

1936

Relation of Light to the Growth and Movement of Plants (Address to the Academy)

William J. Robbins
University of Missouri

Copyright ©1936 Iowa Academy of Science, Inc.

Follow this and additional works at: <https://scholarworks.uni.edu/pias>

Recommended Citation

Robbins, William J. (1936) "Relation of Light to the Growth and Movement of Plants (Address to the Academy)," *Proceedings of the Iowa Academy of Science*, 43(1), 59-79.

Available at: <https://scholarworks.uni.edu/pias/vol43/iss1/7>

This Research is brought to you for free and open access by the Iowa Academy of Science at UNI ScholarWorks. It has been accepted for inclusion in Proceedings of the Iowa Academy of Science by an authorized editor of UNI ScholarWorks. For more information, please contact scholarworks@uni.edu.

RELATION OF LIGHT TO THE GROWTH AND MOVEMENT OF PLANTS¹

WILLIAM J. ROBBINS²

At the meetings of the American Association for the Advancement of Science held at St. Louis last Christmas, the \$1000 prize for the most outstanding paper presented at the meetings was awarded to Dr. P. W. Zimmerman and Dr. A. E. Hitchcock of the Boyce Thompson Institute. The paper for which they received the prize dealt with the results of their experiments on the effect of various chemical substances on the local initiation of adventitious roots on stems and leaves, proliferation, the swelling and bending of stems, the acceleration of growth and epinasty. Certain chemical substances including β indoleacetic acid, β indolebutyric acid, β indolepropionic acid and α naphthaleneacetic acid induce striking responses when applied to plants in solution in water or in lanolin paste. (Figure 1, 2 and 3.)

The striking character of the experiments and their implications has caught the public fancy and a great deal of newspaper and radio publicity has been given to the subject of plant hormones, to the Boyce Thompson Institute, and to Drs. Zimmerman and Hitchcock, all of which is well deserved. Some have predicted that in the near future housewives, gardeners and horticulturists will smear the base of plant cuttings with lanolin paste containing plant hormones purchased from the local drug store, and thus insure successful rooting and propagation; that plants difficult to root may be induced to root by treatment with plant hormones; and that we may look forward to the discovery in the near future of simple chemical means of controlling plant growth, flowering and reproduction, as well as explanations for many phenomena in developmental physiology and in genetics which have hitherto been inexplicable. Whether or not the full expectations of the practical and theoretical importance of plant hormones are realized, we may safely say that the discovery of these substances and their action is one of the outstanding discoveries in botany in the last quarter of a century or more.

I have been interested in this general subject for a number of years. In 1915 Jacques Loeb reported certain experiments on the

¹ Address to the Academy.

² Professor of Botany, University of Missouri.

development of roots at the notches of the leaves of *Bryophyllum calycinum*. He interpreted his results as demonstrating that the leaves produced a substance which was necessary for the initiation of roots and called this substance a hormone. For example so long as the leaf was attached to the plant, roots did not develop because the substance moved out of the leaf to other parts of the plant.

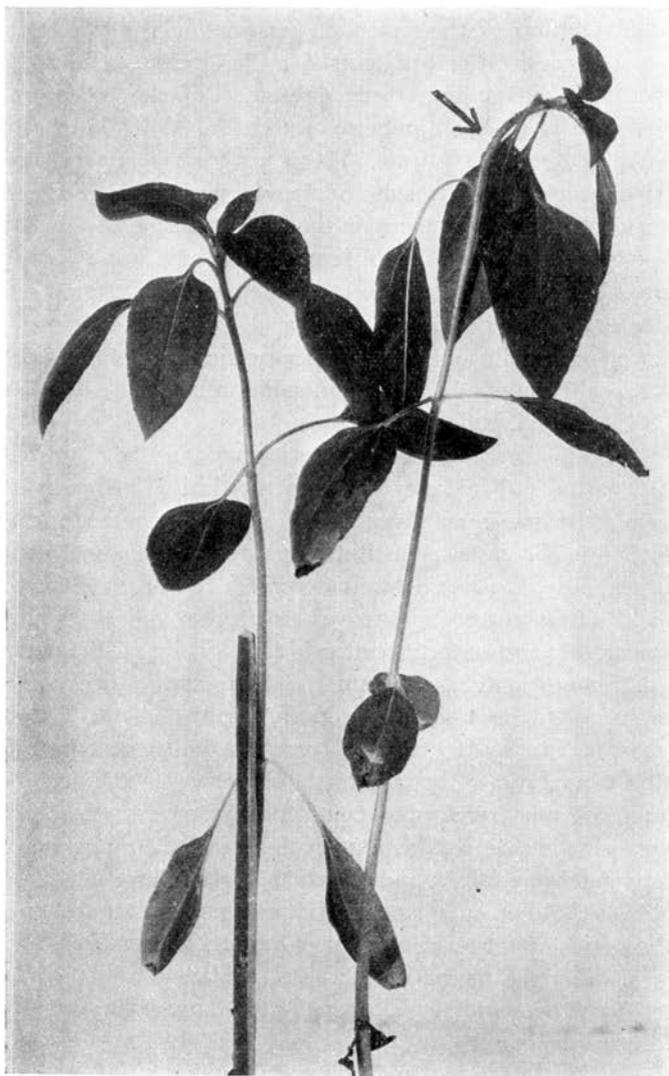


Fig. 1. *Helianthus annuus*. Left, untreated; Right, 10 hours after smearing on left side at arrow with lanum paste containing 0.2% B indoleacetic acid. Note bending away from smeared side and epinasty of leaves. (Experiment by Naylor).

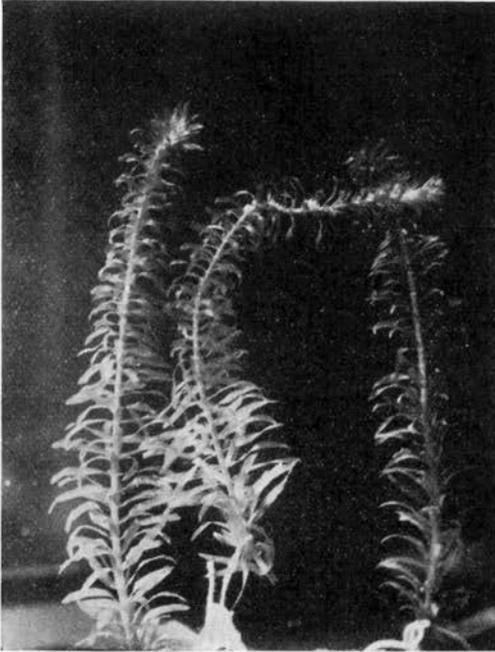


Fig. 2. *Anacharis canadensis*. Left, untreated; center, treated with lanum paste containing 0.2% B indoleacetic acid, right, treated with lanum paste only. (Experiment by Jackson).

