Growth Hormones in Plants

Kenneth V. Thimann

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GROWTH HORMONES IN PLANTS[1]

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[With 2 plates]

The development of our knowledge of the plant hormones is a very interesting example of how a piece of research which seems purely academic may lead to results of considerable practical importance. It also demonstrates rather well the reason for the fascination of scientific work, because one never knows quite where one is going to be led next. Almost any research problem becomes a kind of chase, with all the excitement of an old-time comedian's chase, which may embroil him in all kinds of difficulties and may finally land in the most unexpected places.

No scientific story, of course, has a true beginning, for they all grow out of some earlier one, but this may be regarded for the present as beginning in 1919, when Professor Paál, in Hungary, was studying the response of certain seedlings to light. For this work he used the coleoptiles of the cereals, especially oats.

In a field of oats or wheat, when the crop is still young, one may often see a thin, papery sheath at the base of the stalk. It is soon torn open by the leaves which grow up through it, and withers early. This delicate shoot first attracted the attention of Charles Darwin by its extreme sensitivity to light, and since Darwin many others have studied it. Now Paál was interested in the effect of the extreme tip of the coleoptile on the sensitivity of the part below it. He was anxious to confirm the earlier finding of Boysen-Jensen (1913), which was that if the tip is removed, the sensitivity to light—as shown by the curving of the coleoptile toward the source of light—was lost, and that when the tip was replaced (not grafted but just glued on) this sensitivity returned. He not only did confirm this, but found something even more important. If the tip which had been cut off

[1] Presented at a meeting at the Franklin Institute March 9, 1939. Reprinted by permission from the Journal of the Franklin Institute, vol. 229, No. 3, March 1940.

was stuck on again a little to one side, the side on which it rested grew more than the opposite side, with the result that the plant curved (fig. 1). No light was here involved; the curvature was due to the one-sided influence of the tip. Paál deduced that the growth of the shoot was controlled by a growth substance or hormone which was produced by the tip.

Now the idea of hormones was developed by zoologists to account for those phenomena in which one organ influences tissues in other parts of the body. The heroine of the dime novel, who is suddenly confronted by the villain, or by the family ghost, turns as white as a sheet, her hair stands on end, and her eyes widen with horror. These effects result from her having received a dose of a hormone (adrenalin) which is secreted in a special gland and travels about

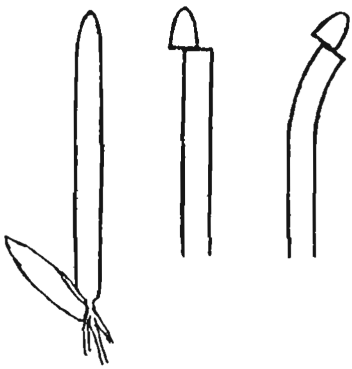


FIGURE 1.—The experiment of Paál. Left, intact seedling; center, tip removed and replaced to one side; right, curvature resulting.

in the blood stream, causing the capillaries to contract all over the skin and scalp. Many other hormones are known. All of them are secreted in some part of the animal body and travel about it to exert their effects in other parts.

In this case growth is controlled by a substance or hormone secreted by the tip and traveling down the side of the plant, which responds by growing faster. In the normal plant, with the tip symmetrically placed, all sides would receive the same amount of the hormone and consequently would grow equally.

It was 10 years before the next step forward was taken by Went, in Holland (1928). He found that if the tips were cut off and placed on a jelly of agar or gelatin, this jelly acquired the property of hastening the growth of a coleoptile stump when applied to one side of it. The growth-promoting hormone had diffused from the tip into the agar. The curvatures which resulted were very regular, and Went found that under constant conditions the reaction could be used as a test for the hormone (fig. 2). Agar pieces of controlled size were used, and the curvature of the plants measured after a definite time. The curvature was then proportional, within certain limits, to the amount of hormone which must have entered the agar.

