of the remarkable way in which it reacts to stimulation. One can stimulate the cell by passing a pulse of electric current through it, by treating it chemically in various ways or simply by poking it gently with a fine probe. The effect is to make the inside of the cell momentarily less negative. If the stimulus exceeds a certain threshold, the membrane potential in the stimulated region does not recover immediately; instead it continues to rise rapidly toward zero and then returns more slowly to its resting value. Examination of the ion flow at this moment shows that the membrane in the stimulated region has become permeable to calcium; it is the inward rush of this positive ion that depolarizes the membrane. The local flow of electric current raises the potential above the threshold in a neighboring region of membrane, triggering the same electrochemical changes there. The disturbance thereby travels over the surface of the cell as a wave.

This is almost exactly what happens when a nerve cell is stimulated, and the wave that sweeps over the plant cell fully merits description as an action potential wave, in the same class of phenomena as the nerve impulse. The shapes of the waves are similar, and both waves are initiated by a stimulus that must reach, in each case, a threshold value [*see illustration at right*]. Of course there are differences also. The plant cell is relatively sluggish. A complete action "spike" for *Chara* takes about 20 seconds, compared with a few milliseconds for a nerve, and it moves only a few centimeters per second along the cell (even more slowly when the cell is bathed in a weakly conducting solution) instead of many meters per second. In the nerve cell it is a sudden inward movement of sodium, rather than calcium, that depolarizes the membrane. An outward movement of potassium ions subsequently restores the membrane potential to its resting value in the nerve and probably does so in the plant cell as well.