When the leaf was detached the substance accumulated and caused roots to form.

It appeared to me that what Loeb called a hormone might be glucose manufactured by the green leaf. I was led to try whether root meristem removed from the plant would grow under sterile conditions when supplied with mineral salts, water, oxygen and sugar. I found that root meristems freshly removed from the plant would make considerable growth, but I never succeeded in cultivating them continuously in a nutrient solution as simple as the one suggested above. Our most successful result with corn has been to produce from a root tip originally 2 millimeters long a root 145 centimeters in length. This was grown in a period of 100 days.

P. R. White (1934) has succeeded in cultivating excised tomato roots indefinitely in a solution and under conditions much similar to those we have used for corn, and we have been able to confirm his results in our laboratory. Even now, however, I am not in a position to say whether or not plant hormones, or substances analogous to them, are involved in the growth of excised roots.

Plant hormones have been hypothesized since the suggestion by

Sachs in 1882 of the action of formative stuffs in the production of flowers and other plant organs. Experiments designed to prove or disprove the existence of such substances by a direct attack on the problem have been suggestive but not definite.

For example, Bottomley (1917) presented evidence that substances, which he called auximones, were essential for the continued growth of the duck weed, *Lemna*. Saeger (1925) in my laboratory, found that by diluting the mineral solution used by Bottomley in which duck weeds ceased to grow, it was possible to keep them growing continuously with no addition of "auxi-

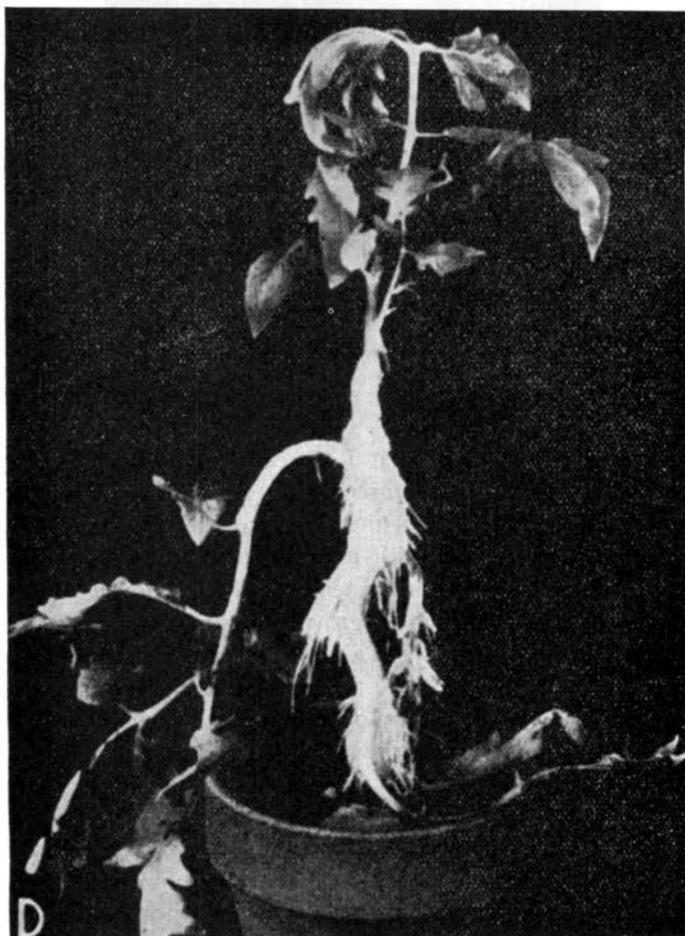


Fig. 3. *Lycopersicon esculentum*. Stem and leaves treated with lanolin paste containing 2% a naphthalene-acetic acid. (After Zimmerman and Wilcoxon).

mones." Clark (1926), at Iowa State College, secured similar results independently.

Our present information on plant hormones is largely an outgrowth of a study of the movements of plants in response to light.

It is common knowledge that plants bend toward the light. The petioles of the leaves of a geranium plant standing in a window and illuminated on one side bend in such fashion that the leaf blades are oriented perpendicularly to the incident light and the stem tip also slowly bends toward the light. This reaction of plants to light is called phototropism or heliotropism and the classical material for the investigation of phototropism has been the coleoptile of the oat seedling.

When an oat grain germinates the first part to appear above the ground is a hollow cylindrical sheath, the coleoptile, within which are the young leaves. When the coleoptile reaches a length of from 3 to 4 centimeters the first leaf pushes through the apex of the coleoptile which remains for some time as a sheath about the base of the young plant. The coleoptile of the etiolated oat seedling is especially favorable for the study of phototropism. At maturity it is a hollow cylinder one or two millimeters in diameter and from 3 to 4 centimeters long. The wall of the cylinder is made up of some six layers of cells. There are small pores near the tip. The growth of the coleoptile, as pointed out by Avery (1936), involves primarily the enlargement of cells and not their multiplication. This is particularly true for the stage at which it is used in experiments on phototropism.

Oat grains germinated in the dark have vertical coleoptiles which are yellowish white in color. When exposed to one sided illumination etiolated seedlings bend toward the light. (Figure 4.) The coleoptile will also grow vertically if the grains are germinated in light which strikes all parts of the plant uniformly, or which falls in a direction parallel to the long axis of the plant. When germinated in a space with one sided light, the coleoptiles grow toward the light. If a dark box with a small hole to admit light is used, each coleoptile will point toward this hole with uncanny accuracy, as was emphasized by Darwin.

From a practical standpoint, from the standpoint of plant production, the study of the bending of oat seedlings to light is of little apparent significance and the contributions made to phototropism in this country, where physiological botany has been largely dominated by its agricultural implications, have been minor and on the whole unimportant. Darwin was interested in this

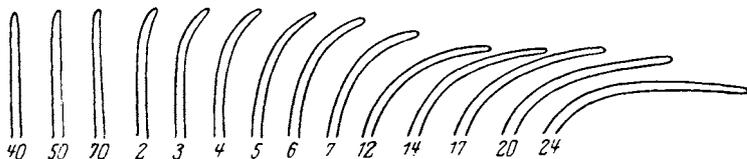


Fig. 4. *Avena sativa*. Response of seedlings to 4 seconds exposure to light of 30 meters candles. After exposure seedlings rotated on horizontal climostat in dark. Time in minutes or hours given below each figure. (After Arisz.)

phenomenon because of the survival value of such a response. Others have studied it because of their interest in the subject of stimulus and response; there are certain resemblances between the responses of an oat seedling to light and those of an animal to a stimulus.

