GEOTROPISM AND THE GROWTH SUBSTANCE

by

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Kenneth V. Thimann, May 1933).

Section I.

INTRODUCTION.

A brief survey of the extensive literature on tropistic movements of plants shows that the study of the response to stimulus has taught us a great deal about growth. Correspondingly, our increasing knowlegde of the growth process has given us a deeper insight into the essence of tropistic movements. It is therefore no longer possible to separate these two fields of plant physiology.

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[1]) Dr. H. E. Dolk was taken away by an early and sudden death in March 1932 before he could prepare a translation of his thesis, which, entitled „Geotropie en Groeistof", was issued in the dutch language in March 1930. Later his widow, Mrs. F. Dolk-Hoek, and his friend V. H. Thimann secured an abridged english version of it. Its publication, however, was delayed, since original papers had to precede in the „Recueil". The redaction believes that the posthume publication of this valuable work will be wellcome to the foreign readers and dedicates it to the memory of the much deplored author. — Red.

Unlike phototropism, the influence of gravity on growth has been little studied. Various investigators, (Zollikofer, 1921, Renner 1922, Weber, 1927) have attempted to explain geotropic curvatures as resulting from independent geogrowth reactions on the two sides of the organ. It is, however, very difficult to explain these two unconnected growth reactions, since the condition stipulated by Blaauw (1918) for phototropism, namely the occurrence of local unequal stimuli, cannot hold for gravity, the intensity of the gravitational field being always the same. Furthermore, merely to state that the curvature is due to unequal growth on the two sides, does not solve the problem of how these reactions arise.

It appears, therefore, that further analysis of the geotropic reaction by means of growth measurements alone is not likely to be fruitful. A much better insight into the process is obtained by starting from a consideration of the conduction of the stimulus. A historical review of the literature on this subject will not be given here, since reviews have been published by Stark (1927) and by Rawitscher (1932). Briefly, it was proved by Paál (1919) that the tip always exerts a correlative influence on the base of a coleoptile. In the tip a substance is produced which accelerates the growth of the base. This substance, according to Paál, also plays a role in the conduction of the phototropic stimulus (Boysen—Jensen, 1913), its production being decreased by light. On unilateral illumination, there is established a light gradient from front to back of the coleoptile, and this therefore leads to a producion gradient for the growth substance. More growth substance is thus produced at the back than at the front of the coleoptile, and a positive curvature results.

This view fits in well with the Blaauw theory, and I have been able to prove (1926) that both in phototropic and geotropic curvature the growth substance plays an important part. In these experiments it was shown that in decapitated coleoptiles of *Avena*, the regeneration of growth substance in the uppermost zones is coincident in time with the return of geotropic and phototropic sensitivity. Cholodny, while agreeing that growth substance is an important factor in the conduction of stimulus, believed, in opposition to Paál, that the effect of the stimulus is to change, not the production of the growth substance, but its distribution, (Cholodny, 1924, 1926, 1927). Unfortunately, Cholodny was not able to prove the theory, for lack of a quantitative method for determining the growth substance, but at the same time a similar view was put forward independently by

Went Jr. (1928 a). Went worked out a method for determining the quantity of growth substance, and with this method was able to show an effect of light both on the distribution and on the production of the growth substance.

As Went points out, a sharp distinction must be drawn between the influence of a stimulus on the production of the growth substance (later abbreviated to g.s.) and on its transport. An influence on the production will, even if acting equally from all sides, produce a growth reaction, while an influence on the transport will only be observed if acting unilaterally. As mentioned above, Went was able to show that, for light, both these effects occur, and that both take part in a phototropic reaction; the latter being, however, quantitatively far greater than the former. This conclusion has been supported by numerous authors, and is only opposed by Beyer, (1928), whose experiments have been shown by Cholodny (1929 a) to be inconclusive.

In contradistinction to the action of light, few quantitative data are available on the influence of gravity. The principal object of this research was to determine how far the theory of Went and Cholodny could be used to explain the geotropic reaction. In order to do this the following phenomena must be studied:

(a) the influence of gravity on the total growth,
(b) the influence of gravity on the production of g. s.,
(c) the influence of gravity on the distribution of g. s.,
(d) the course („Verlauf") of the reaction,
(e) the possibility of explaining geotropism by means of the data from the first three headings.

An attempt has also been made to explain the so-called „tonus effect" on the curving process, exerted by the component of gravity parallel to the length of the plant. This section is incomplete.

As material, *Avena sativa* and *Zea Mays* were used. The *Avena*, („Siegeshafer"), at first obtained from Svalöv and afterwards grown at Wageningen, was soaked for 2 to 3 hours in water and then placed on moist filter-paper for 24 hours at about 27°, at which temperature the growth of the mesocotyl is much slighter than in the cold. Since exposure of the seeds to bright sunlight was found to shorten the length of the coleoptiles, this germination was later carried out in the dark. The *Zea mais*, almost a pure line, was soaked 8 hours and then germinated on filterpaper in the same way as the Avena, and then planted in earth. All experiments were conducted at 25°, in the dark, at 90% humidity, as described by Went (1928 a).

Section II.

RELATION BETWEEN GRAVITY AND GROWTH.

The problem as to whether the production of g.s. is changed by the influence of gravity is of great importance, since an answer to it would decide whether geotropic curvature is due to (a) a change in the amount of g.s. produced, (b) to a change in its distribution, or (c) to some other stimulus-substances, specific for reactions on gravity.

A. *Relation between growth-substance and growth.*

Before the above problem can be answered, it is necessary to know how far the production of g.s. is a direct measure of growth. The relation between the two can be either:
(a) that g.s. produces only an acceleration of the normal growth,
(b) or that without g.s., no growth at all can occur.

