

THE GROWTH HORMONES FOUND IN PLANTS

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INTRODUCTION

Just what is a hormone? This question is the one which first comes to mind if one is not familiar with the subject. The term "*hormone*" is derived from a Greek work meaning "to arouse to activity." It was first suggested by Hardy and used by Starling in 1906 in reference to the substance *secretin*. In 1914 Starling defined a hormone as "any substance normally produced in the cells of some part of the body and carried to distant parts which it affects for the good of the body as a whole." This definition as applied to animal physiology is equally useful to the plant physiologist. Indeed, the naturally occurring plant hormones, as we now understand them in higher plants, are formed or stored in certain regions of the plant and moved to others where they become effective. The common characteristic of these compounds that lets us place them in the category of hormones is the fact that when present in very minute quantities, they bring about *growth* if other conditions such as food and water supply are not limiting. Their influence on growth is out of all proportion to the low concentration in which they occur.

The discoveries during the past 25 years of certain facts concerning the activity of plant growth hormones have given a clue to the long puzzling problem of plant responses to light and gravity, and through studies on these tropisms we have gained much new information regarding normal growth.

In short, the growth hormone theory is this: Assuming an adequate supply of food and water, growth will go on only if growth hormone, or *auxin* (as it is known also) is present. Without auxin, no growth takes place. The presence of auxin in minute quantities promotes cell stretching (elongation) in the direction of the long axis of an organ such as a petiole, or stem, hence auxin may be considered as promoting *polarized* growth—greater growth in length than in any other direction. For the present, at least, this statement must be limited to aerial portions, or shoots, of plants.

The relationship of cell division to the naturally occurring auxins is not sufficiently clear as yet to be discussed here, and so we shall assume for the present, at least, that these substances exercise their effect mainly on cell elongation.

All the earlier studies on auxin were made in connection with grass seedlings, mostly oats, *Avena sativa*. Other more recent work has been done on dicotyledonous seedlings such as lupine, broad bean, sunflower, etc. For the sake of clarifying the discussion that follows, diagrams of the oats and sunflower seedlings are given in Fig. 1. Growth hormones have been

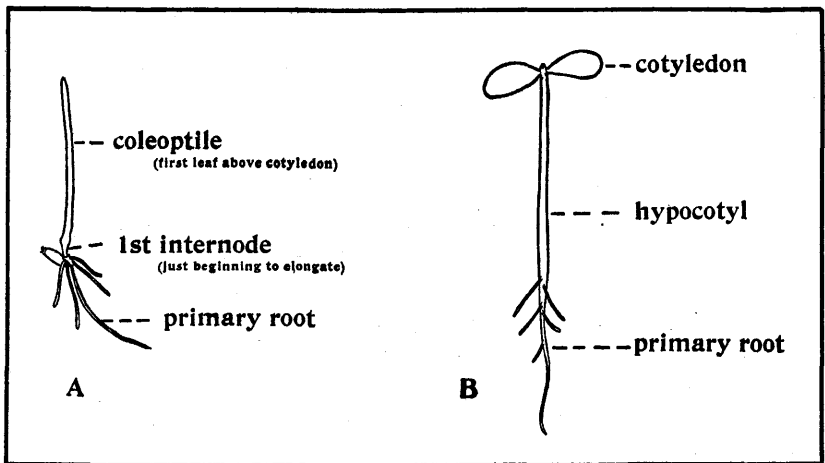


Fig. 1. A, seedling of *Avena sativa*. The coleoptile (cylindrical sheathing leaf and first above the cotyledon) has been used widely in studies on plant growth hormones. The single cotyledon remains enclosed in the old seed coat. B, seedling of typical dicotyledonous plant.

investigated also in the leaves, stems, flowers and roots of various kinds of plants at different stages in their development.

The comments that follow will touch upon such topics as the discovery of plant hormones, how their concentration may be measured, and more briefly on their chemistry, occurrence, effectiveness, formation, nomenclature, translocation, relation to normal growth, tropisms, and other life phenomena. This is essentially the outline followed by Professor Boysen Jensen in his book "Die Wuchsstofftheorie."