The first thing about phototropism likely to impress us is the extreme sensitiveness of the plant to light. The seedlings of many kinds of plants are extremely sensitive to one sided illumination. Darwin, in his book on *Power of Movement in Plants*, published in 1880, says:

“A pot with seedlings of *Phalaris Canariensis*, which had been raised in darkness, was placed in a completely darkened room, at 12 feet from a very small lamp. After 3 hours the cotyledons were doubtfully curved towards the light, and after 7 hours 40 minutes from the first exposure, they were all plainly, though slightly, curved towards the lamp. Now, at this distance of 12 feet, the light was so obscure that we could not see the seedlings themselves, nor read the large Roman figures on the white face of a watch, nor see a pencil line on paper, but could just distinguish a line made with Indian ink. It is a more surprising fact that no visible shadow was cast by a pencil held upright on a white card; the seedlings, therefore, were acted on by a difference in the illumination of their two sides, which the human eye could not distinguish. On another occasion even a less degree of light acted, for some cotyledons of *Phalaris* became slightly curved towards the same lamp at a distance of 20 feet; at this distance we could not see a circular dot 2.29 mm (.09 inch) in diameter made with Indian ink on white paper, though we could just see a dot 3.56 mm (.14 inch) in diameter; yet a dot of the former size appears large *when seen in the light.*” This quotation is of interest not only because it illustrates the sensitiveness of plants to light but also because it shows Darwin’s painstaking record of experimental work.

The sensitiveness of plants to light has been investigated by many others since Darwin’s time. Blaauw (1909) found that etiolated oat seedlings, that is seedlings which had developed in

the dark, would bend toward light of an intensity less than 0.001 that of full moon light and seedlings of *Vicia sativa* are even more sensitive than those of oats.

The extreme sensitiveness of plants to light requires that great care be used in the study of phototropism to exclude light even during the short periods when the plants are examined to note the results. Fortunately the seedlings are not sensitive to red light of weak intensity and may be examined by its aid without risking invalidation of the results. Furthermore, for accurate work the humidity and temperature of the growth chamber used must be controlled. In addition, for some purposes, light sources of known intensity and color composition, photographic means of recording the response, horizontal clinostats to eliminate the effect of gravity, apparatus for the accurate timing of exposures, and other supplementary equipment, may be involved. Altogether the careful study of phototropism is not a simple affair.

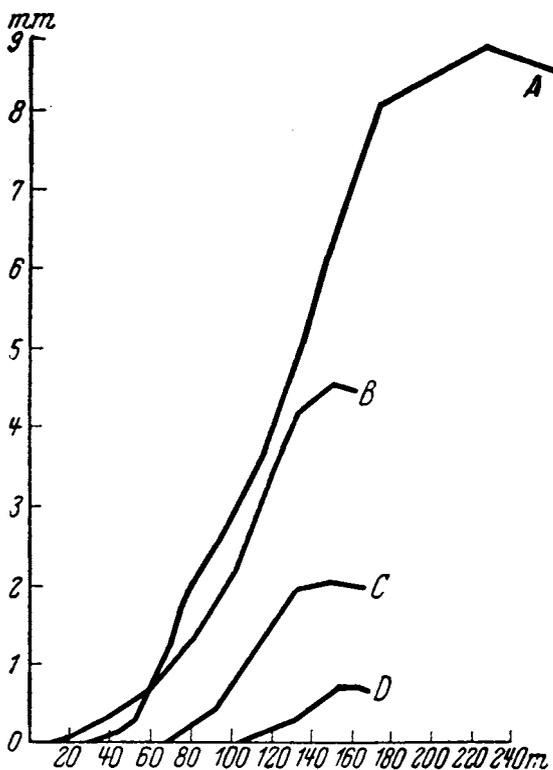


Fig. 5. *Avena sativa*. Bending of seedlings to light, on abscissa time in minutes after exposure; on ordinate millimeters of bending from vertical. A, treated with 700 MCS; B, with 112 MCS; C, with 20 MCS; D, with 5 MCS. (After Arisz.).

I shall review briefly the chief facts with which we are acquainted on the phototropism of oat seedlings.

1st. The oat coleoptile is extremely sensitive to light. This has been elaborated above.

2nd. If exposed for a brief period to light coming from one side and then placed in complete darkness, it will later bend toward the side which had been illuminated. In other words, the time required for the perception of the stimulus and the time required for response to the stimulus are not identical; the perception of the stimulus and the response to it are separate and distinct phenomena. Figure 4 shows the response of etiolated seedlings which had been exposed for 4 seconds to one sided illumination from a lamp of 30 meter candles and then rotated on a horizontal clinostat in the dark. No response is evident at 40 minutes after exposure. At 50 minutes a slight bending at the tip can be noted and this becomes more pronounced as the time increases.

3rd. The perception of the stimulus depends both upon the intensity of the light and upon the time of the exposure; the weaker the light the longer the exposure necessary to produce a response and the stronger the light the shorter the exposure necessary. Blaauw (1909) found that 20 meter candle seconds was sufficient to induce a macroscopically visible response as may be noted in the following Table.

Table 1—The time required to produce a macroscopically visible response in etiolated oat coleoptiles illuminated from one side with light of the intensity shown. (After Blaauw)

Period of Illumination	Light Intensity Meter candles	Product Meter candle seconds
43 hrs.	0.00017	26.3
6	0.00085	18.6
1	0.00477	17.2
4 min.	0.08980	21.6
4 sec.	5.4560	21.8
1/100 sec.	1902.0000	19.0
1/1000 sec.	26,520.0000	26.5

The weakest intensity given in Table 1 is 0.0006 that of full moon light; the strongest is a little over half that of full day light and 0.001 sec. exposure to this light is sufficient to induce a response. It would seem that the oat coleoptile is as sensitive to light as a photographic plate.

4th. The extent of the response varies with the quantity of light and the reaction time also depends to some extent on the amount of the stimulus. The curves in figure 5 show the bending of an oat seedling from the vertical in millimeters after exposure

to various amounts of light. Curve A is the response after exposure to light of 700 meter candle seconds. The bending begins after 30 minutes and the maximum bending is 9 mm. from the vertical. Curve B is for 112 meter candle seconds exposure. Bending begins after 15 minutes and the maximum is 4.5 mm. The response to 20 meter candle seconds is evidenced after 70 minutes and amounts to 2 mm.; 5 meter candle seconds produces a response after 105 minutes and the maximum is less than 1 mm. In fact it has been found that as the amount of light is increased the extent of the bending increases to a maximum and then decreases to zero. With further increases of light the seedling bends away from the light. This negative reaction is followed by a 2nd positive and a second negative. A third positive and a third negative have been reported by some investigators.

