

ON GRAVI-SENSITIVITY IN PLANTS

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SUMMARY

Comments are made on the following controversial points of the theory of geotropism: 1). the efficiency of the gravi-perception apparatus, 2). the candidature of starch for the statolith function, 3). the existence of a gravi-perception sense organ.

THE EFFICIENCY OF THE GRAVI-PERCEPTION APPARATUS

The corrective movements carried out by plants when put in an abnormal position prove that the direction of the gravitational force is "perceived" accurately. According to the starch-statolith theory this is done by special cells called statocysts which contain amyloplasts with large starch grains, the statoliths. When these heavy mobile particles press long enough on the outer tangential wall of the cells, a stimulation would be received. The stimulation of these specialized cells would change the polarity of the whole organ, becoming manifest from a deviation of the auxin transport, and eventually from the geotropic curvature.

In the past the statolith function of starch has been tested repeatedly and in different ways. One way of investigation was to study the effect of removing the starch artificially by starving or chilling the plants or by treating them with chemicals, but this approach of the problem has yielded differing results. The observation of ZOLLIKOFER (1918) with seedlings (see later), that the loss of starch was accompanied by the disappearance of the geotropic sensitivity while the growth and the phototropic sensitivity were scarcely being inhibited, has been cited by WILKINS (1966) as sound support of the statolith function.

PICKARD & THIMANN (1966), on the other hand, go even so far in their recent publication on the geotropic reaction of de-starched coleoptiles as to doubt whether particle sedimentation plays a role at all in geotropism. Since the latter idea goes down to the roots of the theory of geotropism, a few comments may be added to those Wilkins already made on this important investigation.

THIMANN & PICKARD (1965) and PICKARD & THIMANN (1965, 1966) freed wheat coleoptiles from starch by incubating them at 30°C with gibberellin plus kinetin. The geotropic responsiveness was retained but the treatment considerably increased the lag period between the transfer to the horizontal position and the beginning of the curvature (the so-called reaction time). When the curvature was finally set going the curving speed was reduced to about $\frac{2}{3}$ that of the control coleoptiles. However, the ratio of the speed of curvature to the speed of growth was the same in treated and untreated plants. In view of this constant relation the authors set forth the hypothesis "that not only amyloplast

starch is not essential to the geotropic process, but moreover that it does not even enhance the response when present”.

This wording suggests that the authors suppose that the capacity of the perception apparatus can be derived from the speed of the curvature. The fact, however, that the values of the above-mentioned ratio are the same is an indication that in both treated and untreated plants the rate of curving was controlled by the rate of growth and not by the degree of induction. In this situation the rate of curving cannot give information about the efficiency of the perception apparatus.

Wilkins comments on this result that “the slower response of the de-starched coleoptiles might be attributable to the normal role of starch grains as statolith particles being taken over by another particle which sediments at a much slower rate”. From the above-said it follows that this observation of Wilkins can only be brought to bear on the length of the reaction time. The increased reaction time of the starchless coleoptiles indicates indeed that the threshold value of stimulation is passed a few hours later than in the untreated coleoptiles, which points to an imperfect perception. But not even this longer reaction time does prove that the efficiency of the *physical* phase of the perception process (sedimentation and pressure) was reduced by the removal of starch. Extensive studies made by RUTGERS (1912) on the influence of temperature on the presentation time in coleoptiles showed namely that the *cell metabolism* is certainly involved in the perception of gravity. This was confirmed by BRAUNER & HAGER (1958) who report high Q_{10} -values for the induction of the geotropic reaction in *Helianthus* seedlings. Consequently the slow geo-induction observed by Thimann and Pickard may have been caused by a retardation of the metabolic phase of the induction, just as the low rate of curving may have been due to a decreased metabolic activity of the treated plants.

From the foregoing it follows that in the publications of the last-named authors no evidence is present to judge whether the loss of starch had any influence on the perception apparatus. The main point of their results is that in the absence of starch a degree of geo-induction can be attained sufficiently high to be no longer the speed-limiting factor of the geotropic bending.

Opposite results had been obtained before by Zollikofer, as was mentioned above. The seedlings of *Tagetes*, *Helianthus*, and other plants lost the power of geotropic response after the removal of the starch while the growth and the phototropic reaction were not made impossible by the treatment. Now the failing of the geotropic response is not to be identified with an inadequate perception. A small change of the internal auxin concentration may be sufficient to prohibit the geotropic curvature (ANKER 1956). The explanation of the remarkable result of Zollikofer then could be that the preceding period of darkness had so much changed the internal auxin concentration that the geotropic reaction was made impossible, whereas the exposure to unilateral light might have adjusted the auxin level enough to enable phototropism to occur (ZIMMERMANN 1927).