Went was able to show that decapitated coleoptiles, on which g.s. was unilaterally placed, curved, and curved proportionately to the amount of g.s. However, even decapitated plants still grow to some extent, so that it is still possible that while unilateral growth is accelerated proportionally to the amount of g.s., the normal growth is not changed by it. However he also showed that the basal zones of long coleoptiles, in which growth has ceased, were caused to restart growth by the addition of g.s.

In confirmation of the work of Söding (1925), I have previously found (published in Went, 1928 a) that after decapitation growth is greatly reduced, reaching a minimum after 150 minutes, and then restarting. This increase is due to the formation of g.s. in the uppermost zone of the coleoptile. Beyer's claim (1928) that this conclusion was only deduced from the measurements, and not proved, is based on a misunderstanding. On p. 1113 I showed that the uppermost zone of a decapitated coleoptile, cut off after 12 hours and placed unilaterally on a stump gave a definite curvature, whereas when cut off immediately after decapitation, no curvature was produced. This method of detecting the formed g.s. is probably better than that used by Beyer, viz. making a unilateral cut and measuring the resulting traumatotropic curvature, since Weimann (1929) showed that besides the disturbance in correlation (in regard to g.s.) between the two sides, a true traumatotropic effect was also involved. Further (p. 1115, table I) I showed that the above growth accelerating action of the upper zone appears after about 150 minutes, at the same time as the whole decapitated plant shows its growth acceleration. The conclusion was drawn that the increase is due to the action of the upper zone. Later Went (1928 a) was able to extract g.s. from these regenerated tips, thus confirming my conclusions. The failure of Tetley and Priestley (1927) to detect any anatomical change in the regenerated tips proves nothing, since it was never pretended that any anatomical change was involved.

Söding, whose later experiments further confirmed my conclusions, believes that the tip of the coleoptile produces g.s., and that its concentration decreases towards the base, a belief which was shared by Nielsen (1924) and Went (1928 a). If this is true, growth must decrease strongly after decapitation but not entirely cease. If the formation of new g.s. is then prevented by a second decapitation after 150 minutes, the g.s. in the coleoptile will be consumed. Now if growth is proportional to g.s., the growth must fall almost to zero, while if growth is only accelerated by g.s. some residual growth must continue.

The measurements, made in red light at 23° and 85% humidity were carried out with the cathetometer previously used, in which one division of the ocular micrometer = 22.4 μ. The growths of the zone above the earth and of that below the earth („base") were measured separately by means of an ink mark just above earth level (Fig. 1). After decapitation, growth falls considerably but not to zero; the growth of the „base" is relatively less influenced by decapitation than that of the upper zone. This agrees completely with the determinations, made by Söding (1929) of the effect of decapitation on the growth of the upper zone. In these experiments, the parts above and below the earth were 1.5 and 0.5—1.0 cm long, respectively; the mesocotyls were developed to a length of 3 mm. After the second decapitation, growth decreases still more and may reach zero; what growth persists is limited to the „base". In 5 out of 8 cases zero growth was reached, thus confirming Went's opinion (1928 a) that growth cannot occur without g.s.: „Ohne Wuchsstoff kein Wachstum".

Beyer (1928) decapitated coleoptiles twice in the same way, but reached different conclusions, namely, that the growth after decapitation decreases rapidly and then reaches a constant level, this level being that of the residual growth, independent of the presence of g.s. How can this difference be explained? Firstly, the plants used by Beyer were shorter than mine, and therefore contained more g.s. in the base (Went 1928 a, p. 74, and also Söding). Hence the g.s. could not act so rapidly as a limiting

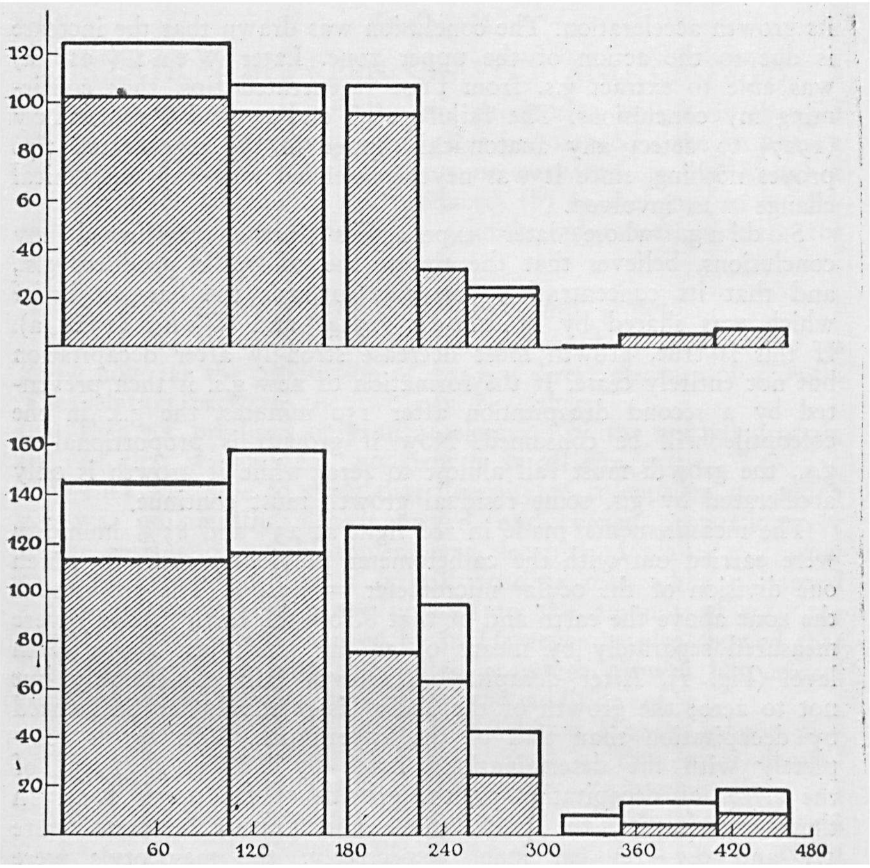

Fig. 1. Growth of coleoptiles before and after decapitation. Abscissae, time in minutes; ordinates, rate of growth in 10 μ per hour. The shaded portion represents the growth of the apical part of the coleoptile, the unshaded portion that of the base. The decapitations are indicated by the breaks in the diagram.

factor. Secondly, Beyer's second decapitation was done far too soon. My former measurements show that even 2½ hours after decapitation the g.s. has not quite all disappeared. Beyer made his second decapitation after 1 hour, and the third after 2 hours, so that g.s. will still remain in the stumps.