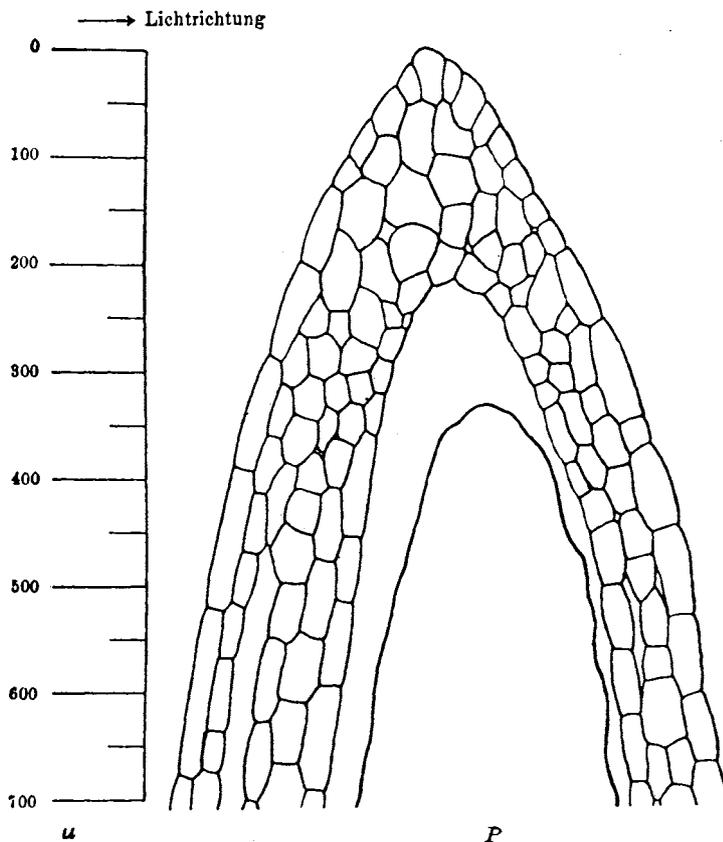


Fig. 6. *Avena sativa*. Median longitudinal section of coleoptile tip. The length in 0.001 mm. is shown on the left. (After Lange).

5th. The tip is the part of the coleoptile most sensitive to light. It may be compared in some respects to a sense organ. It is the perceptive region of the coleoptile. Darwin found this to be true by a simple but ingenious experiment. He covered the coleoptile tip of oat seedlings by caps of black paper, tin foil, or blackened glass, and discovered that such coleoptiles would not bend toward light from one side even though the lower part of the plant was illuminated. Sierp and Seybold (1926) and Lange (1927) investigated this question much more elaborately and more accurately. Lange determined the minimum light necessary to produce a response when a small part of the plant was exposed to light, the balance remaining in darkness. By measuring the area of the part exposed he calculated the light per unit area required to induce a response. The sensitivity he considered to be inversely proportional to the minimum light required per unit area. The first 0.1 mm. of the tip was almost 1,000 times more sensitive than the ninth 0.1 mm.; and the first 1 mm. was almost 2,000 times more sensitive than the third mm. Some of his results are shown in Table 2. The extremely sensitive portion of the tip consists of but a few cells as may be noted in figure 6.

Table II—The sensitivity to light of various portions of the tip of etiolated oat coleoptiles. The minimum light required to produce a response is given in column 2; in column 3 the light per unit area ($10^4 \mu^2$) is given. (After Lange.)

Zone μ	Minimum Stimulus MCS	Minimum Stimulus Per $10^4 \mu^2$ MCS	Sensitivity
0-100	47	154	6475
200-300	35	243	4106
400-500	68	571	1749
600-700	275	2620	382
800-900	817	8470	118
900-1000	1180	12643	79
0-1000	—	—	2304
1000-2000	—	—	14.3
2000-3000	—	—	1.25

6th. The phototropic response is due to unequal growth (elongation) of the two sides of the coleoptile. The shaded side elongates more rapidly than the lighted side, thus bending the plant toward the light.

7th. The stimulus which is perceived primarily by the tip of the coleoptile, travels downwards, the major bending occurring in the base of the coleoptile as may be noted in figure 4. This is evident from the experiments of Lange also; when the tip only was illuminated the response occurred at the base, which necessitates

assuming that the stimulus is transmitted down the coleoptile. If we compare the tip to a sense organ, then the basal portion might be compared to a motor organ. The stimulus perceived by the tip is transmitted downward to the base, where it causes the major movement to occur.

But what is the effect of light on the tip and how is the effect transmitted down the coleoptile? Does light falling on the tip of the plant induce electric currents which moved downward and produce the unequal growth and the resulting bending? Does light cause changes in electrical potential, changes in turgor or permeability? Or does it cause the formation of growth inhibitors or destroy growth accelerators or affect the polarity of the cells or the conduction of food and water?

No answer for these questions supported by experimental evidence was forthcoming until 1910. In that year Boysen-Jensen of Copenhagen reported some simple but fundamental experiments which suggested that phototropism was the result of the movement of a water-soluble substance or substances from the illuminated tip. He made horizontal cuts about half way through the coleoptile tip three or four millimeters from the apex. (Figure 7.) In some he inserted a thin piece of mica or platinum. He then

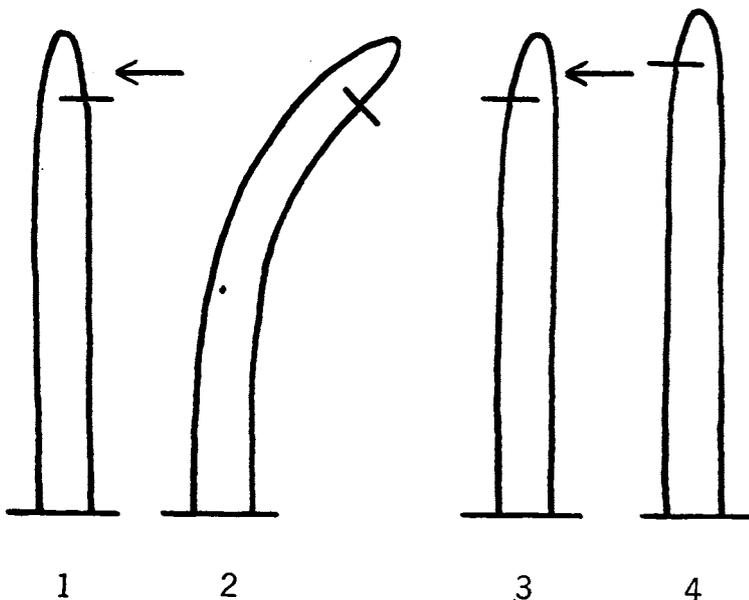


Fig. 7. *Avena sativa*. Diagrams illustrating Boysen-Jensen's experiment suggesting that something travels down shaded side to cause phototropism. 1 and 3 condition at time of illumination; 3 and 4 response. Arrow shows direction of light.

illuminated the tip. If the cut was on the illuminated side a bending toward the light occurred. If the cut were on the shaded side there was no response. The conclusion drawn was that something which would not pass platinum, mica or a dry cut passed from the illuminated tip down the shaded side and caused the lengthening of that side and the bending toward the light.