The most remarkable aspect of this comparison is not that there are differ-

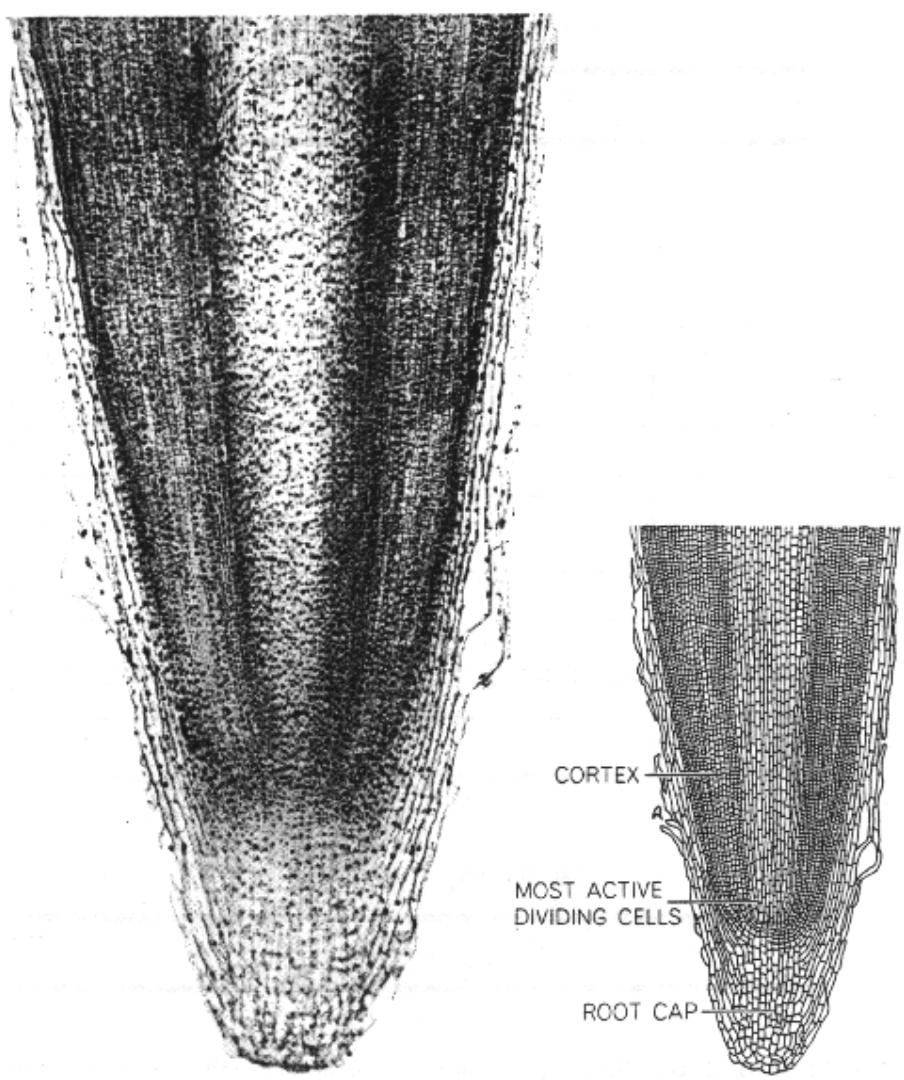



**EFFECTS OF STIMULATION** on squid axon (*top*) and the *Chara* cell (*bottom*) are compared. In both cases stimulation makes the inside of the cell less negative. At a threshold the membrane potential spikes into an action potential wave (*colored curves*) that moves along the cell. The spike is triggered by a change in membrane permeability: sodium ions flow into the nerve cell, calcium ions into the *Chara* cell. Potassium then flows out to restore the resting potential. Note the marked difference in wave velocity in the two cells.

ences but that two cells so far removed from each other on the biological scale should have active membrane properties with so many features in common. One wonders if the action potential wave may not be a characteristic of all cells that has merely been adapted in the nerve cell to the function of communication. If the relative slowness of the process in *Chara* is a feature of plant cells, this could be related to the general quiescence of plants compared with animals. Anyone who has seen a speeded-up movie of a growing plant, however, must have been impressed by the animal-like character of its movement and responses.

In the case of the *Chara* cell no biological function for the action potential wave has yet been established. It is rarely seen to stimulate neighboring cells, but this may be because these cells are in contact only at their ends. In another plant, with cells in more intimate contact, a stimulus from the environment might be transmitted from cell to cell. It is interesting to note that the passage of the wave is closely linked to the streaming of the cytoplasm in the cell. Streaming in a stimulated cell does not cease everywhere at the instant of stimulation but stops progressively along the cell as the action wave moves along it.

Although it is not possible to follow in detail the electrical activity in the tiny individual cells of higher plants, the plant as a whole and its various organs produce fields and currents that can be measured and plotted. The root of a bean shoot growing in a weakly conducting medium, for example, is found to act as an electric generator sending tiny currents into the medium and back through the root [*see top illustration on opposite page*]. This is probably because the growing plant is actively absorbing ions through its roots. The flow of ions into the root and their movement to other locations in the plant produce a macroscopic electric field that can be mapped by exploration with a voltage-measuring probe connected to a sensitive electrometer. The instrumentation must be highly sensitive, because only about a hundredth of a microampere flows across a square millimeter of root surface. The electric output of 100 billion roots would be needed to light a 100-watt lamp.