That the cessation of growth in the experiments above described is not due to a wound effect is shown in the following experiments, (Fig. 2). In these, agar containing g.s. was placed on the stumps after the second decapitation. When placed centrally growth increased immediately; when placed unilaterally strong (15°) curvatures appeared.

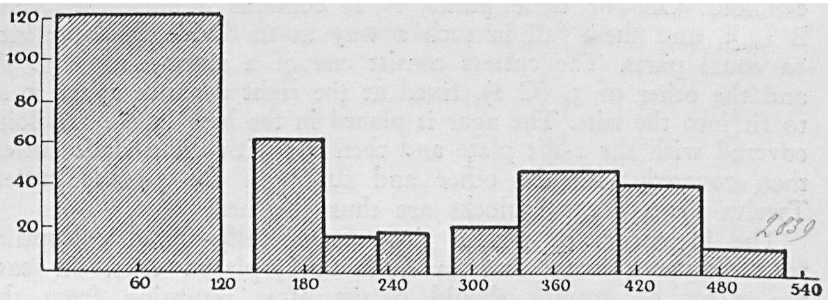

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Fig. 2. Growth of coleoptiles before and after decapitation. Abscissae, time in minutes; ordinates, rate of growth in 10 μ per hour. The decapitations are indicated by the breaks in the diagram. After the second decapitation agar containing growth substance was applied.

B. *Influence of gravity on the production of growth-substance.*

A preliminary study in this field was made by Went (1926) but only roughly. The experiments were therefore repeated using a better method for determination of g.s. (Went, 1928 a.)

This method consisted of cutting off a number of tips and placing them on agar, removing them after a definite time, allowing a further time for the g.s. to distribute itself evenly throughout the ager, and finally cutting the agar into 12 equal parts, which were placed unilaterally on decapitated coleoptiles. For cutting the agar a special instrument was devised, (Fig. 3); a sheet

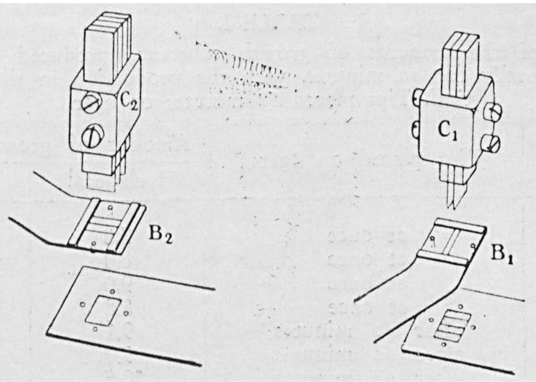


Fig. 3. Explanation in text.

of celluloid has a rectangular hole in it, the exact size of the piece of agar; either of 2 copper plates can be placed on top of the celluloid so that 2 projecting pins in each fit into holes in the celluloid. One of these plates, B 1, contains 2 slits, the other, B 2, 3, and these fall in such a way as to divide the agar into 12 equal parts. The cutters consist one of 2 razor-blades, (C 1), and the other of 3, (C 2), fixed at the right distance apart so as to fit into the slits. The agar is placed in the hole in the celluloid, covered with the 2-slit plate and then cut with the 2-blade cutter, then covered with the other and cut with the 3-blade cutter. Twelve exactly equal blocks are thus obtained.

The formation of g.s. in tips of vertically-placed coleoptiles was compared with that in horizontally-placed ones. In case the effect of gravity should persist after returning from the horizontal position, the g.s. was isolated (a) directly after geotropic stimulation, and (b) after a further period of rotation on the horizontal axis of the clinostat. The plants could not be placed vertical during this further period, since the curvature resulting from the previous stimulus would then introduce a stimulus in the opposite direction. Two series of experiments were carried out, in which the plants were exposed to gravity 10 and 30 minutes respectively. The procedure was not completely described in the earlier communication (Dolk, 1929 a) and was therefore not fully understood by Stark, who, in his review (Zeit. f. Bot. 22, 284) thought the formation of g.s. in vertical coleoptiles was being compared with that in coleoptiles rotated on the clinostat. Stark considered these experiments therefore inconclusive. The results, (Table I and II) show that the production of g.s. in the horizontal

TABLE I.

Comparison of the amounts of growth substance produced in coleoptiles placed horizontally for 10 minutes, with the production in those kept vertical. Tips placed 60 minutes on agar.

No. of tips.	Tips placed on agar:	Amount of growth substance	
		Horizontal	Vertical
6	at once	7.8	8.2
6	at once	8.0	8.2
6	at once	9.0	8.9
8	at once	8.8	8.6
8	after 60 minutes	9.1	9.9
8	after 60 minutes	9.0	8.8
8	after 60 minutes	10.5	10.8

TABLE II.

Comparison of the amounts of growth substance produced in coleoptiles placed horizontally for 30 minutes, with the production in those kept vertical. Tips placed 60 minutes on agar.