Instead of placing the agar on one side of the coleoptile stump it can be placed symmetrically on it, thus taking the place of the tip, with the result that the coleoptile grows faster on all sides. With a traveling microscope the straight growth can also be used for the assay of the growth hormone. This is important in principle, but the curvature method has certain technical advantages for use as a routine test.

Now there are a good many natural conditions under which plants curve. Plants are not free to move about as the higher animals are, since their base is usually fixed. When one is confined to bed by doctor's orders, one's base is similarly fixed, and about all that one can do, when receiving visitors, is to curve in various ways.

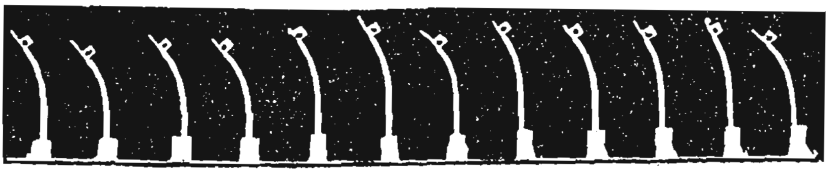
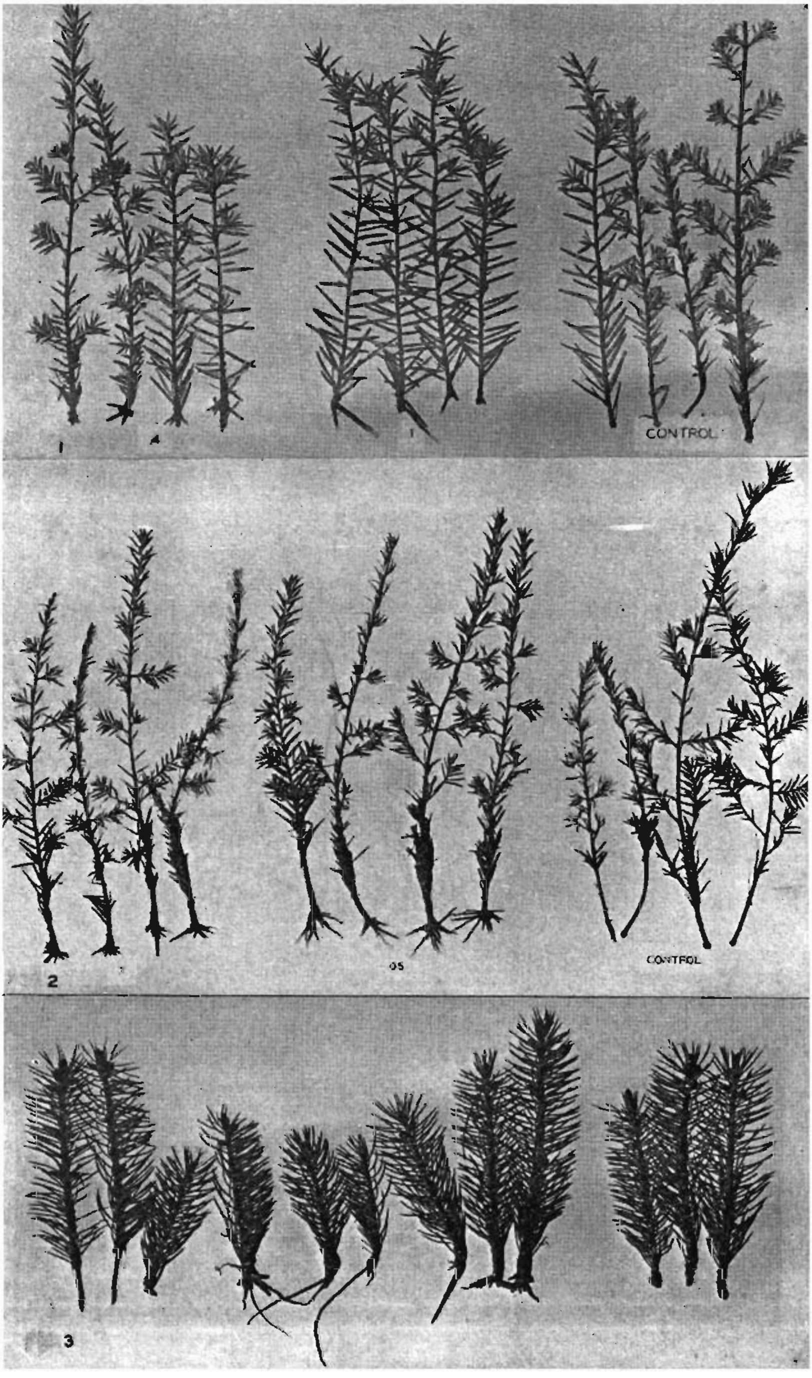
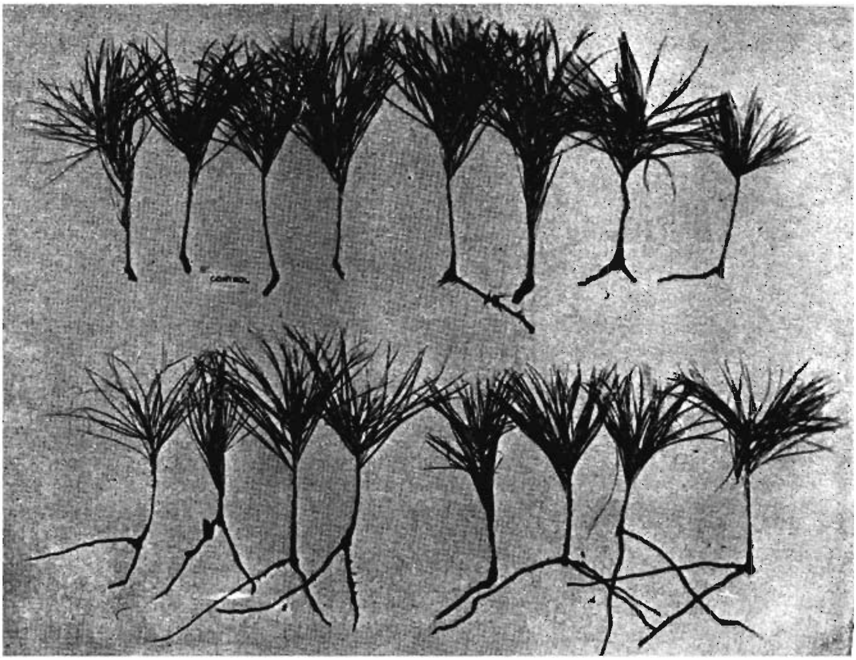