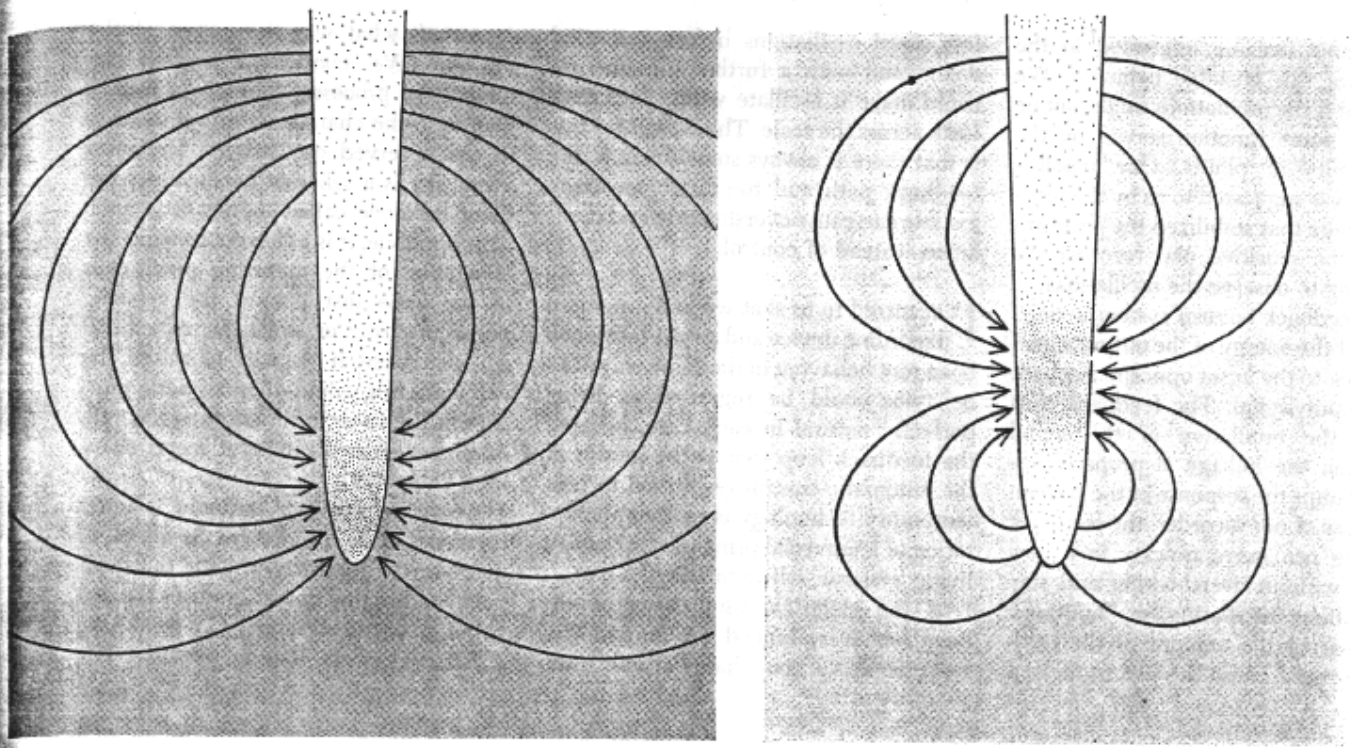



**BEAN-ROOT TIP is enlarged about 50 times in the photomicrograph at left. It is composed of a great number of individual cells in various stages of growth, division and development. The root cap protects the tip; cell division is concentrated above the cap; cellular elongation occurs primarily higher in the root, above the three-millimeter section depicted.**

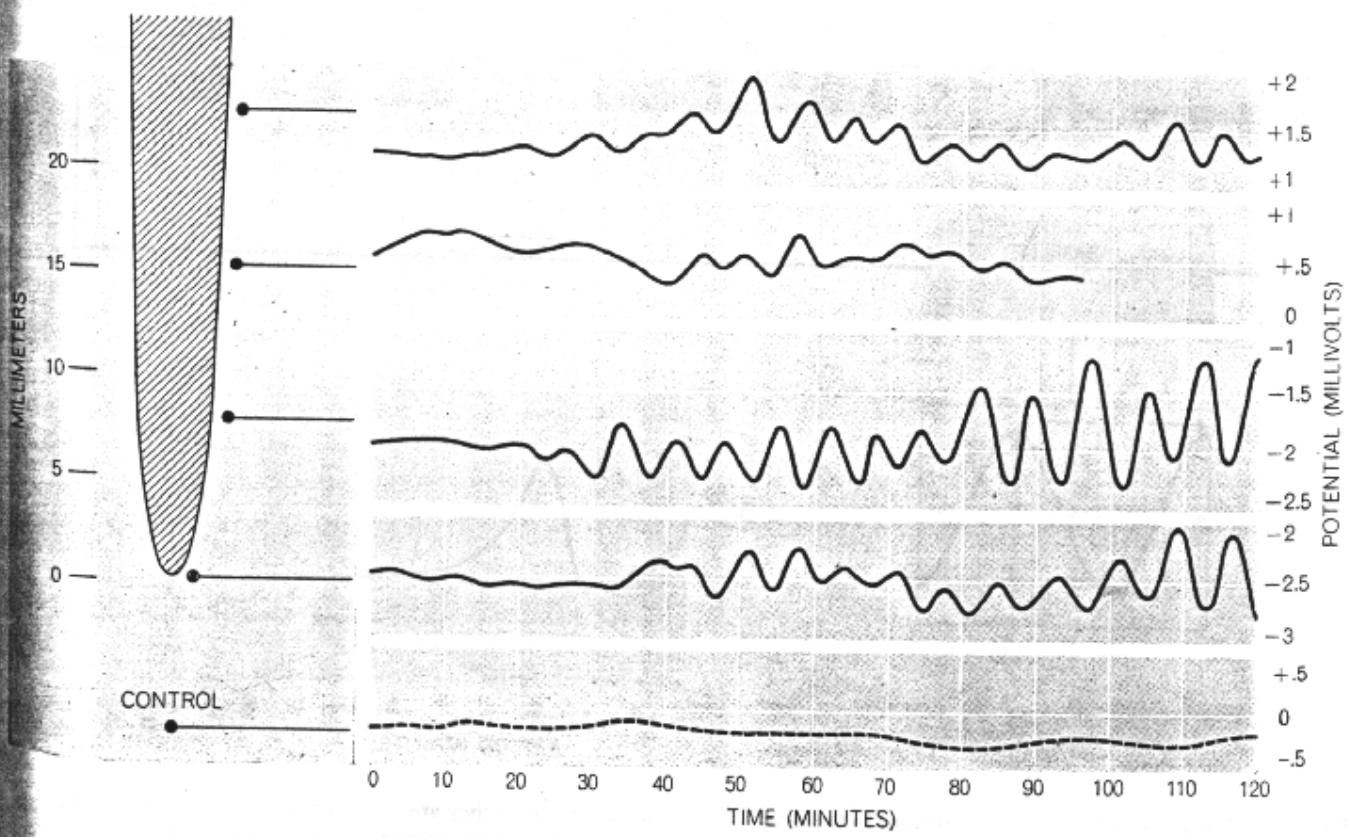
Observation of the flow of current tells some interesting things about what is going on in the plant. In a medium containing potassium, for instance, a root sends out a current from its upper part and back into itself near the tip. Because the cells at the tip are actively dividing and the creation of new cytoplasm sets up a high demand for potassium, one may deduce that the inflow of positively charged potassium ions is associated with the inflow of current at the tip. On the other hand, if the growth medium is rich in sodium, the root sends a current outward from both the tip and the base of the root and inward most strongly where the cells have almost reached their maximum length. This suggests that these cells are now filling their vacuoles with the sodium, contributing to the build-up of osmotic pressure that gives the root its turgor. Analysis of the ion content of successive small cross sections of root tissue from the tip upward confirms these deductions. Further confirmation is supplied by experiments with radioactive sodium and potassium that show that their paths of entry into the root follow the paths indicated by our bioelectric observations.