No. of tips.	Tips placed on agar:	Amount of growth substance	
		Horizontal	Vertical
8	at once	10.3	10.1
8	at once	8.4	8.4
8	at once	5.5	6.4
8	at once	2.2	2.8
8	at once	7.8	7.9
8	after 60 minutes	9.0	9.0

position is exactly the same as in the vertical position, confirming Went's original approximate findings. The differences between the determinations are not only so slight as to fall well within the experimental error, but are also of different signs. These experiments also make it highly improbable that specific stimulus substances play any part in the gravitational stimulus (top of Section II, alternative c), for should the geotropic stimulus produce in the lower side a substance which accelerates growth, then it must produce in the upper side a substance which retards growth in the same ratio, so that the total growth is unchanged. These results are not in accord with those in the literature, which indicate a true „geo-growth reaction". It is, of course, possible that gravity may influence another phase of the growth process, in the same way as light does. According to du Buy and Nuernbergk (1929 b) light has an influence on the cellwall as well as on the g.s. transport. Van Dillewijn (1927) believes light to have an influence on the permeability of the cell, and Sierp and Seybold (1926) believe in an influence on the growth itself as well as in the g.s. production. F. W. Went (1925) considers the growth reaction of the base to result from a direct influence of light on growth, and thinks the case may be the same for gravity, (cf. also Jost and Wissmann 1924). It was therefore of interest to study the influence of gravity on the growth itself.

C. *Influence of gravity on growth.*

A survey of the literature on the influence of gravity on the growth of various parts of plants reveals that different investigators of this subject have arrived at various and opposing conclusions. The reason for this lies in the fact that different experimentators have used different objects, and also that the methods used were very primitive and sometimes even wrong in principle. It seemed therefore desirable to make a further investigation in this field.

1. *Methods.* It must be borne in mind that growth reactions are frequently sinusoidal, i.e. consist of an acceleration and a retardation, so that if the increase in length of a plant is determined only over long time intervals, it is possible for the growth reaction to become obscured. Measurements must therefore be made over as short a time interval as possible. For this purpose the cinematographic camera may be used, as was done by Lundegardh (1918) and Buder (1926). An objection to this is that measurements cannot be made during rotation on a clinostat. The auxanometer of Koningsberger (1922) is however very suitable and was therefore used. Koningsberger has already made a series of measurements of the geogrowth reaction. His measurements have been criticised by Bremekamp (1925), who points out that if a plant, on the horizontal axis of the clinostat, curves in the dorsoventral plane, the tip is no longer perpendicular to the gold contact-plate of the auxanometer, and has therefore to travel further to reach it. This would register as an apparent retardation of growth, and when the plant is replaced vertically the subsequent straightening will appear as an acceleration of growth. For exact data such dorsoventral curvature must therefore be excluded. This was first attempted by use of the intermittent clinotsat, the plants being so placed that gravity acted always perpendicularly to the plane of symmetry of the coleoptile. If the dorsoventral curvature arises from unequal sensitivity of the coleoptile to gravity in different planes, no curvatures should then result. However, the plants were found still to curve in the dorsoventral plane. It follows that dorsoventral curvature is autonomic, as was thought by Lange (1925) and Pisek (1926).

Since dorsoventral curvatures could not be excluded in this way, use was made of the method described by van Dillewijn (1927). This is designed to exclude small nutations, since even nutations invisible to the naked eye cause distinct irregularities in the registration of growth. Van Dillewijn allows the coleoptiles to grow through a very narrow ring, so that the part immediately below the tip is fixed. With this method growth proved to be absolutely constant, and even after 1 hour's rotation on the horizontal axis of the clinostat no curvatures appeared. The auxanometer was mounted on the clinostat of de Bouter (F. A. F. C. Went, 1922) which has the advantage that even with very excentric loading the rotation remains regular. The time for a complete rotation was 6 mins., ant the total growth in each 6 mins. was noted, i.e. the increase in length was determined between successive returns of the coleoptile to the same position, and hence the mistake pointed out by Koningsberger, viz. the apparent irregularity in growth caused by sagging of the coleoptile, was avoided. The plants were grown in cylindrical zinc boxes which were fixed to the auxanometer with a screw clamp. The occurrence of slides in the earth immediately after changing the position of the coleoptile, which appeared as small jumps in the growth record, was largely but not entirely avoided by placing over the earth a small perforated brass plate which by means of a spiral spring pressed the earth firmly in place. Immediately after the plant had been fixed to the auxanometer rotation was begun on a vertical axis; after a few hours, when growth had become completely constant, the axis was turned through 90° and rotation continued. Two series of experiments were carried out each consisting of a great many determinations, the horizontal rotation times being 30 and 60 mins. respectively. This was done in order to eliminate the „manipulation reaction" of Zimmermann (1927 a). It was, in fact, found that both on placing horizontal and on replacing vertical small growth irregularities, not always in the same direction, occurred. By taking the mean of all experiments, (Fig. 4 & 5), these variations were almost completely eleminated. If the growth reaction were truly sinusoidal but with the peaks of the curves occurring all at different times, the mean of a number of experiments would result in the effect being cancelled out and would therefore not be allowable. However, the variations found were absolutely irregular, showing no signs of sinusoidal shape, and furthermore, many plants showed absolutely no change after rotation on the horizontal axis. In figs. 4 & 5 the first measurements after the change of axis are not included, since for the reasons above, they

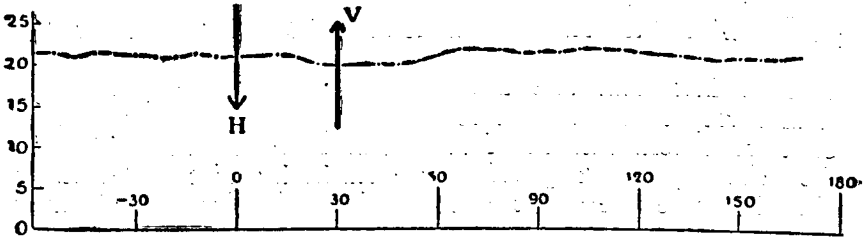


Fig. 4. Mean growth of coleoptiles before and after rotation on the horizontal axis of the climostat. Abscissa, time in minutes; ordinate, growth rate in μ per minute. At H, placed horizontal, at V, vertical. Rotation for 30 minutes. Mean of 13 reactions.

