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Geotropism and Geoelectric Effect.

Summary

A short summary is given of the two classical theories of geotropism of plants, the statholith theory and the geoelectric theory.

A new mechanism for developing potentials from gravity is given , which could explain the potentials in plants. The reason is thought to be an ion-exchange process.

A new method for measuring the geoelectric potentials in plants without touching them is described.

Some results of the measurements on plants are given.

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Geotropism and Geoelectric Effect

In the following report work will be described which has been carried out in the Department of Physics, Lund, to examine the two phenomena known as geotropism and geoelectric effect.

Geotropism is a common name for the movements which various parts of a plant make as a result of the action of gravity. We can talk about at least two kinds of geotropism, positive and negative - positive for parts of plants which grow in the direction of gravity (e.g., roots) and negative for parts which grow in the opposite direction (e.g., stem parts).

There are two classical theories for explaining the gravity perception of plants. The oldest one is the so-called statholith theory, according to which the perception of gravity is due to sedimentation of small particles (starch grains). By falling on the lower side of the cells , the growth of those parts should be accelerated or inhibited depending on whether it is a root or a stem part , and by an unequal growth effect (compare a bi-metal thermometer) the green parts of the plant bend upwards and the root bends downwards.

The newer and more detailed theory explains the phenomenon of geotropism in the following way:

When, for example , a stem part of a plant (e.g., a maize coleoptile) is displaced from its normal vertical position into a horizontal position it can be shown that an electrical potential in the order of magnitude of 50 millivolts is developed. This potential is known under the name of geoelectric effect and was first examined by Brauner in the Nineteen Twenties (1). Various growth-controlling substances , auxins , which are produced in the tips of the plants and transported backwards , are electrophoretically unsymmetrically distributed in the plants . Because of the unsymmetrical distribution of auxin the rate of growth is no longer equal in upper and lower sides of the plant part , and as before the bending is an unequal-growth effect. The fact that root and stem parts bend in various directions is explained in the following way. In the roots the auxin concentration is more than optimal and in stem parts less than optimal. If the underside of a root receives more auxin its growth is inhibited , but if the underside of a stem part receives more auxin its growth is accelerated. The result is that the root bends downwards and the stem upwards.

This was the starting point for the work which has been done in Lund. The first problem to be investigated was the mechanism for developing an electrical potential from gravity . The old theory (2) , which supposed that the potentials resulted from the various influence of gravity on the mobilities of cations and anions in the membranes of the cell walls , was not satisfactory. It could soon be shown that the experiments which had been made on model systems were not free from objections.

To find another theory for the geoelectric potentials in plants, we have among other things examined what happens when rather insoluble substances, e.g., $CaCO_3$, are deposited on an ion-exchange membrane(3, 4). We found a potential across the membrane with the right polarity for a cation-exchange membrane and with a realistic order of magnitude . The process has been investigated in detail in Lund.By using various combinations of membranes ,salts and ions in the membrane, it could be shown that the mechanism is the following.

When the salt, e.g., $CaCO_3$ is deposited on the ion-exchange membrane containing K^+-ions an ion-exchange process starts. The result of this is that Ca^{++}-ions go into the membrane replacing the K^+-ions there. By this process there is formed a rather concentrated solution K_2CO_3 over the membrane. Thus we have a concentration difference across the membrane and as a result thereof the voltage across the membrane is the difference between the two Donnan-potentials at the boundaries electrolyte-membrane. As is expected from the proposed mechanism potentials with the opposite sign are obtained if an anion-exchange membrane is used instead of the cation-exchanger. The reason is that the Donnan-potentials have opposite signs.

Various salts with different solubility e.g., $BaCO_3$ and $BaSO_4$ have been used. The results agree with what can be expected, that is, more readily soluble "statholith"-salts give greater potentials. If a rather insoluble salt e.g., AgCl is formed as a result of the process, smaller potentials are obtained.

Making use of the OH^--ions which are formed from the K_2CO_3 the process could be made visible by adding a pH-indicator of suitable range to the electrolyte.

Theoretically the process has been investigated by solving the diffusion equation with the proper boundary values. The theoretical time-variation of the electrical potential agreed very well with the experimental curves. The investigation of the process will be described in detail elsewhere (4).

The next step in our investigation was to look at the measurement of geoelectric potentials in plants (6). The classical method for measuring plant potentials by applying fluid electrodes to the plants was shown to be unsatisfactory because of the risk of disturbances at the measuring points and the risk of shortcircuiting along the plant surface . An ideal method for measuring would be one where the plant is not touched by the electrode . This was achieved in the following way by making use of the vibrating reed principle (5). Five coleoptiles in parallel , extending from a container filled with gelatine and a calomel electrode for electrical contact , form one of the condenser plates . The other is a small plane gold electrode , vibrated at a frequency of about 250 c/s. If a potential exists between the plants and the vibrated electrode, an AC-signal is generated at the latter. The AC-signal is fed to a cathode-follower stage (electrometer tube in order to be able to use sufficiently high grid resistance), and after further frequency-selective amplification (to minimize noise) made visible on a cathode ray oscilloscope. By changing the DC- potential of the plants by an external variable voltage , this AC-signal can be reduced to zero. If the plant potential changes during the experiment the external potential has to be adjusted . This adjustment, which can be measured by a usual instrument, is equal to the plant potential change . The compensation can be made automatically , using a phase-detector . The potentials are then recorded on a recording instrument.

At present a modification of the described method is being developed . In order to get rid of longitudinal potential changes in the coleoptiles, experiments are made with a 120 degree sector of a cylinder condenser , which rotates around the coleoptile tip. By coupling through a condenser , formed by the unsectored end of the cylinder and an outer cylinder an AC-signal is fed to the grid of an electrometer tube and further to an amplifier as before.

Concerning the results of our measurements on plants we can say briefly that we have found three new things . The first one is that the potentials developed when a plant is geotropically stimulated are about four times greater than those values reported before. This might be explained to be a result of the very high input impedance (because our measuring device does not touch the plant) which we have compared to earlier workers.

Secondly we have found a time-delay of about 15 minutes from geotropic stimulation to the rise of the potential. Probably this effect has been masked earlier by electrochemical changes of the potentials at the contact points. The reason of the time-delay still awaits an explanation.

Thirdly we found that geoelectric potentials disappear reversibly when the plant is placed in a nitrogen atmosphere. Also we found some effect with substances which inhibit respiration, e.g., DNP, NaN_3 and KCN. This fact led us to believe that the particles which are deposited and give rise to the potential are the mitochondria, which are responsible for the plant respiration. This theory is supported by the fact shown by Ziegler (7) that mitochondria are falling through the cytoplasm of the cells and accumulated on the lower side. However, this new theory that mitochondria are responsible for the geoelectric potentials still has to be tested.

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