That the multicellular root tissue responds like the single cell of *Chara* to stimulation can be demonstrated by simply giving the root a gentle poke. The potential at any point near the root changes suddenly and usually makes one or two oscillations before settling down to a steady state. A few roots behave in a more mysterious way. Without any stimulation the potential near the root starts to oscillate in a rhythmic fashion, the oscillations continuing for perhaps several hours before the root reverts to its normal steady electric behavior. The periods of oscillation for the roots we have studied are about five minutes. Evidently in these cases there is an alternating-current generator in the root as well as a direct-current source.

My colleagues and I at the University



ELECTRIC CURRENTS are found around bean roots growing in salt solutions and are related to the concentration of specific ions in the roots. The root at left is growing in a solution of potassium chloride, the one at right in a sodium chloride solution. Concentrations of potassium (*gray*) and sodium (*color*) are indicated by density of shading. Apparently each of the two positive ions is concentrated where it is most needed: potassium in the region of actively dividing cells and sodium in a region of maturing cells.




SPONTANEOUS OSCILLATIONS in electric currents of the kind mapped in the illustration at the top of the page are sometimes recorded near a bean root growing in water. The potentials recorded by probes at various points near the root suddenly start to oscillate, with periods of about five minutes, as shown in the four solid-line graphs. The oscillations are strongest near the root tip.