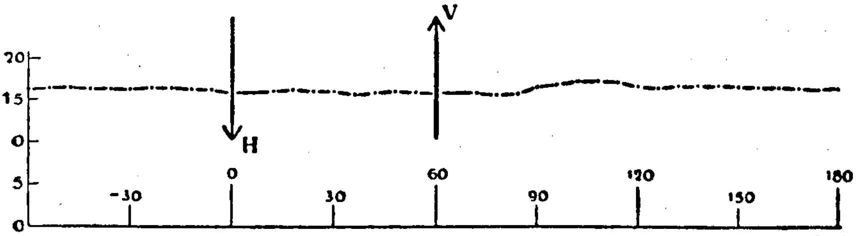


Fig. 5. As Fig. 4. Rotation for 60 minutes. Mean of 19 reactions.

are not reliable. It is clear that no considerable growth reaction occurs either after placing horizontal or after replacing vertical. To the very slight increases in growth which appear after replacing vertical I dare not attach significance; they are probably due to very slight nutations. *There is therefore no geogrowth reaction.*

The results of Koningsberger, which indicate the existence of a geogrowth reaction, are probably due to the appearance of autonomic curvatures during rotation in the horizontal axis. Some experiments were therefore carried out in which the plants were absolutely free under the contact-plate of the auxanometer (table III). In this case, after replacing the plants vertical, the growth

TABLE III.

Growth of a coleoptile standing freely under the contact-plate of the auxanometer, before and after rotation on the horizontal axis of the clinostat. Rotation for 30 minutes. At ↓ placed horizontal, at ↑ vertical.

Minutes	0					30						60		
									horizontal			↑	vertical	
Growth in μ per minute	16.5	16.8	17.0	17.8	17.5	↓	17.8	17.7	17.3	17.2	15.7		14.8	15.3

Minutes			90					120					150
Growth in μ per minute	14.5	13.8	14.0	16.0	18.0	18.2	20.5	20.5	19.5	18.7	18.3	18.2	17.5

becomes inconstant and a „growth acceleration" appears. The figures vary rather widely. It must be pointed out that in none of these experiments the dorsoventral curvature was visible to the naked eye, — a proof of the sensitivity of the method of Koningsberger, but also proof of the extreme slightness of curvature needed to affect the results.

2. *Discussion of results and comparison with those in the literature.*

It was pointed out above that different investigators in this field have arrived at different results, principally on account of the very different methods used, to some of which serious objections can be raised. Some of the earlier, cruder, experiments will not be discussed at all here, since they were carried out with many different objects. The observation of Luxburg (1905) that, on being suddenly placed horizontal, coleoptiles of *Avena* and *Triticum* showed no change in growth is in complete agreement with my own results. Unfortunately, however, Luxburg measured the growth over a short time only, since he restricted himself to the period of the reaction time, before curvature commences. His results therefore indicate nothing as to the relation between growth and curvature. That Zollikofer (1921) obtained completely different results is probably due to faults in he methods. To measure the total growth of a curving plant by means of a horizontal microscope, in which only a part of the plant is visible, is certainly very difficult. Koningsberger correctly points out the large error which would necessarily arise from the necessary shifting of the object with respect to the microscope. It is also remarkable that her results vary so widely. The growth seems to be sinusoidal but no regularities can be detected. The differences between my results and those of Koningsberger have already been discussed; his results were also rather irregular. In those of his experiments which were continued over long periods dorsoventral curvatures have without doubt obscured the true course of the reaction.

The experiments of Zimmermann, (1927 b), indicating a growth acceleration when roots of *Lepidium* are inverted, seem to be in conflict with my results. The growth acceleration found, as mean of 10 reactions, was however slight. Inspection of the separate experiments shows that a clear reaction was only given by one root. In most of the roots growth was very irregular both before and after inversion. The resulting impression is that this is a case of the „Manipulationsreaktion" and that the mean of a larger number of experiments would have shown no effect. The experiments of Weber (1927) on the influence of gravity on the total growth of *Avena* and *Hordeum* were carried out with somewhat different methods. The coleoptiles were grown in glass tubes into which they just fitted, as described by Schtscherback (1910). After having been placed horizontal for some 30 minutes, which is about the geotropic reaction time, strong retardation occurred, and on replacing vertical a considerable acceleration was found. Weber compares this growth reaction with those found by Koningsberger, but his results are in my opinion due to the „straitjacketed" state of the coleoptiles. Weber himself states that the tip of the coleoptile was so close to the glass that accurate observations of it were impossible on account of the refraction. In later observations he adjusted the coleoptile so that the tip just protruded from the glass, but even this did not prevent a certain amount of sticking. The growth in these experiments was so far removed from normal that the results can scarcely be considered as significant. Schtscherback had previously found that growth almost stops in glass tubes. In those experiments in which Weber measured the increase in lenght of the centerline of freely curving coleoptiles, almost no change in growth was found. Where a slight change did occur, the growth was somewhat irregular before placing horizontal. Comparison of his figures 5 and 11 shows that the plants in the glass tubes have given a much greater acceleration after replacing in the vertical position than those which were free to curve. Weber's conclusion, therefore, that the growth changes in coleoptiles are the same whether they are confined in glass tubes or free to curve, is not justified.

The experiments of Nemecek (1924), in which geotropic curvatures were also eliminated by growing in glass tubes, are open to the same objection. Although he himself was clearly aware of this, he still considers the growth changes found to be due to the geotropic effect. On the other hand, the results of Cholodny (1929 b), although obtained in quite a different way, are in complete agreement with my own. Cholodny measured not elongation, but increase in volume, before and after placing horizontal. This was done by determining the water uptake under conditions in which transpiration was prevented. Hypocotyls of *Helianthus* and *Lupinus* showed no change in growth under these conditions.