FIGURE 2.—Oat seedlings with tips removed and blocks of agar containing growth hormone applied. Photographed 100 minutes later.

Plants curve in particular in response to light and gravity. In these curvatures there is a characteristic difference between the response of the shoot and that of the root. Shoots curve toward a weak light, while the roots are either indifferent or (in some plants) curve away from the light. Shoots curve upward away from the earth, roots typically downward. As mentioned above, it was from studies of the curvature toward light that the role of the growth hormone was discovered. Naturally, therefore, it occurred to these workers that the curvatures caused by asymmetric application of the growth hormone are probably related to those due to light and gravity. Cholodny, in Russia (1927), suggested that all such curvatures were due to a displacement of the hormone within the plant, more going to the lower side when the plant is placed horizontal, or to the shaded side when exposed to a one-sided source of light. That this is the correct explanation was proved in the following way: tips were cut off and placed on two small pieces of agar so that the hormone diffusing from the two sides would be collected in separate pieces. On now exposing to light from one side, the agar on which the dark side rested was found to contain more growth hormone than the



Top, Canada hemlock. Left to right, 400, 100, and 0 mg. auxin per liter for 24 hours.
Middle, Canada hemlock, variety *pendula*. Left to right, 100, 50, and 0 mg. auxin per liter for 24 hours.
Bottom, Blue spruce. Left to right, 400, 200, 100, and 0 mg. auxin per liter for 24 hours All photographed after 9–10 weeks in peat-sand medium. (From Thimann, K. V., and Delisle, A. L., Journ. Arnold Arboretum, vol. 20, pp. 116–136, 1939.)