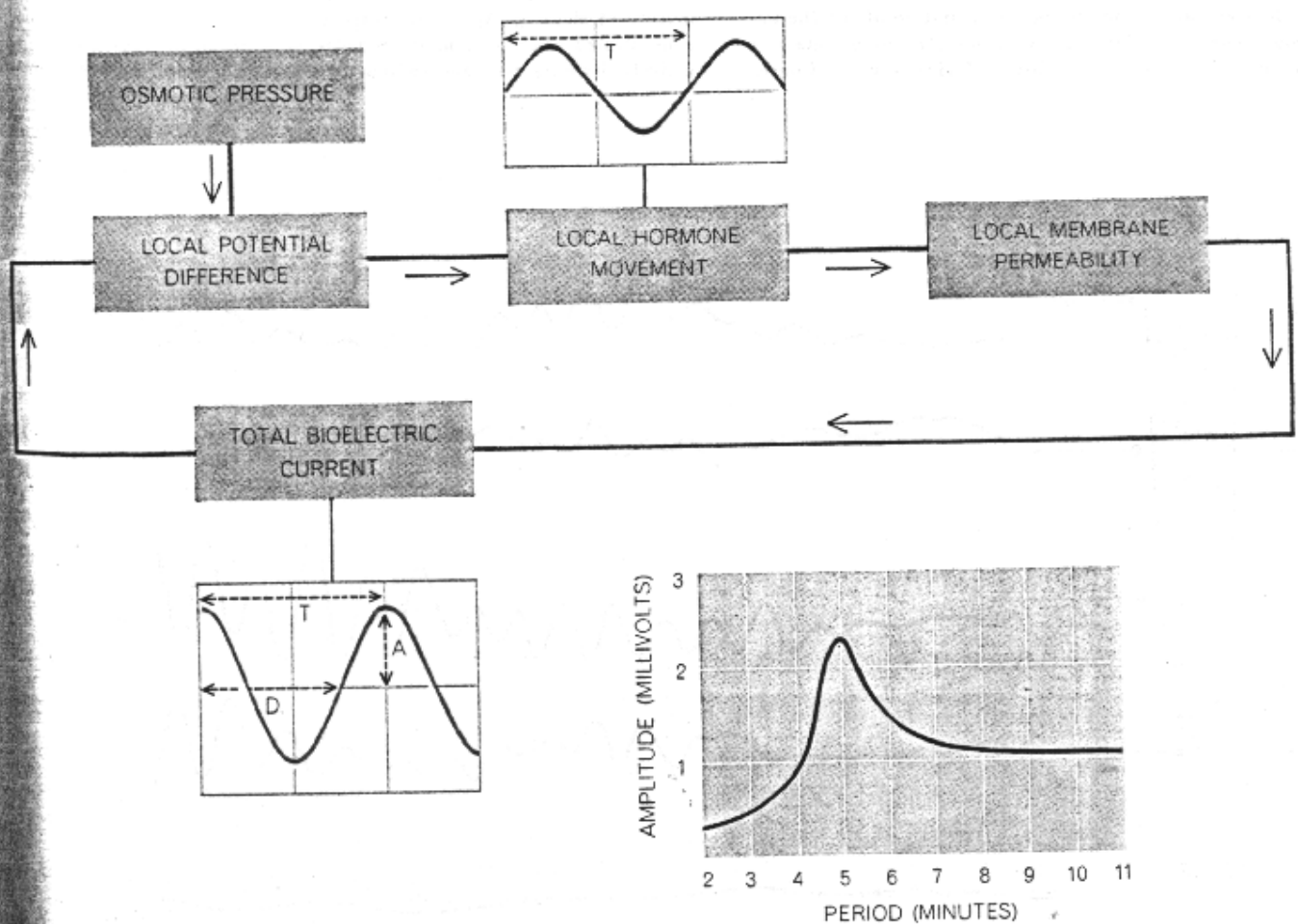
of Tasmania became interested in the reasons for this unstable behavior. We wondered if the oscillations might not be a clue to some function served by the bioelectricity of plants. One possible function was suggested to us by the feedback linkage that stabilized the performance of the sensitive pen recorder we were using to observe the oscillations.

In a feedback control system a small portion of the energy of the output signal is fed back to the input opposite in phase to the input signal. The feedback thus opposes the oscillation of the signal and, when the linkage is properly adjusted, damps the response of the system. In the case of our recorder, the feedback made the pen move quickly to a new position without overshooting and stay there without oscillating, or "hunting." By increasing the amount of the feedback we could cause the pen to make a few rapid oscillations before it settled down, and with a further increase we could make it oscillate wildly back and forth across the scale. The reason for this is that there is always some delay in the feedback path and too much feedback too late can cause overshooting and oscillation instead of control.

It occurred to us that we had a modern recording device and an old-fashioned bean root behaving in the same way. The behavior could be regarded as being perfectly natural in each case, because the feedback loop that is the genius of the automatic-control revolution in contemporary technology is really an adaptation of a universal principle that makes living systems self-regulating.

If the electrical oscillations of the bean root were indeed a symptom that some feedback loop had become overcorrected, what was the nature of the linkage? We considered various sequences of processes that might form a loop with the characteristics required to fit the observed oscillations. The most promising is a scheme that involves the plant hormone called indoleacetic acid. This hormone, it is believed, controls the elongation of the maturing plant cells in the zone just behind the growing point of a root or shoot. In very small concentrations it appears to soften the cell wall; this would allow osmotic pressure in the vacuole to lengthen the cell. At higher concentrations it seems to inhibit elongation.