Section III.

INFLUENCE OF GRAVITY ON GROWTH-SUBSTANCE DISTRIBUTION.

Since it was shown above that neither growth nor the production of g.s. were influenced by gravity, the influence of gravity on the distribution of g.s. was next investigated. This involves measurement of the amounts of g.s. passing downwards on the two sides of a coleoptile exposed to gravity.

A. *Method.*

To separate the amounts of g.s. being transported on the two sides of the coleoptile, the following instrument was constructed (Fig. 6).

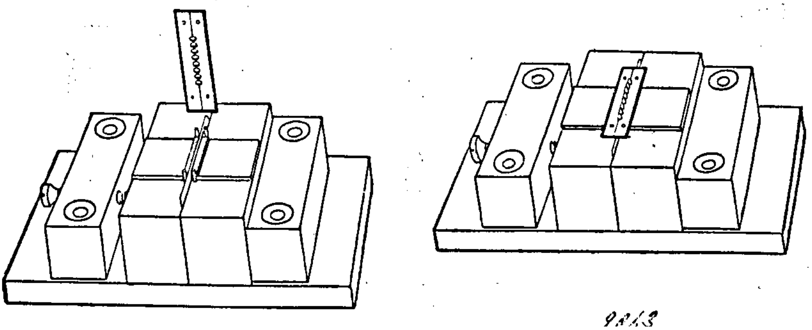


Fig. 6. Explanation in text.

Two blocks of ebonite, between which a sharp razorblade protruded about 2 mm, were pressed together by means of a screw. On either side of the razor blade a coverslip was fixed to the ebonite, and on these were placed small strips of agar, above which the razor blade thus protruded about 0.25 mm. In order to place the tips centrally over the blade, they were slipped through holes in a platinum plate, which was provided with a groove fitting just over the blade. The platinum was kept in place by means of pins in the ebonite. The top of the platinum was covered with another, very thin, plate of ebonite, since a dark surface facilitated the placing of the tips in the weak red light used. A very thin coating of paraffin on both razor-blade and platinum plate prevented diffusion of g.s. from one side to the other by capillarity. A number of coleoptiles, grown in earth, were placed horizontal in such a way that gravity was acting perpendicular to the plane of symmetry. After a definite time the coleoptiles were decapitated and the tips placed in the apparatus so that all those sides which had been lower were to the left and those which had been upper were to the right. After leaving for some time on the agar, the tips were removed and the amount of g.s. in the agar determined in the usual way.

B. *Experiments on tips.*

Results from the first series of experiments, carried out with *Avena,* are given in table IV. A distinct difference between the

TABLE IV.

Distribution of growth substance in tips of Avena coleoptiles after horizontal stimulation.

Time horizontal in seconds	No. of tips	Time on agar in minutes	Amount of growth substance	
			Upper side	Lower side
660	6	60	8.5	9.5
1800	6	90	2.0	6.2
1800	6	90	7.8	9.0
1800	7	60	4.4	7.0
1800	8	60	3.0	6.2
1800	8	60	3.2	4.0
1800	8	60	2.4	9.0

amounts of g.s. in the two sides is apparent, more g.s. always coming out from the side which had been the lower. The sum of the amounts of g.s. on the two sides was found to be about the same as the total amount in controls which had not been placed horizontal. The rather wide variation in the results is attributed to the experimental errors, since in spite of all precautions the tips were probably not placed exactly centrally over the razor-blade. As an error of this kind would have a greater effect, the smaller the coleoptiles, the experiments were repeated with *Zea Mays,* whose tips are about three times as large. The resulting error should therefore be three times as small. To determine whether the g.s. from *Zea Mays* can in fact be measured with *Avena,* 8 tips of mais were first placed for 60 mins. on agar. This was then divided into 12 and placed unilaterally on decapitated coleoptiles of *Avena.* Curvatures of 20.5° resulted. The growth substance is therefore not specific, as has already been shown by numerous investigators. The amount of g.s. in mais tips is furthermore rather large, — about three times that in *Avena,* — and mais was therefore used later for the isolation of g.s. for various experiments.

In table V the results are given of the experiments with *mais* tips. Here also in every case the amount of g.s. diffusing out from the under side is greater than that from the upper side. The differences are considerable, but even here the data vary rather widely. This variation may be partly due to the inadequacy of the method, since the g.s. may be partly transferred from one agar plate to the other by capillarity. Later, however, another explanation for these variations was found. As will be shown in the next section, geotropic sensitivity is not confined exclusively to the tip, but is also present to some extent in the lower zones.

TABLE V.

Distribution of growth substance in tips of Mais coleoptiles after horizontal stimulation.

Time horizontal in seconds	No. of tips	Time on agar in minutes	Amount of growth substance	
			Upper side	Lower side
2700	5	60	12.4	19.5
1800	4	60	9.6	14.0
1800	4	60	10.5	16.2
1800	4	60	13.4	16.7
1800	4	60	8.3	22.5
1800	4	60	6.3	11.2
1800	4	60	2.5	8.5
900	4	60	4.6	8.7
1800	4	60	2.6	6.6
900	4	60	2.5	5.3
1800	4	60	3.2	7.0
1800	6	60	12.7	14.6
1800	6	60	12.3	16.7

The asymmetric transport of g.s. will therefore also be spread over some distance in the coleoptile. Since the length of the tips in the above experiments was never quite the same, asymmetric transport will have occurred to varying extents. This explains, in large part, the variations in the results of tables IV and V. It was in fact found that the longer the tips the larger the resulting difference in g.s.

Following on the experiments described in section 5, an attempt was made to determine how long the asymmetric transport of g.s. persists, after the application of the stimulus has ceased. Coleoptiles of *Avena* were placed horizontal for 30 mins. then

TABLE VI.