THE DISCOVERY OF HORMONES IN PLANTS

The history of hormone investigations extends over the past twenty-five years, and Boysen Jensen should doubtless receive credit for the discoveries which later led to the unquestioned demonstration of the presence of growth hormones in plants. His studies, published in 1910-11, indicated the presence of some sort of a chemical substance which streamed from the tip of the *Avena* coleoptile downward toward its base. If the light came from one side (hereafter referred to as *unilateral* light), the substance apparently streamed downward on the darkened side, and the coleoptile elongated on the dark side. The result was that the tip bent toward light. This was demonstrated by inserting a mica plate in a transverse direction into the back and front sides of coleoptiles, just below their tip (Fig. 2, A and B). When inserted into the back side this usual phototropic response to unilateral light did not occur. He then removed the tip of the coleoptile and placed a thin sheet of gelatin on top of the coleoptile stump. Following this, the tip was replaced in its original position—except that a layer of gelatin lay between it and the stump. When the coleoptile was exposed again to unilateral light, the usual phototropic bending took place. This led to the important conclusion that the movement of a chemical substance must be involved in this growth response.

A series of experiments by other workers followed. Paal (1918), removed the tip of the coleoptile and set it back on one side of its stump (Fig. 2 C). The result was a curvature away from the replaced tip (positive curvature), which indicated that a growth substance of some sort was moving downward from the replaced tip. Stark (1921) extracted juice from coleoptiles and made it up in agar blocks. When such an agar block was placed on one side of the coleoptile stump (see Seubert, Figure 2 D), curvature took place toward the block; this *positive* curvature indicated the presence of some sort of a growth inhibiting substance. Seubert (1925) was the first to demonstrate that growth hormone could be extracted from plant and animal material; agar blocks were prepared with saliva, diastase and malt extract, and when these were applied to coleoptile stumps (Stark's method), positive growth curvatures occurred (Fig. 2 D).

This line of investigation was followed up by Went (1928). He showed that the decapitated coleoptile tips such as Paal had

replaced on one side of the stump, could be placed on a small agar surface, and that growth hormone would diffuse out of the

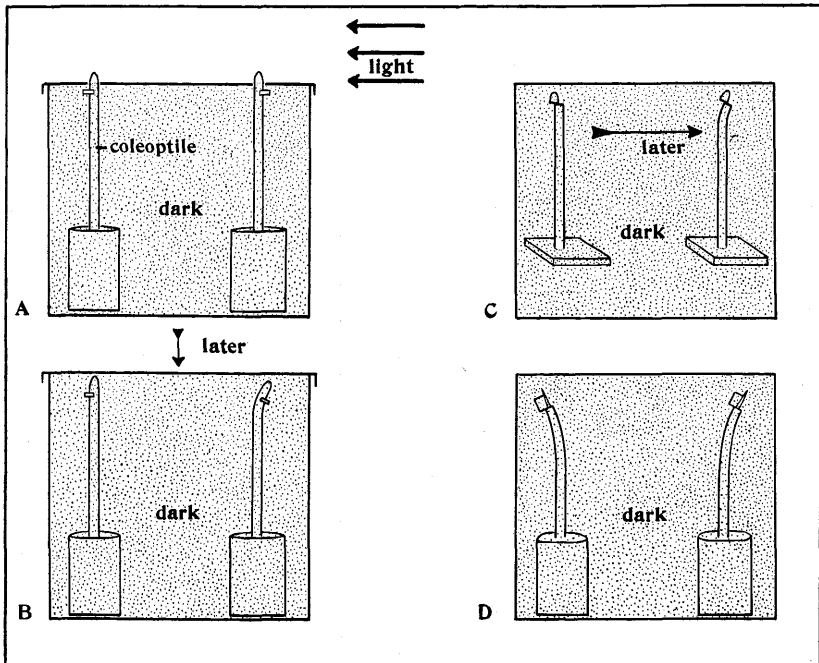


Fig. 2. A and B, diagrammatic representation of the experiments of Boysen Jensen (1910-11). A, *Avena* seedlings growing in soil in small glass containers, in total darkness except for the coleoptile tips which extend into the light (light coming from the right hand side, *unilateral* light). Before receiving the unilateral light, small sheets of mica were inserted on the front and back sides, immediately below the tips of the coleoptiles. After a short exposure to light, the coleoptiles were in total darkness. B, later, the coleoptiles with the mica insert on the side which was illuminated bent in the direction of the illumination while those with the mica insert on the back side did not bend. This indicated that a growth stimulus of some sort ordinarily passed down the coleoptile on the side away from the light, causing it to bend toward the light. (When the coleoptile tip was severed from the stump, then replaced in its normal position but with a layer of gelatin between it and the stump, the response to unilateral light took place as usual—not illustrated.) Boysen Jensen interpreted these experiments as indicating that the stimulus was chemical in nature, thus laying the ground work of the hormone theory. C, Paal (1918) worked with empty coleoptiles of *Coix*. After severing from the seedlings, the coleoptiles were supported in moist sand. He showed that the coleoptile tip could be removed and replaced on one side with a resulting curvature away from the tip. This indicated that growth stimulating substance was being dispersed from the coleoptile tip. D, by decapitating coleoptiles and using agar blocks according to the method of Stark (1921), Seubert (1925) was the first to show that growth hormone could be extracted from plant and animal material. When the agar was infiltrated with saliva, diastase, or malt extract, and small blocks of such agar were placed unilaterally on *Avena* coleoptile stumps, growth curvatures occurred (right). Curvatures toward the block were induced (left) when growth inhibiting substances were present in the agar.