According to our scheme electric forces set up in the root by the action of indoleacetic acid may provide the feedback linkage that in turn controls the distribution of the hormone. As a weak acid it forms negative ions in solution. The




**FEEDBACK LOOP is proposed to explain oscillations in the bean root's field. Rhythmic variation of the indoleacetic acid (IAA) content of the medium induces oscillations of the same period ($T$) in the bioelectric current near the root. But these oscillations lag behind the input oscillations. As the input period is varied, the time delay ($D$) of these oscillations in the bioelectric current, the amount by which they are out of phase with the input oscillations, is found to vary in a manner consistent with a feedback loop. Moreover, resonance, or maximum amplitude ($A$), occurs for periods of about five minutes, indicating that the natural oscillation observed in bean-root currents is caused by feedback. Varying the osmotic pressure instead of the IAA content gives similar results.**

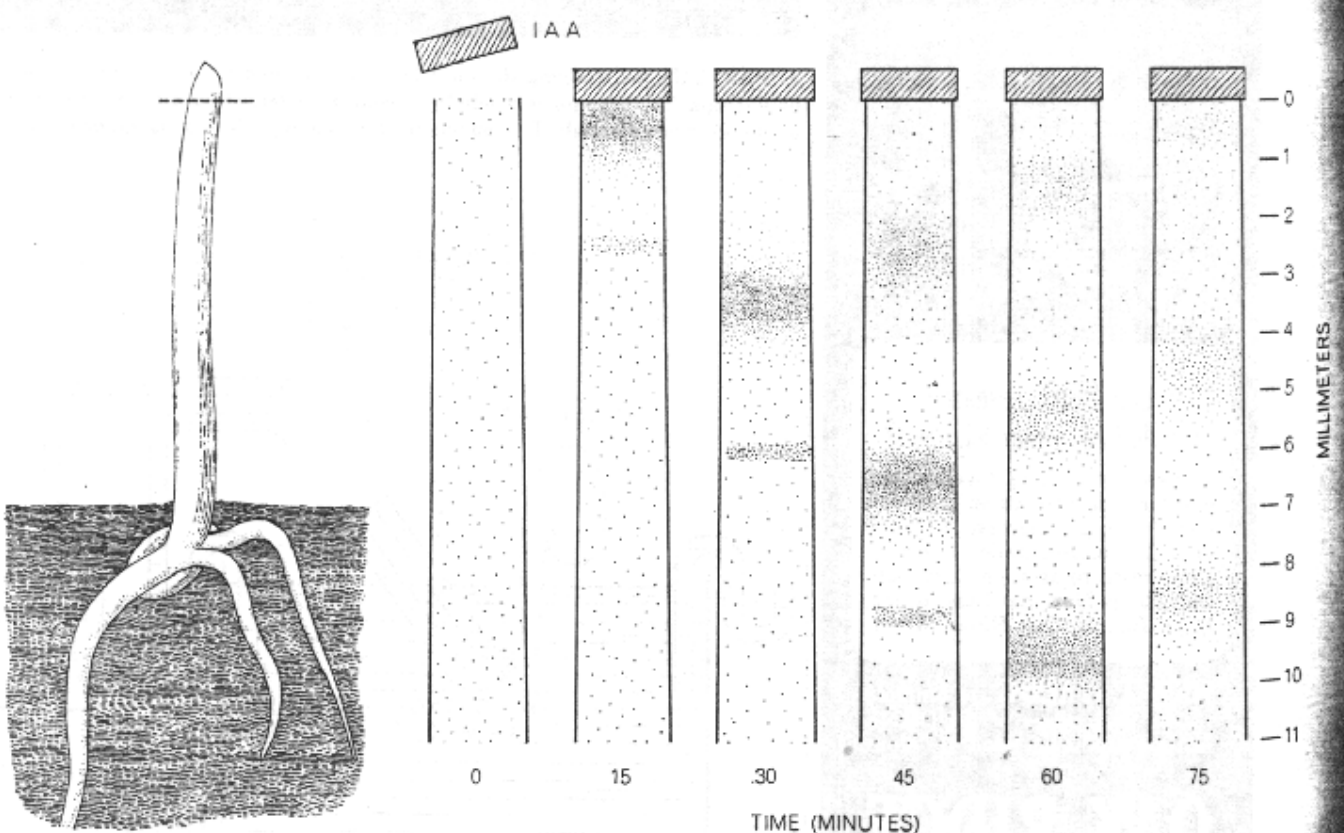
amount of indoleacetic acid reaching sites in the cell where it is active is therefore likely to depend on local electric forces, particularly voltage changes across cellular membranes. Since it appears to modify the permeability of the membrane to various inorganic ions, the movement of indoleacetic acid in the plant tissue may affect the pattern of current flow around the root. These current changes would in turn influence local potential differences in the root tissue through which the negative ions of indoleacetic acid pass. In this way the bioelectric current observed in the vicinity of the root may serve to close the feedback loop between events in the individual cell and processes in the root as a whole.