In addition to these experiments Boysen-Jensen performed one still more enlightening. (Figure 8.) In this experiment he severed the tip completely, covered the decapitated base with gelatine and replaced the tip. When the tip of such a plant was illuminated it bent toward the light. This showed clearly that the effect of the stimulus is transmitted over a discontinuity.

It is worth noting that Boysen-Jensen tried these experiments in spite of the fact that Fitting in 1907 had reported somewhat similar experiments with negative results, probably because the experimental plants were kept in too moist an atmosphere. Under such conditions the cut was filled with water through which the active substance could diffuse. This is worthy of note because it shows the way in which we gain scientific knowledge. In science no man's word is taken as law. What he states as truth must be susceptible to confirmation by others and until it is tested and con-

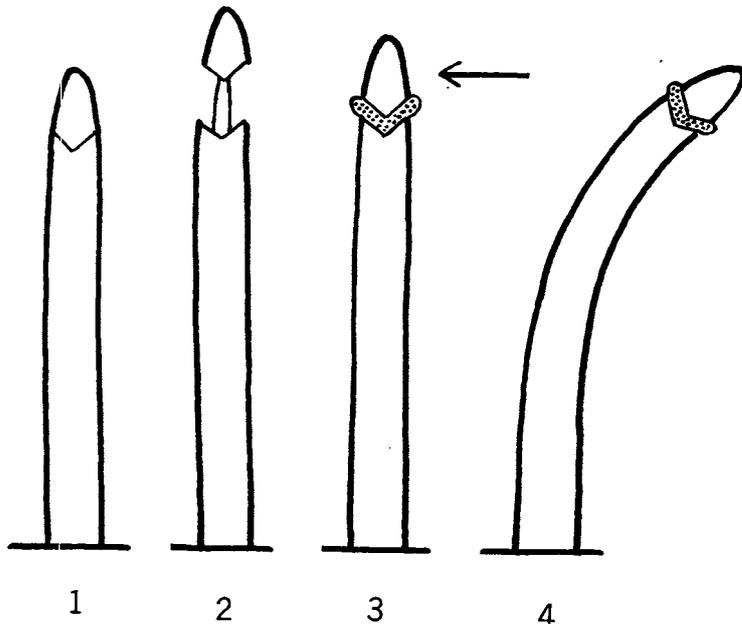


Fig. 8. *Avena sativa*. Diagrams of Boysen-Jensen's experiment demonstrating that the material responsible for phototropism may pass a discontinuity. 1, coleoptile tip severed; 2, tip removed; 3, tip replaced with intervening layer of gelatine and illuminated; 4, response.

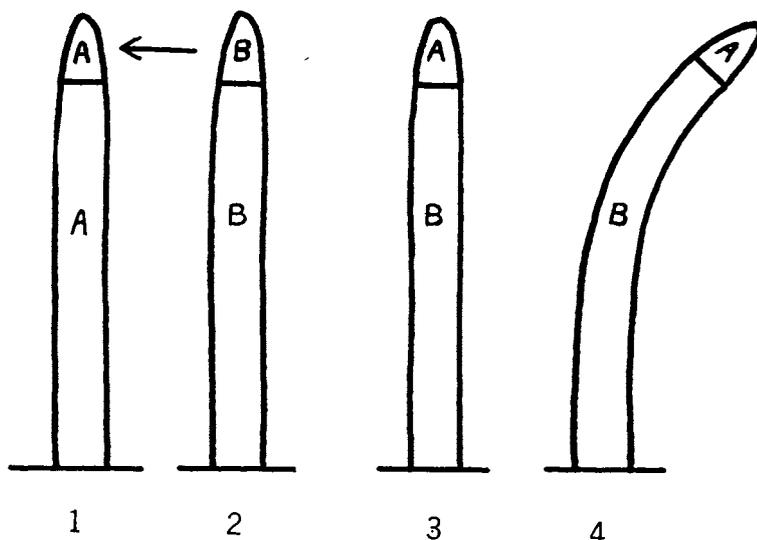


Fig. 9. *Avena sativa*. Diagram of experiments by Stark and Dreschel demonstrating that the tip from an illuminated coleoptile may function on a non-illuminated decapitated base. 1, coleoptile tip illuminated; 2, not illuminated; 3, illuminated tip placed on non-illuminated base; 4, response.

firmed we view it with reserve. In accordance with that principle Boysen-Jensen repeated Fitting's experiments and in turn the botanical world was slow to accept Boysen-Jensen's experiments at their face value.

But confirmation followed. Paál (1914, 1918) confirmed and extended Boysen-Jensen's experiments and showed further that in the dark an amputated tip set on one side of a decapitated base would cause curvature away from the side on which the tip rested.

Stark (1921) and Stark and Dreschel (1922) substituted the tip from a coleoptile stimulated by one sided illumination for the tip of a plant not so stimulated. When this was done the base of the unstimulated plant on which the stimulated tip rested responded as though it had actually received light. (Figure 9.) They found also that the tip of one kind of plant could be substituted for another. Evidence continued to accumulate showing that the explanation for phototropism might be briefly put as follows:

The tip of the oat coleoptile produces a substance which accelerates the growth in length of the coleoptile. When the tip is illuminated from one side this growth substance is unequally distributed, more of it existing on the shaded side. The growth substance diffuses down the coleoptile more of it on the shaded side, where it causes a more rapid lengthening and hence a curvature toward the light.

Purdy (1921) repeated and confirmed Boysen-Jensen's original experiments and extended them to the phenomenon of geotropism.

Söding (1923) observed that a decapitated oat seedling without a tip grew about one-third as much as a decapitated seedling on which the severed tip had been replaced, which suggested that the coleoptile tip produces something which accelerates the growth of the base.

Snow (1924) showed that it was possible to produce a bending away from the light if a severed tip was placed on one side of the base and illuminated from that side.

Boysen-Jensen and Nielsen (1925) found that the light was probably effective, not by destroying the growth substance on the illuminated side or by changing the rate of its movement down the coleoptile but by affecting its movement crosswise; away from the lighted side and toward the shaded side. They split the coleoptile tip lengthwise and inserted a thin piece of glass. When such a tip was illuminated perpendicularly to the glass no response occurred. (Figure 10.) This was interpreted to mean that the growth substance moved transversally in the tip but could not pass the glass barrier. When the tip was illuminated with the glass plate parallel to the light the response was normal.