tips into the agar (see diffusion from leaf in Fig. 3). He cut the agar into small blocks, and if such blocks were placed unilaterally on coleoptile stumps, positive curvatures were obtained, like those of Seubert a few years before. Then Went discovered that this curvature was proportional, within limits (angles of 15° to 20°) to the amount (later shown to be concentration) of growth hormone present in the agar. This marked the discovery of a *quantitative* method for working with plant hormones; the method (Fig. 3) makes it possible to determine hormone *concentration*, and its importance cannot be overestimated. The field has been an increasingly active one ever since Went's discovery.

METHOD FOR DETERMINING THE CONCENTRATION OF AUXIN IN AN UNKNOWN

No chemical test has been devised which provides a ready and simple means of qualitative or quantitative detection of the minute amounts of auxin present in living plants. This means that some other means must be used for detection. Just as the animal physiologists resort to rabbits, guinea pigs and rats for tests with animal hormones, the botanist also resorts to a biological measuring stick. The botanical "guinea pig" or test object for plant hormones, is the *Avena* coleoptile, and Went's technique, as modified by others and himself, is illustrated in Figure 3.

The laboratory in which the tests are carried on should be maintained at 79° F. and approximately 90% humidity, and pure fresh air should be supplied at regular intervals. It should be lighted only with red or orange light, of wavelengths which bring about no phototropic response in the test plants.

If for any reason it is not possible to apply the agar blocks approximately 40 minutes after decapitation, the coleoptiles may be decapitated a second time by removing a short segment at the top of the stump. After such "double" decapitation, maximum sensitivity is reached after about 3 hours.

A little more than 2 hours before a test is made, it is necessary to prepare the material in which the hormone concentration is to be determined. Let us assume that it is a vigorously growing leaf, or stem tip of the tobacco plant that is to be tested. Not knowing just what to expect at first, it would be well to use the tips of 2 or 3 plants. These are cut from the plants and placed on rectangular pieces of agar, prepared as indicated in Figure 3