It is one thing to suggest such a cycle of feedback interactions and quite another to test it in a living plant in which the individual reactions cannot be isolated. In one test we have used we subjected a root that was not itself producing oscillations to deliberately timed oscillation in the concentration of indoleacetic acid in the fluid medium bathing the root. The root responded by producing electric oscillations all of the same period. We found that we could elicit maximum oscillation from the root at a period of about five minutes. This resonance identified the natural period of the loop, because it marked the time required for the imposed disturbance to travel around the loop and return, just one cycle later, to reinforce the next oscillation. The hormone oscillation and the resulting electric oscillation are out of step with each other. This is another expected characteristic of a feedback loop, in which there are always time lags. It gives further clues to the way the components may be linked up in the loop.

We have subjected the root to a similar "frequency response" test by varying the salt content and thereby the osmotic pressure of the culture medium. This variable does not directly form part of the proposed feedback loop, although variation in osmotic pressure intimately affects the system. It quickly alters the membrane potential in the root's outer cells, probably by rapid water movement and change in the salt concentration in these cells. Resonance again occurs at periods of about five minutes. This, we expect, is close to the period of any spontaneous oscillatory behavior of the root.

We are confident that there is a feedback system in the root in which the interactions appear to be as described. It may even be that the over-all growth of the root is co-ordinated by the indicated interaction of hormone and electric field. We have not, however, been able to observe any departure from normal growth in roots that have been subjected to sustained overcorrection and oscillation of the postulated feedback system.

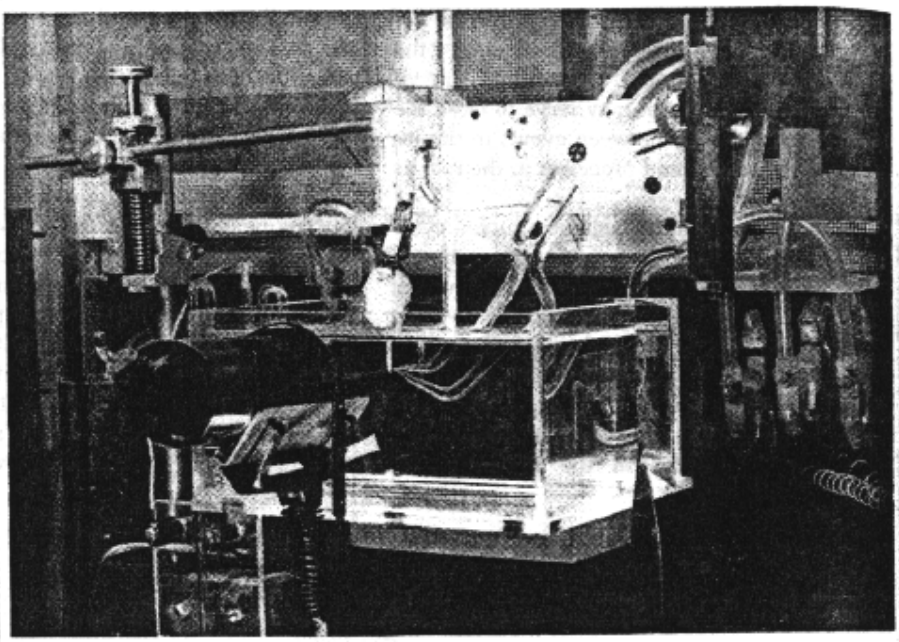
The demonstration in a lower organism of a feedback system with characteristic periods of oscillation is of interest in still another connection. This is the time sense, or "biological clock," of such organisms. It is now well known that all living systems from higher animals down to single-celled organisms behave in ways that vary rhythmically