Stark (1921) and Seubert (1925) showed that it was possible to affect the bending of coleoptiles by placing blocks of agar con-

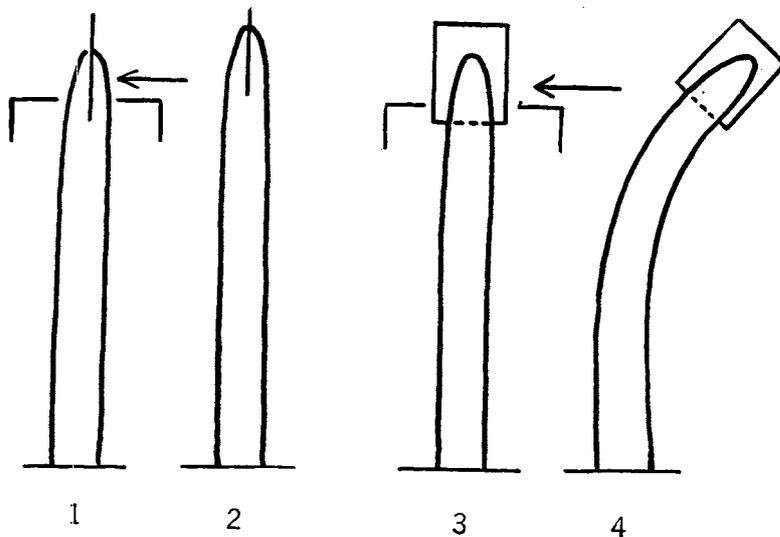


Fig. 10. *Avena sativa*. Diagram of experiment by Boysen-Jensen and Nielsen demonstrating that unilateral light causes substance responsible for phototropism to be transported horizontally to shaded side. 1, tip illuminated perpendicular to glass plate; 2, response; 3, tip illuminated parallel to glass plate; 4, response.

taining tissue extracts, certain salts, diastase or saliva on one side of the decapitated base of an oat coleoptile.

And thus in the years since Darwin's study of the power of movement in plants more and more complete and accurate information on the phototropism of oat coleoptiles accumulated. We continued to learn more and more about less and less; a procedure frequently criticized by socially minded administrators and others, who would apparently prefer to have less and less learned about more and more — a process which I must point out approaches as a limit complete ignorance about everything.

No one knows how much time has been devoted to the study of the responses of this small object to light. Perhaps 500 man-years have been expended on it and if we consider that each investigator must have had preliminary education and training and that minds above the average in intelligence have been devoted to it during their most active and productive years the above figures should probably be doubled or trebled.

I feel sure that many a practical man must have asked what difference it makes whether we know why oat seedlings bend toward light or nor. They would still bend whether we know why they do it or whether we don't. I feel sure, too, that some of those working on the problem haltingly discoursed on the importance of knowledge even of little things, of the value of truth, and of the significance of fundamental research.

At any rate the fundamental experiments of the Dane, Boysen-Jensen, demonstrating that phototropism was probably due to a diffusible substance and the further work of the Hungarian, Paál; the Germans, Stark, Drechsel, Söding and Seubert, and the English, Snow and Purdy, prepared the way for the final and complete demonstration by a Hollander, Went, of the existence in plants of growth substances or growth hormones. In truth science knows no national boundaries.

Although Boysen-Jensen's experiments of 1910 now seem so significant and convincing, not everyone was willing to accept them and the interpretations which Boysen-Jensen had placed upon them.

Brauner (1922) considered the process of bending in response to light to involve.

- (1) Increase in permeability and increase of growth inhibitor on the lighted side.
- (2) Movement of the growth inhibitor down on the lighted side to the growth zones.
- (3) Strong inhibition of growth on the lighted side.

(4) Bending toward the light.

Priestley in 1926 said, "It may be permissible to point out what a pyramid of conceptions are struggling to maintain themselves upon the one general experimental fact — the phototropic response of a coleoptile stump when its severed apex is replaced and alone laterally illuminated."

Priestley then points out the frequency of the exudation of drops of water from coleoptile tips (guttation). He assumed the permeability of the apical tissues of the coleoptile to be increased by light, and, therefore, light falling on the apex to increase apical guttation. Lateral light falling on the apex increases the rate of guttation on the lighted side, decreases the turgor and causes, in his opinion, the bending toward the light. The results of the various decapitation experiments he considered explainable on the basis that decapitation opens the veins and increases water loss.

It remained for Went (1928) to give the final convincing evidence for the occurrence of a growth accelerating substance in plants and its function in phototropism. But note how the way had been prepared for him by Boysen-Jensen's original fundamental experiments, by Paál's and Purdy's confirmation of them, by Stark's and Seubert's use of agar blocks, by the experiments of Snow, Söding and others. Furthermore, F. A. F. C. Went's

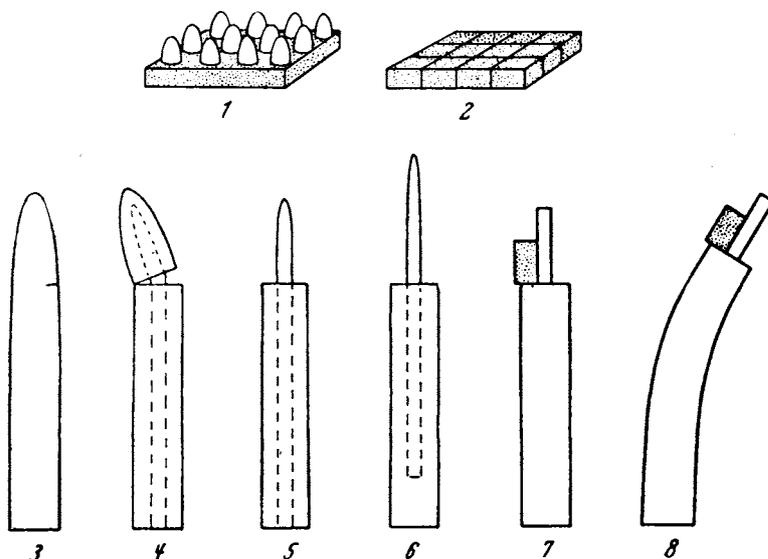


Fig. 11. *Avena sativa*. Method used by F. W. Went to isolate and to determine quantitatively the growth hormone. 1, Agar plate with coleoptile tips; 2, Tips removed and agar plate cut into blocks; 3 to 8, Etiolated coleoptiles decapitated and crowned on one side with agar blocks bend as shown in 8. Experiments carried on in darkness (After FAFC Went in Kostytschew Lehrbuch der Pflanzenphysiologie 2nd Bd.).

