

## THE MECHANISM OF AUXIN ACTION<sup>1</sup>

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(WITH ONE FIGURE)

Plant growth hormones are known to produce a number of striking effects on various processes including cell enlargement, root initiation, bud inhibition, etc. It has also been shown that the auxins, and indole-3-acetic acid in particular, participate in some general protoplasmic processes. Support for this view has been most recently afforded in the demonstration by COMMONER and THIMANN (1) that this hormone is involved in part of the respiratory metabolism of plant cells.

The mechanism of the action of indole-3-acetic acid in the various growth processes which it influences is as yet unclear, however, even in the most favorable case of cell enlargement. Two theories concerning this auxin effect have been put forth. One suggests that the hormone lowers the resistance of the cell wall to turgor pressure, thereby permitting cell enlargement to take place. The other theory, suggested by CZAJA (2), holds that cell enlargement is the result of an increase in the intensity of an osmotic driving force. Although it has been the practice to consider these as two opposing theories it must be pointed out that both agree that the actual driving force in cell enlargement is osmotic in nature for it is clear that the turgor pressure is itself a consequence of osmotic forces.

No conclusive evidence in support of the wall-resistance theory has been presented thus far. The second theory has been objected to on the ground that growing plant cells do not show any increase in the osmotic pressure of their vacuole contents. The very failure of growing cells to exhibit a *reduction* in osmotic pressure while the vacuoles rapidly absorb water and increase in volume indicates, however, that the absolute solute content of the sap must be *increased* during this process.

Thus it becomes important to know whether indole-3-acetic acid influences the solute content of the cell sap and so by momentarily increasing the osmotic pressure, affects water uptake and cell enlargement. It would be expected that no observable increase in osmotic pressure would occur, since the uptake of water would counteract the increase in solute content. Increase in sap solute might result from the hydrolysis of stored material such as protein and starch or from the absorption of salts. Attention toward the latter alternative was drawn by the observation of THIMANN and SCHNEIDER

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(5), that the stimulation of the growth of *Avena* coleoptile sections by auxin is greatly enhanced by the presence of KCl in the medium.

The experiment reported here was designed to determine the effect of auxin on the salt absorption process in potato tuber slices, in order to learn whether the hormone may increase the sap solute content by stimulating this activity. Potato slices were prepared according to the method of STEWARD (3) and vigorously aerated for a period of eight days in solutions containing 0.001 M KCl and various concentrations of indole-3-acetic acid. Salt absorption was followed by determining the electrical conductivity of the solutions and wet weight was determined in a highly reproducible manner by weighing the tissues after blotting twice.

Since the slices were not previously rinsed they all went through the expected period of salt loss during the first 24 hours and then began to absorb salt actively. During this time all the slices absorbed water, since the external solution was hypotonic, but the relative amount absorbed in the different auxin concentrations followed a curve with an optimum at about 10 mg. per liter.

Figure 1 represents the data for the two-day period following the initial day of salt loss. The upper curve represents the amount of salt absorbed during this 48-hour period; the lower curve indicates the corresponding changes in wet weight during that time. It is obvious that these processes are affected by the concentration of auxin to which the slices are exposed. The parallelism between the two curves is clear and there is a definite maximum in both salt absorption and water uptake rates at a concentration of 10–20 mg. of auxin per liter. It should be noted that in the non-maximal auxin concentrations there is some salt absorbed while water is lost. The inverse relation holds for these concentrations only during this period of the time-course of the experiment, and when the changes during the total eight-day period are calculated there is a close correspondence between the positive absorption of both salt and water. An experiment similar to the one cited above but involving large numbers of *Avena* coleoptile sections gave the same results.

These data indicate that the salt absorption mechanism of these plant cells is affected by auxin in a manner which parallels the hormone's influence on cell enlargement, for the function relating auxin concentration to growth always follows a curve of the type shown in figure 1. Furthermore, the data indicate that the absorption of salt is at least in part the driving force for the uptake of water and the consequent cell enlargement. This conclusion is also supported by the observation that potato slices placed in hypertonic sucrose solutions (0.2 M) and treated with KCl and a maximal concentration of indole-3-acetic acid actually gain water while slices which are not supplied with auxin lose water and become limp. This evidence contradicts the

“wall-softening” theory of auxin action, for it shows that auxin can exert its effect even when the cells are flaccid and no turgor pressure exists. It is strongly indicated, therefore, that the effect of auxin on water uptake and cell enlargement is a direct consequence of its effect on the salt absorption process.

These conclusions necessitate a careful consideration of the connection between the available information on salt absorption and cell elongation in plant cells. The work of STEWARD, HOAGLAND *et al.* (4) has already shown

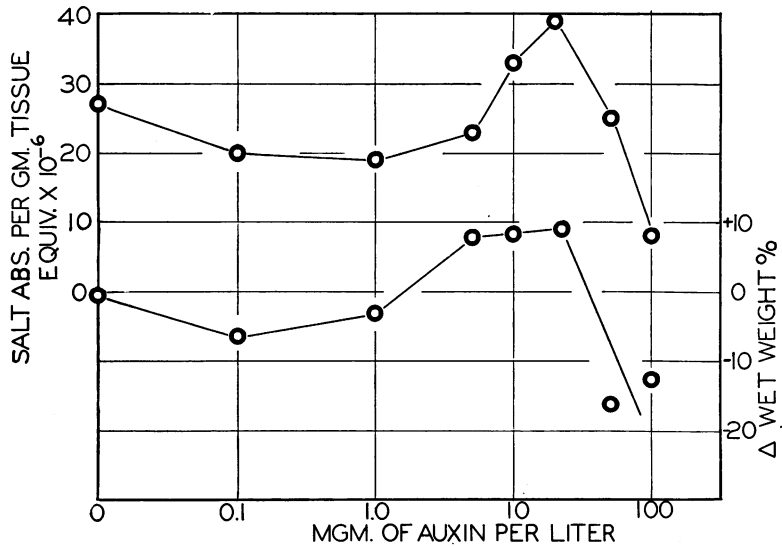


FIG. 1. The effect of various concentrations of indole-3-acetic acid on the amount of salt absorbed and the change in wet weight of potato slices during a 48-hour period.

that salt absorption depends on the activity of the cellular respiratory processes and will occur only under aerobic conditions. The metabolic changes which seem to be related to salt absorption involve, among other substances, the four-carbon dicarboxylic acids. These workers also report that salt absorption is always accompanied by an increase in cell size, and indicate that only those tissues which are capable of growth are able to absorb salt. This information bears a significant relation to the findings of COMMONER and THIMANN (1) on the relation between growth and respiration in the *Avena coleoptile*. Their data showed that the effect of auxin on cell enlargement is related to a parallel influence on the activity of that part of the cell respiration which involves the four-carbon dicarboxylic acid hydrogen transport systems. The similarity of the respiratory relations of both sets of phenomena is very apparent and indeed it seems likely that both salt absorption and cell enlargement depend on the same source of energy. Further sup-

porting evidence can be found in the fact that certain succulents such as the Crassulaceae are noted for the predominance of their four-carbon acid metabolism as well as for their water-binding powers.

It seems likely therefore that the effect of auxin on cell enlargement is a consequence of its effect on salt absorption and the water uptake which inevitably accompanies such an increase in sap solute. Auxin stimulates the enlargement of cells by augmenting the intensity of the osmotic driving force. The dependence of cell enlargement on respiratory processes may be viewed as a consequence of the respiratory dependence of the salt absorption process, and the evidence points to the four-carbon acid metabolism as the respiratory agent particularly related to these phenomena. A further report on the interrelations of these factors will appear soon.

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