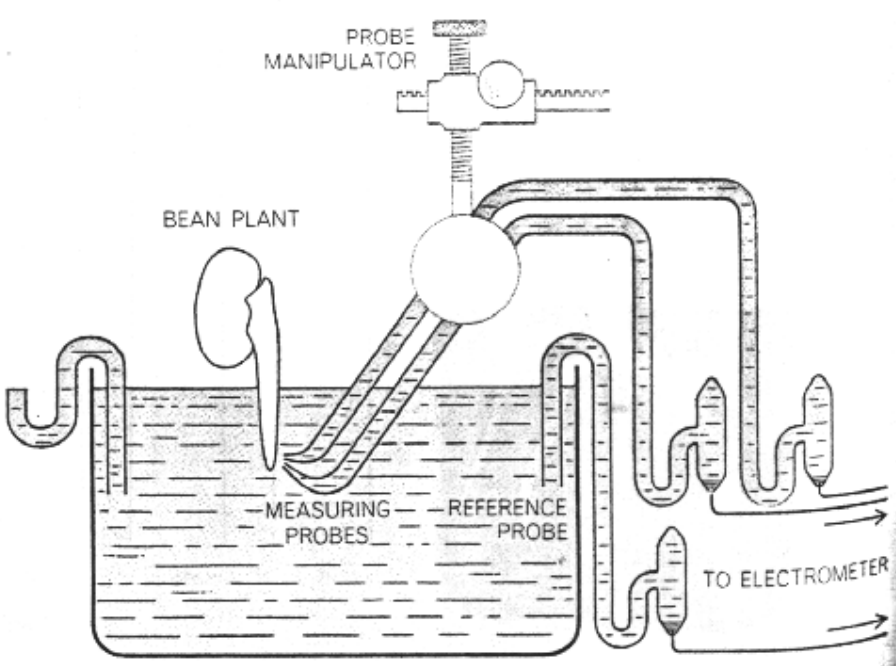

**IAA manufactured by the tip of the coleoptile that sheathes a young oat shoot moves down the coleoptile to its growing region. When a block of agar containing IAA is placed on a decapitated coleoptile, the IAA's progress down the shoot is accompanied by an electric wave. The density of the gray shading indicates the strength of the downward potential gradient that is recorded. A small upward gradient (*color*) precedes the initial downward pulse. The downward gradient may influence IAA movement**

even when there is no apparent periodic change in their environment. A built-in electrochemical oscillator governed by a feedback loop nicely fits the specifications for a biological clock.

No less than the roots, the above-ground portions of the plant generate electric fields that may have significance in growth processes. As long ago as 1932, Frits W. Went, now director of the Missouri Botanical Garden, suggested that indoleacetic acid moves down in the coleoptile of the grasslike plants under the influence of electric forces. The coleoptile is a hollow sheath that grows upward in the seedlings of these plants and serves as protection for the developing shoot; it is a favorite subject for study of the effects of light, gravity and various hormones on the plant bending. Like the root tip, the tip of the coleoptile manufactures indoleacetic acid,



**APPARATUS** for studying the electric field generated by a bean root is shown in this photograph. The bean plant is held by a clamp at center. The glass tubes are probes to measure bioelectric potentials. The lens at left foreground projects a magnified image of the root.




**POTENTIALS** are measured as shown in this diagram of the apparatus in the photograph at the top. Two glass probes explore the vicinity of the root and another probe is used as a reference. Probes are connected to an electrometer through mercury-calomel cells.

which moves down the coleoptile to the growing region, where it controls the rate at which the cells elongate. Winslow R. Briggs and his co-workers at Stanford University showed in 1957 that light shining on one side of the tip of a corn coleoptile makes some of the indoleacetic acid that would have traveled down the lighted side move down the darkened side instead. The extra amount of hormone on the darkened side makes the cells there elongate more than those on the lighted side, and the coleoptile bends toward the light.

Recently, in partial confirmation of Went's prediction, A. R. Schrank at the University of Texas has found lateral differences in potential around a coleoptile corresponding to the distribution of indoleacetic acid when the coleoptile is illuminated from one side. C. H. Hertz at the University of Lund in Sweden has found a similar distribution of potential in coleoptiles placed horizontally and in process of bending upward against the force of gravity.

We have addressed our experimental effort in this connection to the question of how the indoleacetic acid moves down the coleoptile as fast as it does. It moves at the relatively high speed of 15 millimeters per hour through tissue that does not appear to contain any long, pipelike cells that might carry it downward in a flowing solution. Our observations show that a change in indoleacetic acid concentration in the coleoptile is accompanied by a change in electric field along the coleoptile surface. As the hormone moves down the plant, the electric change moves with it as an electric wave.

We can initiate these waves either by lighting the coleoptile from one side or by cutting off the tip and placing some of the hormone on the cut end. The association of the hormone and the electric field suggests a possible explanation for the rapid movement of the hormone. Through a feedback interaction, such as that postulated for the root, the advancing front of indoleacetic acid sets up an electric field that in turn may push the hormone farther down the coleoptile.

Observation and speculation so far have not answered the question of whether or not the electric fields set up by a growing plant influence its development. There are encouraging indications that they do play such a role. The discovery of more conclusive evidence awaits further refinement in techniques for the detection and perhaps the manipulation of these fields.