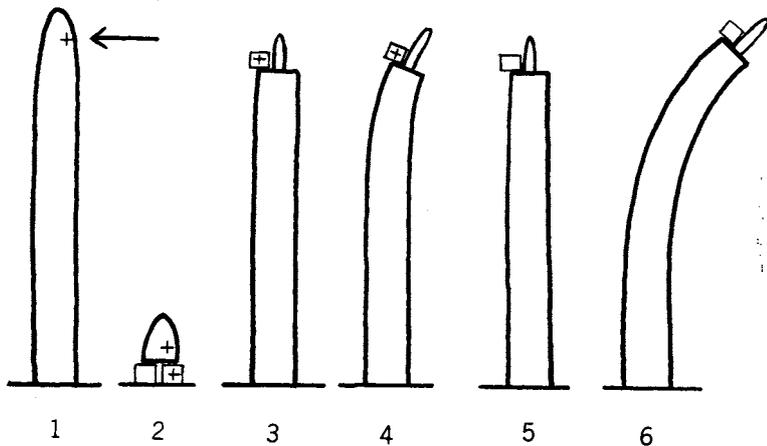


Fig. 12. Diagram of Went's experiment showing more growth hormone on shaded side of coleoptile tip than on illuminated side. 1, tip illuminated; 2, tip removed and placed on two agar blocks; 3, decapitated plant crowned on one side with block from illuminated side of decapitated tip; 4, response; 5, decapitated plant crowned on one side with agar block from shaded side of decapitated tips; 6, response.

laboratory in Utrecht, in which the son, F. W. Went worked, had for many years been concerned with a careful and extended study of phototropism.

Went showed that the active material would diffuse from the coleoptile tip into a block of agar, which would then act as effectively as the tip itself. (Figure 11.) He found it possible to determine the concentration of the growth hormone, by allowing it to diffuse into agar, and then measuring the amount of bending of the oat coleoptile under standard conditions. From its diffusion rate he calculated its molecular weight to be in the vicinity of 376. He demonstrated that the concentration in the tips of illuminated coleoptiles was less than those left in the dark, and that there was more on the shaded side of an unilaterally illuminated tip than there was on the illuminated side. (Figure 12.) The great contributions of Went were the final demonstration of the growth substance and his method of quantitative determination by the use of agar blocks placed laterally on the decapitated base of oat coleoptiles under standard conditions.

From this time on a widening circle of investigators busied themselves with the problem.³ Nielsen (1930) found that *Rhizopus suinus* and other molds produced an active substance, (later identified as β indoleacetic acid which is probably formed from tryptophane). Boysen-Jensen (1931) found that bacteria also produced

³ No attempt has been made to give a complete summary of the voluminous literature on plant hormones. The reader may be referred to Babicka (1934), Boysen-Jensen (1935) and Thimann (1935).

it, Dolk and Thimann (1931) that the active substance in cultures of *Rhizopus suinus* is an acid with about the dissociation constant of acetic acid. Kögl, Haagen-Smit and Erxleben (1931, 1933) found active substances in urine and eventually (1934) isolated three materials in crystalline form, Auxin A, an organic acid of molecular weight 328; Auxin B, a lactone M. W. 315; and heteroauxin or indole acetic acid. Laibach (1932) found considerable quantities of growth hormone in the pollinia of tropical orchids. He prepared (1933) a paste of lanolin containing an acid extract of the pollinia and found the paste effective in causing curvatures. Heyn (1930) found the growth substance was chiefly effective in increasing the plasticity, or ease of stretching, of the cell wall. Skoog and Thimann (1934) reported that auxin A, auxin B and heteroauxin had the same inhibiting effect on the development of lateral buds as does the terminal bud. Avery (1935) found the auxin concentration associated with differential growth in tobacco leaves. Boysen-Jensen (1933) and Hawker (1932) found the differential distribution of auxin under the influence of gravity to be responsible for the movements of roots in response to gravity. Bouillenne and Went (1933) found boiled malt diastase, extract of rice polishings and water extract of cut leaves induced root formation. Thimann and Went (1934) observed that crude auxin preparations from *Rhizopus* and from urine were effective in inducing the formation of adventitious roots. Thimann and Koepfli (1935) found pure indol acetic acid effective. Zimmerman, Wilcoxon and Hitchcock (1935) extended the number of substances which induce curving, overgrowths, epinasty and root formation and used them in both liquid form and in lanolin.

Are these substances, 16 or more, all to be considered plant hormones, or are they effective by influencing the production or functioning of specific growth hormones themselves? How does light cause the lateral movement of the growth hormones in the coleoptile tip? Are there other hormones which affect cell division or the differentiation of plant parts such as flowers? Why do the same substances accelerate the growth of stems and inhibit the growth of roots? How is it possible for the same substance to inhibit the elongation of roots but to favor the initiation of adventitious roots? Are dwarf varieties of plants the result of a deficient production of the growth hormone? For these questions and many others on the phytohormones we have as yet no answer. Scientific knowledge is rarely complete, rarely free from error.

This history, brief and fragmentary as it is, is one more demon-

Be shut forever in an iron sleep,
 Their eyes shall see the kingdom of the law.'
 They could not understand this life that sought
 Only to bear the torch and hand it on." (Noyes)⁴