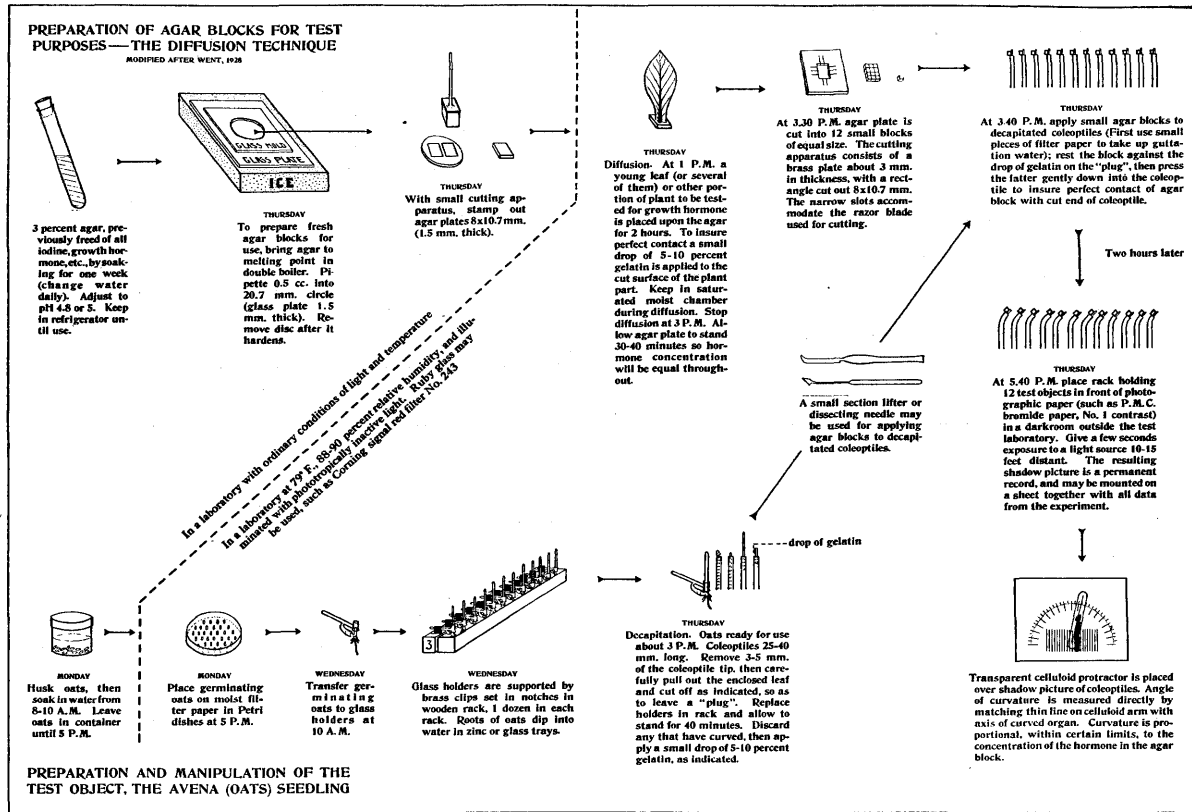


Fig. 3. Went's (1928) quantitative method of demonstrating the hormone content of plant parts. The time schedule is indicated by days for convenience sake only. The curvature of the *Avena* coleoptile is proportional, within certain limits, to the concentration of the growth hormone.

In our laboratory we use the size agar plate suggested by Dolk and Thimann: 8 x 10.7 x 1.5 mm. It dries out less rapidly than the smaller blocks. A small amount of 5 or 10% gelatin is applied to the cut end of the young tobacco stems and they are placed upright on the agar, then allowed to stand in a moist chamber for 2 hours. After removing the tobacco tips at the end of the 2 hour period, the agar is cut into 12 small pieces of equal size. In the meantime the coleoptiles have been decapitated, and we are ready to proceed. Each of the blocks is placed as indicated (Fig. 3) on a decapitated coleoptile. After the agar blocks have been in place 2 hours, the rack of 12 test plants may be photographed (shadow picture on bromide paper is simplest). The angles of curvature can then be determined with a protractor, and the results may be expressed in degrees of coleoptile curvature, or in the various units suggested by different authors. Curvatures up to about 20° are directly proportional to the concentration of the hormone present in the agar block.

If a liquid of unknown hormone content is to be tested, the agar should be made up with various dilutions of the unknown. Each of these dilutions should be tested, so that certain of them, at least, will fall within the range of quantitative results.

A typical schedule for diffusion of plant material and the subsequent tests is as follows:

Material	Start Diffusion	Stop Diffusion	Decapitate	Apply Agar Blocks	Photograph
A.....	9:00 a. m.	11:00 a. m.	10:50	11:32	1:32 p. m.
B.....	9:15	11:15	11:05	11:47	1:47
C.....	9:30	11:30	11:20	12:02	2:02
D.....	9:45	11:45	11:35	12:17	2:17
E.....	10:00	12:00	11:50	12:32	2:32
F.....	10:15	12:15	12:05	12:47	2:47
G.....	10:30	12:30	12:20	1:02	3:02
H.....	10:45	12:45	12:35	1:17	3:17
I.....	11:00	1:00	12:50	1:32	3:32
J.....	11:15	1:15	1:05	1:47	3:47
K.....	11:30	1:30	1:20	2:02	4:02
L.....	11:45	1:45	1:35	2:17	4:17
M.....	12:00	2:00	1:50	2:32	4:32
N.....	12:15	2:15	2:05	2:47	4:47
O.....	12:30	2:30	2:20	3:02	5:02
P.....	12:45	2:45	2:35	3:17	5:17

For one operator to run 16 dozen test plants in a little more than 8 hours, as outlined above, requires experience. It is

possible to run half as many with greater ease. With half the number, diffusion can be started at 5 minute intervals, then the operations will not overlap. With a little practice it is possible to decapitate a rack of one dozen coleoptiles in 2 or 3 minutes. Agar blocks can be applied in a similar length of time. In order not to get behind schedule if anything unforeseen happens, it is well to allow at least 5 minute periods between diffusions.