WHITE PINE.

Left to right: Above, 0 and 100; below, 200 and 400 mg. auxin per liter for 24 hours. Photographed after 4 months.

Although the results of auxin treatment in rooting of cuttings are in general very striking, there are some plants which do not respond markedly even to this. Recently we have studied some of these so-called "difficult" plants. It appears that some of them, such as Canadian hemlock and blue spruce, may be readily rooted if care is used and auxin in the right concentration is applied (pl. 1). Some others, such as white pine and Norway spruce, can also be rooted, but only when the plants from which cuttings are taken are themselves young (pl. 2). It is important to note that it is not the age of the cutting which is important, but the age of the tree from which it is taken. Occasionally, too, other substances, such as sugar, vitamin B_1, etc., when used together with auxin, promote the formation of roots.

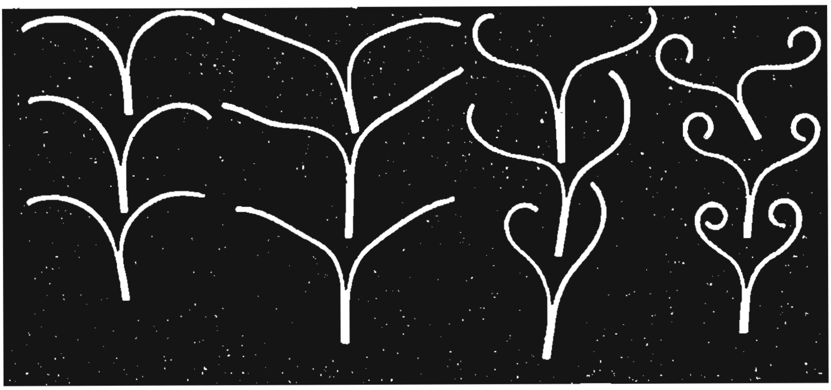


FIGURE 4.—Inward curvature of slit stems in auxin solutions. Left to right: water, 0.2, 1, and 5 mg. auxin per liter. Photographed after about 30 hours.

Another fact of some importance in the rooting of woody cuttings is the type of shoot used. In some of the conifers it is clear that there is a difference in response between the side shoots (laterals) and the apical or terminal shoot. The latter, even if supplied with sufficient auxin, roots less readily and dies more quickly than the side shoots. Thus here again the response to auxin varies with the part of the plant.

Perhaps the most remarkable variation within the plant is shown by the different responses of different parts within the same section of stem. If stems of young pea plants are slit in two and placed in auxin solution, the two halves curl inward toward each other. The extent of the curvature varies with the concentration of the solution, and the reaction can thus be used as a test for the auxins (fig. 4). Many other plants show the same phenomenon; dandelion stalks are very responsive. The development of the curvature can best be shown in the form of a movie, taken by lapse-time photography. The halves first curve outward, then after an hour or so the inward curvature begins and is complete in about 20 hours.

Now in this reaction the auxin is being supplied to all the tissue, since the piece of stem is immersed in the solution, yet nevertheless the curvature which results shows that the tissues on the outside grow more than those on the inside. It is evident that this phenomenon is quite different from those described at the beginning, in which curvature results because the auxin is only applied to one side. We have accumulated a good deal of evidence to prove that here there is truly a difference in the response of the outer and inner sides to the same auxin concentration.

Such subtle differences as this between closely appressed layers of tissue, or those described above between the rooting response of different parts, can now be investigated for the first time by the use of growth hormones. These substances are a powerful tool for studying all kinds of phenomena in plants and especially that most obscure process of all, whose understanding is one of the most fundamental things with which biologists are concerned, the phenomenon of growth.

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