Distribution of growth substance in tips of Avena coleoptiles, after horizontal stimulation and subsequent rotation on the horizontal axis of the clinostat.

Time horizontal in seconds	No. of tips	Rotation time in minutes	Time on agar in minutes	Amount of growth substance	
				Upper side	Lower side
1800	6	64	105	5.0	4.7
1800	7	60	90	5.8	5.6
1800	7	60	90	6.7	7.0
1800	7	60	90	6.8	6.6
1800	7	60	90	5.3	5.7
1800	7	60	90	11.0	10.6
1800	7	60	90	10.2	12.5

rotated for 60 mins. on the horizontal axis of the intermittent clinostat; the amounts of g.s. in the upper and lower sides of the tips were then determined as before. Table VI shows that the same amount of g.s. diffused into the agar from each side, i.e. the asymmetric transport soon ceases. These experiments are discussed further in section V.

C. *Experiments on coleoptile cylinders.*

After having established that geotropic perception is also located in the lower zones (see section V), I endeavored to demonstrate that asymmetric transport of g.s. also occurs in these zones. The tips of a number of *Avena* coleoptiles, grown in earth, were cut off at a length of 1 mm. The upper 2 mm of the stumps was then cut off so as to leave the primary leaf in place. In these coleoptile cylinders g.s. transport is easily demonstrated, (Went 1928 a) by placing them on agar and placing another piece of agar, containing g.s., on top of them. The g.s. diffuses through the cylinders to the lower piece of agar, in which it can then be determined. To study the influence of gravity on this transport, use was again made of the apparatus in Fig. 6, but with the razor-blade now protruding 0.5 mm above the agar so that the coleoptile cylinders could be ifxed on to it by a slight pressure. On each cylinder was placed a small piece of agar containing g.s. and the whole apparatus was then turned through 90°. After 90 mins. the cylinders were removed and the amount of g.s. transported through each side was determined. Table VII shows that the g.s. transport has been changed by the influence of gravity. More g.s. came out at the side which had been lower that at that which had been

TABLE VII.
Distribution of growth substance transported through horizontally-placed cylinders of Avena coleoptiles.

Time horizontal in seconds	Amount of growth substance applied to cylinders	Amount of growth substance obtained	
		Upper side	Lower side
120	11.7	6.3	9.8
120	11.7	7.5	10.3
120	9.5	4.0	8.8
126	9.5	6.5	8.0
120	16.3	6.3	8.8
120	16.3	3.4	6.8
120	16.3	3.8	8.8

the upper. Another point of importance in these experiments is that controls showed that no g.s. was formed in the cylinders. Gravity, therefore, can here only have influenced the transport. To the experiments with the tips the objection can always be raised that gravity can still have influenced the actual production of the g.s., the increase in amount on the lower side being at the expense of a corresponding decrease on the upper side, so that the total production remains unchanged. The experiments with the cylinders render this explanation highly improbable.

D. *Discussion of results and literature.*

1. These results make it clear that, while the total growth does not change during a geotropic curvature, its distribution does. In this respect geotropic curvature differs from phototropic, for the effect of light is to influence both the total growth as well as its distribution.

2. The unequal distribution of growth is due to an unequal distribution of g.s. Gravity induces a „polarity" in the cells of the coleoptile, so that the transport of g.s. becomes „polar". The word „polarity" here has no special significance in regard to the actual nature of the process, but is used only in the sense of Zimmermann (1927 a) as indicating an axis with two unequal poles.

3. The coleoptile, in regard to its production of a geotropic curvature, must be considered as a whole, i.e. the two sides are not independent, but react together in harmony.

The published data on the growth of the different parts of horizontally-placed plants show that most investigators have reached the same conclusion, namely, that the negatively geotropic parts show a growth acceleration on the lower side and an accompanying retardation on the upper. Positively geotropic parts show the reverse effect, (Sachs 1873 b, Noll 1888, Luxburg 1905, Schtscherback 1910 and Weber 1927). As to the quantitative relationship between the acceleration and the retardation, opinions are divided. This growth distribution is now explained as due to the unequal distribution of the g.s.

To explain geotropic curvature on the basis of the action of specific stimulus substances, as has been suggested by some other investigators, becomes correspondingly more difficult. Pürdy (1921) draws the conclusion form her experiments that the conduction of the geotropic stimulus takes place only in the lower part of the coleoptile, — an opinion which was at one time shared by Stark (1927). How Purdy can explain the growth retardation which occurs in the upper part of the coleoptile is not clear, since, as explained op p. 517, it would be necessary to assume the formation of a growth retarding substance. That her experiments were inconclusive, since she takes no account of the regenerative processes following the wounding, has been pointed out by numerous writers, among others by Beyer (1928). Working on the horizontally-placed stems of the *Labiatae,* Gradmann (1925) considers that the growth-accelerating substance is only formed in the lower side. To explain the retardation in the upper side he invokes the statolith theory. In his opinion the growth-accelerating substance is only formed when the statoliths are pressing against the tangential wall of the cell. Owing to the fact that, in the normal vertical position, the statoliths still exert a slight pressure on the tangential wall, small amounts of the growth-accelerating substance are still produced. On placing horizontally, this pressure on the tangential wall ceases altogether in the upper half, and this explains the resulting slight retardation in this half. This view is shared by Zimmermann (1927 a). Such an explanation for the occurrence of a growth retardation is, in my view, highly hypothetical, particularly when it is considered that the pressure which will be exerted on the tangential wall when the plant is vertical must be extremely small, while on the other hand the growth retardation, when placed horizontal, is very great. It has also been shown by Cholodny (1927) that split stalks, placed horizontally with the cut surface downwards, are certainly able to undergo geotropic curvature, while on the view of Gradmann this would be impossible. Similar results were obtained with split coleoptiles by Weber (1927).