There are other ways than the *Avena* method of detecting the presence of the auxin, but they have not been as satisfactory in terms of quantitative results. Of course the *Avena* technique does not work for all kinds of plant material, but in most instances it has proved itself useful. Skoog (in press) has shown that by removing the cotyledon and endosperm from the *Avena* seedling ("de-seeding"), its sensitivity as a test object can be increased. *Cephalaria* is a sensitive test object, but it does not give curvatures proportional to concentration over a very wide range.

CHEMISTRY AND OCCURRENCE

To date three hormones have been demonstrated as occurring naturally in plants. In certain fungi it has been possible to demonstrate the presence of a growth hormone which Kögl, Haagen Smit & Erxleben have referred to as *heteroauxin*. From various higher plants and other sources these same investigators have isolated two other hormones, designated by them as auxin *a* and auxin *b*. The information they have given us constitutes the greater part of our present knowledge of the chemistry of auxins. The empirical formula of heteroauxin is $C_{10}H_9O_2N$; of auxin *a*, $C_{18}H_{34}O_5$; and of auxin *b*, $C_{18}H_{30}O_4$. Auxin *a* is a monocyclic tri-hydroxy-keto carboxylic acid with one double bond, and heteroauxin is 3-indole acetic acid, a compound known for 50 years before its potency as a plant hormone was discovered.

Pure crystals of auxin *a* are reported to have a melting point of $196^\circ C$; auxin *b* of $183^\circ C$ and heteroauxin of $165^\circ C$. Auxin *a* is stable in the presence of acid and is sensitive to alkali. Heteroauxin is just the opposite, while auxin *b* is destroyed by both acids and alkalies. Auxins *a* and *b* lose their activity after a few months. They have not yet been synthesized.

Although the above compounds have diverse chemical characteristics, they apparently all promote cell elongation (in their naturally occurring state) in the direction of the long axis of stems or other parts of the shoots of plants.

The chief experimental source of auxins has been from human urine, about 80% of the growth hormone concentration of which is auxin *a* and 20% heteroauxin. The content in urine is appreciable following the ingestion of butter, salad oil and other fats at meals. Normal and pathological animal tissues have been shown to have auxin present in them. Auxins have been shown to occur also in numerous plant products, such as corn oil and malt, and in the vegetative and reproductive parts of many kinds of mono- and dicotyledonous plants. Pollens of many kinds of plants are an especially rich source, as are the embryo and endosperm of many seeds. Fungi such as *Rhizopus* and *Aspergillus* produce heteroauxin, and the alga *Valonia* has been found to contain auxin. There is every reason to suppose that these or similar growth hormones occur universally in plants.

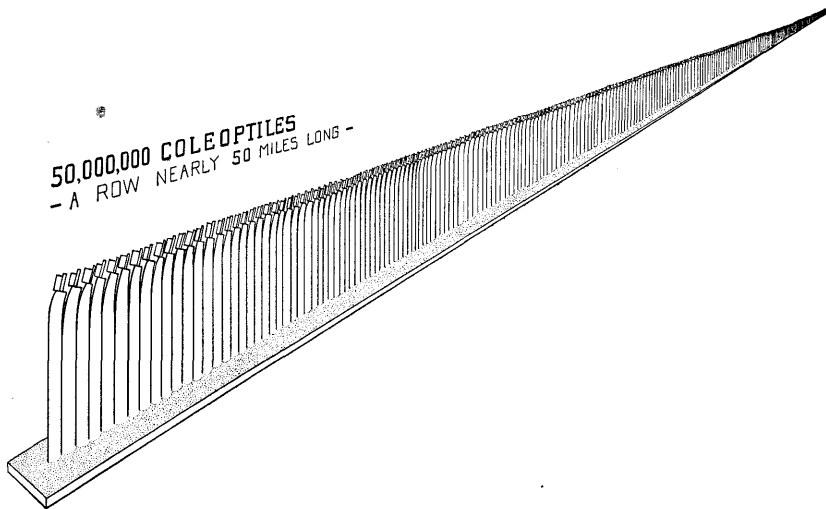


Fig. 4. One milligram of pure auxin *a* is sufficient to bend 50,000,000 coleoptiles to an angle of 10° , if applied unilaterally in agar blocks. 50,000,000 coleoptiles, if placed side by side, would make a row nearly 50 miles long. At this rate, four pounds of auxin *a* would bring about a 10° curvature in a row of coleoptiles extending from earth to sun!