BIBLIOGRAPHY

- ARISZ, W. H. 1915. Untersuchungen über den Phototropismus. Rec. trav. bot. Nierl. 12:44-216.
 developing leaf of *Nicotiana*, and its relation to polarized growth. Bul. AVERY, G. S. JR. 1935. Differential distribution of a phytohormone in the Torrey Bot. Club 62:313-330.
 AVERY, G. S. AND P. R. BURKHOLDER. 1936. Polarized growth and cell studies on the *Avena* coleoptile, phytohormone test object. Bul. Torrey Bot. Club. 63:1-16.
 BABICKA, J. 1934. Die Wuchsstoffe. Beihefte z. bot. Centrbl. 52:449-484.
 BLAAUW, A. H. 1909. Die Perzeption des Lichtes. Rec. trav. bot. Nierl. 5:209-372.
 BOTTOMLEY, W. B. 1917. Some effects of organic growth-promoting substances (auximones) on the growth of *Lemna minor* in mineral culture solutions. Roy. Soc. London. Proc. B 89:481-507.
 BOUILLENNE, R. ET F. WENT. 1933. Recherches experimentales sur la néoformation des racines dans les plantules et les boutures des plantes supérieures (substances formatrices des racines). Ann. d. jard. bot. d. Buitenzorg 43:1-175.
 BOYSEN-JENSEN, P. 1910. Ueber die Leitung des phototropischen Reizes in *Avena* keimpflanzen. Ber d. deut. bot. Ges. 28:118-120.
 BOYSEN-JENSEN, P. 1931. Ueber Wachstumsregulatoren bei Bakterien. Biochem. Ztschr. 236:205-210.
 BOYSEN-JENSEN, P. 1933. Die Bedeutung des Wuchsstoffes für das Wachstum und die geotropische Krümmung der Wurzeln von *Vicia faba*. Planta 20:688.
 BOYSEN-JENSEN, P. 1935. Die Wuchsstofftheorie und ihre Bedeutung für die Analyse des Wachstums und Wachstums-bewegungen der Pflanzen. 166 pp.
 BOYSEN-JENSEN, P., AND N. NIELSEN. 1925. Studien über die hormonalen Beziehungen Zwischen Spitze und Basis der *Avena*-koleoptile. Planta 1:321-331.
 BRAUNER, LEO. 1922. Lichtkrümmung und Lichtwachstumsreaktion. Ztschr. f. Bot. 14:497-547.
 CLARK, N. A. 1926. Plant growth-promoting substances, hydrogen-ion concentration and the reproduction of *Lemna*. Plant Physiol. 1:273-279.
 DARWIN, CHARLES. 1880. The power of movement in plants. London.
 DOLK, H. E. AND K. V. THIMANN. 1931. Studies on the growth hormone of plants. Proc. Nat. Acad. Sci. 18:30-46.
 FITTING, H. 1907. Die Leitung tropischer Reize in parallelotropen Pflanzenteilen. Jahrb. f. wiss. Bot. 44:177-253.
 HAWKER, L. E. 1932. Experiments on the perception of gravity by roots. New Phytol. 31:321-328.
 HEYN, A. N. J. 1930. On the relation between growth and the extensibility of the cell wall. Proc. Kon. Akad. v. Wet. Amsterdam 33:1045.
 KÖGL, F. UND H. ERXLIEBEN. 1934. Ueber die Konstitution der Auxin a und b. X Mitteilung über pflanzliche Wuchsstoffe. Z. f. physiol. Chem. 227:51-73.
 KÖGL, F. AND A. J. HAAGEN-SMIT. 1931. Ueber die Chemie des Wuchsstoffs. Proc. Akad. Wet. Amsterdam 34:1411.
 KÖGL, F., A. J. HAAGEN-SMIT AND H. ERXLIEBEN. 1933. Ueber ein Phytohormone der Zellstreckung. Reindarstellung des Auxins aus menschlichen Harn. IV. Mitteilung über pflanzliche Wuchsstoffe Z. Physiol. Chem. 214:241-261.
 LAIBACH, F. 1932. Pollenormon und Wuchsstoff. Ber. d. deut. Bot. Ges. 50:383.

- LAIBACH, F. 1933. Versuche mit Wuchsstoffpaste. Ber. deut. bot. Ges. 51:386-392.
- LANGE, S. 1927. Die Verteilung der Lichtempfindlichkeit in der Spitze der Haferkoleoptile. Jahrb. f. wiss. Bot. 67:1-51.
- LOEB, J. 1915. Rules and mechanism of inhibition and correlation in the regeneration of *Bryophyllum calycinum*. Bot. Gaz. 60:249-302.
- NIELSEN, N. 1930. Untersuchungen über einen neuen wachstums-regulierenden Stoff: Rhizopin. Jahrb. f. wiss. Bot. 73:125-191.
- NOYES, ALFRED. 1922. The Torch Bearers. Watchers of the Sky. Frederick A. Stokes. New York City.
- PAÁL, A. 1914. Ueber phototropische Reizleitung. Ber. d. deut. bot. Ges. 32:503-506.
- PAÁL, A. 1918. Ueber phototropische Reizleitung. Jahrb. f. wiss. Bot. 58:406-458.
- PRIESTLEY, J. H. 1926. Light and growth. III. An interpretation of phototropic growth curvatures. New Phytol. 25:213-247.
- PURDY, HELEN A. 1921. Studies on the path of transmission of phototropic stimuli in the coleoptile of *Avena*. Kgl. Dan. Videnskab. Selskab. Biol. Med. 3:1-29.
- ROBBINS, W. J. 1922. Cultivation of excised root tips and stem tips under sterile conditions. Bot. Gaz. 73:376-390.
- SACHS, J. VON. 1882. Stoff und Form der Pflanzenorgane. Arbeit. bot. Inst. Würzburg 2:452-488, 689-718.
- SAEGER, A. 1925. The growth of duck weeds in mineral nutrient solutions with and without organic extracts. Jour. Gen. Physiol. 7:517-526.
- SEUBERT, E. 1925. Ueber Wachstumregulatoren in der Koleoptile von *Avena*. Ztschr. f. Bot. 17:49-88.
- SIERP, H. AND A. SEYBOLD. 1926. Untersuchungen über die Lichtempfindlichkeit der Spitze und des Stumpfes in der Koleoptile von *Avena sativa*. Jahrb. f. wiss. Bot. 65:592-610.
- SKOOG, F. AND K. V. THIMANN. 1934. Further experiments on the inhibition of the development of lateral buds by growth hormone. Proc. Nat. Acad. Sci. 20:480-484.
- SNOW, R. 1924. Further experiments on the conduction of tropic excitation. Ann. Bot. 38:163-174.
- SÖDING, H. 1923. Werden von der Spitze der Haferkoleoptile Wuchshormone gebildet? Ber. d. deut. bot. Ges. 41:396-400.
- STARK, P. 1921. Studien über traumatope und haptotrope Reizleitungsvorgänge mit besonderer Berücksichtigung des Reizübertragung auf fremde Arten und Gattungen. Jahrb. f. wiss. Bot. 60:67-134.
- STARK, P. AND O. DREHSEL. 1922. Phototropische Reizleitungsvorgänge bei Unterbrechung des organischen Zusammenhangs. Jahrb. f. wiss. Bot. 61:339-371.
- THIMANN, K. V. 1935. Growth substances in plants. Ann. Rev. Biochem. 4:545-568.
- THIMANN, K. V. AND J. KOEPLI. 1935. Identity of the growth-promoting and root-forming substances of plants. Nature 135:101-102.
- THIMANN, K. V. AND F. W. WENT. 1934. On the chemical nature of the root-forming hormone. Proc. Akad. Wet. Amsterdam 37:456-459.
- WENT, F. W. 1928. Wuchsstoff und Wachstum. Rec. trav. bot. Neerl. 25:1-116.
- WHITE, P. R. 1934. Potentially unlimited growth of excised tomato root tips in a liquid medium. Plant Physiol. 9:585-600.
- ZIMMERMAN, P. W. AND F. WILCOXON. 1935. Several chemical growth substances which cause initiation of roots and other responses in plants. Contrib. Boyce Thomp. Inst. 7:209-229.

Missouri State University.