2. THE CANDIDATURE OF STARCH FOR THE STATOLITH FUNCTION

Although there exists almost general agreement on sedimentation being the primary mechanism of gravi-perception, there is a difference of opinion as to the question whether mobile starch is the only possible candidate for the function of statolith. In the previous section we have met with an example of geotropism without starch. In that case the starch was artificially removed. HABERLANDT (1900), one of the originators of the starch statolith theory, cites already examples of geotropism of organs in which starch is naturally absent.

The fact that mobile starch is always found in those parts of the organs where the highest sensitivity to gravity is localized is in support of the statolith function. But these places of highest sensitivity are at the same time the places of highest metabolic activity. The abundance of starch, therefore, can also be connected with the adjacency of the zones of meristematic activity and of cell elongation. At these places great amounts of carbohydrate are broken down in the respiration to provide energy and starting-products for the synthesis of nucleic acids, proteins, cell-wall material and of a great variety of other organic compounds. Moreover, sugars and organic acids are necessary to preserve the osmotic value of the vacuolar sap during the auxin-induced uptake of water in the process of cell elongation. The starch grains, therefore, represent a big source of osmotically inactive carbohydrate, close to the places where the consumption of it is excessive.

This interpretation does not preclude statolith function of starch. The notion that cell parts have more than one function is not new. The cell wall, for instance, individualizes parts of the protoplasm of the plant and at the same time gives mechanical support.

3. THE NECESSITY OF A GRAVI-PERCEPTION SENSE ORGAN

The significance of starch might, finally, be broached by investigating the connection between the presence of mobile starch in a cell and the capacity of the latter to transport auxin in the lateral direction. To this purpose the method, so successfully used by KONINGS (1967) to determine the transversal transport of radio-active IAA in the apical part of the *Pisum* root, might be applied with de-starched roots and coleoptiles. The theoretical background of a similar investigation may be formulated in the words of AUDUS (1962): "If statolith starch grains are the gravi-perceptors, then this implies either that auxin must travel primarily in the gravi-sensitive statenchyma or that some influence modifying transport must spread from that tissue to the other cells mediating auxin flow".

The latter possibility would mean that in stems where the statenchyma is represented by the starch sheath (endodermis), the bulk of the cells would depend on this single layer as for "transport instructions". This is not impossible since the principle of stimulus conduction is not limited to the animal kingdom. But it has been shown through decapitation experiments that the rate

of the geotropic curvature of a coleoptile is not decreased by the removal of the tip, provided auxin is given in the right concentration (ANKER 1954, 1956). This proves that the ability to transport auxin in the lateral direction was not impaired by the removal of the "apical statenchyma".

As to the longitudinal and lateral transport of auxin an important hypothesis has been published by HERTEL (1962), HERTEL & LEOPOLD (1963a, b), and HAGER (1967). Auxin molecules would move from cell to cell by secretory processes. The structures necessary for secretion (permeases in the plasmalemma?) would be accumulated near the basal part of the cell thus causing polar transport. Pressure would activate the secretion, possibly by changing the allosteric configuration of the hypothetical permeases (Hager). The authors explicitly do not identify pressure with mobile starch, so that their hypothesis is not limited to the explanation of the lateral auxin transport in the statenchyma. In support of this explanation Hager cites the investigation of SKOU (1959) who demonstrated that the activity of the surface-spread enzyme acetylcholinesterase is increased by small pressures of 2 to 10 dyn/cm². Since this is about the weight of the cytoplasm in a cell of 20 μ in diameter (AUDUS 1962), further investigations along these lines might become of great interest to the theory of geotropism.

After these comments and considerations it does not seem rash to put the question whether the basic principles of the statolith theory, to wit sedimentation and stimulation, must be preserved. But in search of other principles we must beware of over-simplification. A seemingly unsuccessful attempt to find a substitute for the principle of stimulation has been made by SIEVERS (1967). He reports that in the horizontal parts of the positively orthotropic rhizoid of *Chara foetida* the statoliths will gather along the lower wall. There they would block the normal transport of the Golgi vesicles so that the growth of the lower wall is inhibited while that of the upper wall would be stimulated by the accumulation of the Golgi apparatus in that place. Thus, in his paper called "Zum Wirkungsmechanismus der Statolithen in der pflanzliche Zelle", he proposes a very simple mechanism of the positive geotropic curvature (Die Function von Statolithen und Golgi-apparat lässt sich demnach als ein recht einfaches selbstregulierendes System darstellen).

Increased growth of a cell wall, however, requires in the first place a hormone-induced change of its plastic and elastic properties. Without these changes deposition of cell wall material by the Golgi vesicles would cause only a thickening of the wall.

Another objection to Sievers' hypothesis is that it leaves unexplained the function of the starch grains in the negative geotropic curvature of the stem and the coleoptile.

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