EFFECTIVENESS

Auxins *a* and *b* are about equally effective in promoting growth. It has been estimated that one milligram of either compound is capable of bringing about a curvature of 10° in fifty million decapitated coleoptiles, if applied unilaterally in agar blocks, as previously indicated. Convert this into some figure that is more nearly comprehensible. There are a few over

one million coleoptiles to the mile if they stand closely side by side, so one milligram of either compound is capable of bringing about a 10° curvature in nearly 50 miles of coleoptiles (Fig. 4). Heteroauxin is approximately one-half as effective, i. e., one milligram of it would bend only 25 miles of coleoptiles!

Substances of synthetic origin (other than 3-indole acetic acid) have been tested on the *Avena* coleoptile, but none tested so far has been quite as effective as the naturally occurring auxins. For example, one milligram of one of the indole propionic acids would bend 5 miles of coleoptiles, and the same amount of a methyl-indole acetic acid would bend only $1\frac{1}{2}$ miles of coleoptiles, etc. These synthetic substances have been designated as "growth substances," and indeed many of them do appear to behave as such. It may be that the concentrations in which it is necessary to use them to get a given effect will be so high that they cannot be considered hormones. They do not need to concern us for the present for they have not been shown to occur naturally in plants. But that they are of the utmost practical importance, whether hormone-like or not, cannot be denied, and their applications in horticulture with regard to rooting and other phenomena will be discussed by Dr. Zimmerman in a later lecture in this series.

NOMENCLATURE

Any chemist would tell us that even with our present knowledge of the chemistry of plant growth hormones, we ought to call them by their chemical names. For example auxin *a* is auxentriolic acid, auxin *b* is auxenolonic acid, and heteroauxin has already been referred to as 3-indole acetic acid. But there are many brands of chemical nomenclature. 3-indole acetic acid is also known as β -indolyl acetic, β -indole acetic and indole-3-acetic acid. We might well adopt the names botanists have provided, such as growth substance¹, growth regulator², growth hormone and phytohormone; they refer more particularly to the physiological response. The animal hormonists have outdone the botanists, and a score or more of physiological names have been applied to sex hormones alone. The nomenclature will become more settled as our knowledge of the field advances.

¹⁻²The terms "growth substance" and "growth regulator" probably ought to be dropped gradually from the literature, because the nutritional substances even when present in very small amounts (minerals, gases, and organic foodstuffs) are also growth substances and growth regulators.

FORMATION, STORAGE, AND PHYSIOLOGICAL REGENERATION

We are almost entirely in ignorance regarding the synthesis of auxin by the living plant. The production of heteroauxin by molds and bacteria has been studied in relation to the character of the nutrient substratum; it has been found that glucose, peptone, glucose ammonium tartrate, tryptophane and other compounds favor its formation. Within limits, higher temperatures have been found to result in increased production of growth hormone. It has been found too, that its formation in young leaves and other growing parts of green plants will not take place in the absence of light. Seedlings are enabled to grow for many days in darkness because they have a stored supply of auxin present in the seed; when this is exhausted they cannot grow further, even though they possess adequate food and water. Just how this auxin is stored in seeds we do not know. Presumably it is in an inactive form, and does not become active until the seed absorbs water. Some seeds require a short exposure to light before they will germinate. This doubtless indicates that light in some instances activates in some way the inactive stored form of auxin.

There are many references in the literature which indicate that growth hormone is formed at the tip of the *Avena* coleoptile, from which point it moves downward, bringing about growth. From what we know now, this interpretation seems untenable. It is more likely that the auxin, probably in its inactive form, is moved from the endosperm and cotyledon upward through the vascular bundles to the tip of the coleoptile, where it becomes activated before being dispersed downward.

There are many studies pertaining to "physiological regeneration," a phenomenon peculiar to the coleoptile of grasses, and which may be explained as follows: When the coleoptile tip is removed, the immediate source of the growth hormone supply is removed also and the growth of such a decapitated coleoptile, as would be expected, gradually comes to a stop, i. e., the hormone present in the tissues of the coleoptile stump is used up. At this time the coleoptile is not responsive to unilateral light or to gravity. But after a few hours a new "physiological tip" becomes established at the upper end of the stump; as the auxin moves downward through the tissues from this new center of dispersal, growth starts again, and the organ again is sensitive to unilateral light and to gravity. This physiological regenera-

tion, as it is called, is probably not "regeneration" in the sense originally intended. As we now understand it, the endosperm and embryo are places of storage of growth hormone, and its probable movement upward in the vascular bundles has been indicated above. If the endosperm is removed, physiological regeneration does not occur after about ten hours have elapsed. From this it might reasonably be expected that it would move upward (in its inactive form) in a decapitated coleoptile as well as in an intact one, and that it would similarly be dispersed downward (in its active form) after the wound shock has subsided. There is considerable evidence to support this interpretation but the secret of "activation" at the tip, if this is what happens, still remains to be discovered.

MOVEMENT OF THE GROWTH HORMONE IN PLANTS

This is a subject of utmost interest. The naturally occurring growth hormones apparently move only in a morphologically basipetal direction, as for example, from the tip downward in the *Avena* coleoptile, or from the embryological regions of young stem tips downward in stems, or downward from the storage place in the cotyledons into the hypocotyls of dicotyledonous seedlings. This one-way movement has been designated as "polar" transport. It apparently holds true in young or moderately mature tissues, but in old tissues the growth hormone has been demonstrated to move in either direction. Of course it does not ordinarily occur in mature tissues. Anesthetization disturbs the "polarity" of transport.

It has been discovered recently that certain of the synthetic growth hormones can be applied to the plant and be transported upward. This apparently is due to their getting into the transpiration stream, in which they are carried upward through dead xylem ducts. This is not out of harmony with the facts given above in regard to polar movement through living tissues.

The velocity of movement is about 1 centimeter per hour, a rate considerably greater than could be accounted for by diffusion; the *rate* apparently is not affected by ordinary ranges of temperature and is independent of any concentration gradient existing in the plant. Anesthetization reduces this rate to that of simple diffusion.

Several explanations have been offered to explain the mechanism of movement: diffusion, protoplasmic streaming, electrophoresis, etc. The latter has found considerable support

in studies of the past year or two. The acid character of the growth hormones suggests that they might be moved toward the positively charged pole in an electrical circuit, an explanation which has been reported as verified experimentally *in vivo* and *in vitro*, under an applied electric potential. This does not mean that protoplasmic streaming and other factors are not involved. Our information on this, as on other things, is as yet incomplete.

GROWTH HORMONES AND NORMAL GROWTH

From what has been said it is clear that we are dealing with minute amounts of certain chemical substances which are synthesized by plants. These substances move and "behave" characteristically, and most important of all, *growth* depends upon their presence. Cells apparently cannot elongate without them.

If auxin applied in agar blocks to decapitated *Avena* coleoptiles gives curvatures proportional to concentration, there ought to follow a direct correlation between growth intensity and hormone concentration in normally growing plant organs (within limits, of course). This has been demonstrated in a few plants—in the *Avena* coleoptile, lupine hypocotyl, and the foliage leaf of tobacco. The implication is an important one: growth vigor, other things being equal, must be associated with the synthesis, accumulation, effective use, or destruction of auxin. Van Overbeek (1935) reports that a dwarf strain of maize derives its dwarf character from the fact that enzyme systems are present which destroy the hormone more rapidly than in normal plants.

The facts regarding the normal growth of *roots* seem, at first glance, to be in opposition to the thesis of the growth substance theory. Root growth is inhibited by concentrations of the hormone which ordinarily promote growth in stems, coleoptiles, petioles of leaves, etc. While this may give us a clue to the inherent difference in roots and shoots, it is without an entirely satisfactory explanation in terms of growth hormone. But certain investigators regard it as the normal and expected behavior. The argument is this: When a root is decapitated, the growth of its stump is accelerated for a short time, and if the root tip is placed unilaterally on the stump, growth is *inhibited* on that side (curvature *toward* the root tip); the response is the same if a coleoptile tip is placed unilaterally on the root stump, although

we know that a root tip or coleoptile tip placed unilaterally upon a decapitated coleoptile gives a growth promoting effect (curvature *away* from the applied object). If a root is immersed in an auxin solution, its growth in length may cease entirely. This can mean but one thing: the normal response of roots to auxin applied in the manner indicated is to slow down their growth rate, i. e., growth inhibition. As regards roots, then, the auxins are not growth promoting hormones; they are growth inhibiting! Concentration of hormone may turn out to be the answer to this puzzling difference between roots and shoots.

A discussion of normal growth ought to include some mention of how hormones actually work, i. e., their mechanism of action. There is evidence that they are used up in the process, not as building stones, but as activators influencing in some way the plasticity of cell walls. The walls become stretched in growth and do not shrink back to their previous smaller size. There must be either a rearrangement of the structural units of the cell wall, or an active deposition of new wall building material. The first urge for a cell to grow may come from wall extension, the wall taking the lead and thus making possible the entrance of more water. Although in its movement the auxin passes through the end walls of cells, only the side walls are affected—they are the ones which increase their length. There is a real challenge here. We do not know the fundamentals.

TROPISMS

It was brought out in the brief history of the subject that Boysen Jensen's discovery came about through experiments on the response of the coleoptile to unilateral light. This phenomenon of phototropic response is well known, and we expect it whenever a potted plant is placed near a window in our house. Its younger stems always bend toward the light. Any such response must be due to unequal growth on the opposite sides of a light-stimulated organ. The darkened side grows more rapidly than the lighted side. It has been shown that when a young stem is given light from one side only, the growth hormone becomes unequally distributed. More of it is transported to the darkened side, hence a greater concentration of it on the darkened side. Greater concentration of the hormone on the darkened side of the stem gives what might be expected, i. e., greater growth on that side. The result: bending toward the light. Exactly how light brings about this differential distribu-

tion of the hormone, we do not know, but from the suggestions already made in connection with movement of auxin in the plant, we would be led to suspect that it is at least partly due to a light-induced change in the electric potential across the organ.

The usual responses of stems of plants to gravity are well known also; if a potted plant is oriented on its side we know that in a short time the young main stem and leaves will turn upward—the so-called “negatively geotropic” response. The work of Dolk and others has shown that this is due to the greater accumulation of the hormone on the under side of an organ such as a coleoptile or stem, hence *more rapid cell elongation on the under side*, and the resulting upward curvature.

Roots behave differently. That the main roots of most plants grow directly toward gravity is common knowledge. If they are placed in a horizontal position, the young growing tip turns downward, i. e., *the cells on the upper side* elongate more rapidly, and cause the growing tip to bend downward. It has been shown that this is due to the accumulation of the hormone on the lower side of the root, where its presence inhibits cell elongation; hence the root tip turns downward in its growth.

Here, then, is the connecting link between the environment and the growing plant. The tropic responses of plants to two of the most important stimuli in their environment, light and gravity, are brought about by the same agent, the growth hormone which occurs naturally in their tissues. This has come to be known as the growth hormone explanation of tropisms. Although some of the details of our explanation may be incorrect, the evidence is overwhelming, and strikingly simple.

Tropic responses can be induced in young portions of plants by applying growth hormone to the outside of the plant in some suitable solvent such as lanolin, but this is to be discussed by others.

THE RELATION OF HORMONES TO OTHER LIFE PROCESSES

Most of what has been said up to this point finds its explanation in the fact that plant growth hormones regulate cell elongation. Other work reported in the past year or two suggests that numerous other effects may be due in whole or in part to the activity of these same hormones: (1) It has been reported that they stimulate the production of new roots. (2) The so-called apical dominance of the terminal bud over the lateral buds has been attributed to the inhibition of the lower axillary buds by

growth hormone moving downward from the terminal bud past them. (3) Cell division in the cambium and in callus tissue has been attributed to auxin, also. These observations are of great interest and are very suggestive. Whether the effects mentioned will ultimately be attributed to hormones remains for future investigations to determine.

SUMMARY AND CONCLUSIONS

Plant hormones (auxins), like animal hormones, are produced in very small quantities in one part of the organism (young, vigorously growing parts) and moved to another part where they become active. Their main role, as we now understand it, is the regulation of cell elongation; other roles have been attributed to them.

The tropic response of plants to two of the most important stimuli in their environment, light and gravity, are brought about by the movement of auxin from one part of a stimulated plant organ to another. This has come to be known as the growth hormone explanation of tropisms.

Three different hormones have been found to occur naturally in plants: auxin *a* and auxin *b* in higher plants, and heteroauxin in the fungi. Although chemically distinct, they are not yet known to differ in their effect on growth.

A few years hence the picture presented here will change materially. We have just started to work with a new tool that should aid in probing further the secrets of plant development. Every great surge of progress in our understanding of growth has come about from the discovery and use of just such a new tool. This augurs well for the future of our knowledge of chemical correlation in plants, and, indeed, for our understanding of plant morphogenesis as a whole.

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No attempt has been made to cite all the authors whose work has been discussed. The work of those referred to and others whose names are not mentioned may be found in the following:

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