Both Zollikofer (1926) and Beyer (1928) have advanced theories on the mechanism of geotropism, but in neither case do these theories explain all the facts. Brauner (1923), whose conclusions were confirmed by different experimental methods by Seubert (1925), and Went (1926), showed that the g.s. from the tip was indispensable for the production of geotropic curvature in the coleoptile. However, this did not prove that the g.s. plays a direct role in the formation of a geotropic curvature. It was still possible to claim, with Stark (1927) and Zimmermann (1927 a), that the substance simply accelerates growth and thus allows geotropic curvature to take place, i.e. the action of the g.s. is one of „tonus" production. The same explanation could have been given for some, at any rate, of the experiments of Cholodny (1926).

Many investigators have tried to show that in plants exposed to geotropic stimulus, the behaviour of the two sides is independent. Sachs (1873 b) showed that in stems split lengthwise with the cut surface downwards the upper half shows a retardation in growth and the lower half an acceleration. These experiments have been frequently repeated, always with the same results, (Copeland, 1900, Schtscherback 1910, Weber 1927), so that the facts must be considered established. It is, however, questionable whether the reactions of split stems are comparable with those of intact plants. This objection has been raised both in my previous communication (1929 a) and by Cholodny (1928). If geotropic curvature results from a change in the direction of transport of the g.s., then in the split stem the g.s. of the upper half will become concentrated in the cut surface, where its action will be obscured by the growth-retarding action of the wound (Schtscherback). On the other hand the g.s. of the lower half is concentrated in normal tissue and can consequently produce a reaction there. There are indications that this view is correct. Thus Cholodny (1927) showed that a split stem placed horizontal with the cut surface downwards shows no geotropic curvature until after 36 hours, by which time the tissue has to some extent recovered. One may also conclude, indeed, from the experiments of Schtscherback that there is a movement of g.s. towards the cut surface. When hypocotyls of *Lupinus* were split in such a way that one half contained the central cylinder, (in which, according to Cholodny, the g.s. is produced) only this half grew, while the other half, consisting only of cortex, stopped growing. Such stems placed horizontally with the larger half on top showed two different phenomena; (a) only the upper half curved, the lower half remaining straight, or (b) both halves curved, the resulting total curvature appearing like that of a normal plant. In the first case the contact between the two halves was incomplete, while the second type of curvature resulted when precautions were taken to insure good contact. This shows clearly that some substance is interchanged between the two halves, and therefore that they cannot be considered as acting independently.

The same conclusion can be drawn from the experiments of Gradmann (1925). In these, split stems of *Labiatae* showed distinct geotropic curvature when the two halves were tied tightly together, but when they were separated by tinfoil the curvature was much slighter. Gradmann claims that the stimulus substances, formed in the lower half, diffuse into the upper half, but in the view expressed here the decrease in curvature is due to the fact that g.s. from the upper half cannot diffuse into the lower half.

It is clear from the above that experiments with split stems are susceptible of quite different interpretations, but the conclusion that geotropic curvature is the result of independent action of the two sides, — a conclusion arrived at by all these investigators, and shared by Zimmermann in his review (1927 a), — is entirely unjustified. On the contrary, all these data show that geotropic curvature can be completely explained on the theory of Cholodny and Went. An exception may be made in those cases where geotropic curvature takes place by means of nodes, since in these cases my view is that a change in total growth is involved.

Section IV.

DISTRIBUTION OF GEOTROPIC SENSITIVITY IN THE COLEOPTILE.

A. *Introduction.*

Since the amounts of g.s. diffusing on the two sides of the coleoptile can be determined quantitatively, it had been hoped that a quantitative explanation of geotropic curvature could be arrived at on this basis. However, tables IV and V show that the results are too variable for this to be possible. The reason for this great variability was found by studying the behaviour of stumps which were decapitated for isolation of the g.s., after geotropic stimulus had been applied. Such stumps are still capable of curving geotropically, as has been frequently reported (Rothert 1896). It follows from this fact that a part of the curvature of intact plants occurs independently of the g.s. in the tip. From a measurement of the g.s. in the tip only it would therefore be impossible to calculate the resulting curvature. Nevertheless, since the experiments reported in the previous section show that the tip has at any rate a marked influence on the curvature, experiments were carried out to determine the extent of this influence.

A number of coleoptiles of *Zea Mais* were stimulated by placing them horizontally for 30 minutes, and thereafter rotated on the horizontal axis of the clinostat. Some of the coleoptiles were decapitated immediately after stimulation and the remainder 60 mins. later. After a time the coleoptiles were photographed and the curvatures measured. Table VIII shows that plants decapitated 60 mins. after stimulation give greater curvatures than the others. The difference between the two sets of curvatures is a measure of the influence exerted by the tip during the 60 mins. Now table V has shown that the amounts of g.s. in tips placed on agar for 60 mins. after stimulation are unequal on the two sides. From the differences therein found it should be possible to calculate the differences in curvature given in table VIII, since the unequally distributed g.s. in the tips will have diffused into the base during the 60 mins. By repeating these experiments accurately it had been hoped to make a quantitative comparison between these differences. Unfortunately, however, closer consideration showed that this would be impossible under the existing conditions, since in the experiments of the previous section the tips remained vertical on the agar, while in the experiments described here they were horizontally rotating. We shall see in section VII that gravity acting on the longitudinal axis of the plant has a marked influence on any geo-induction which has taken place previously. The distribution of g.s. will therefore be different according to whether the tips have stood vertical or have been rotated on the horizontal axis of the clinostat. In order to make comparisons, the isolation of g.s. from tips would have to be carried out on the horizontal axis of the clinostat also. This involved very great technical difficulties and such experiments were therefore not carried out. It is also impossible to leave the

TABLE VIII.

Geotropic curvature of coleoptiles of Zea Mays stimulated horizontally for 30 minutes and then at once rotated on the horizontal axis of the clinostat. Some of the coleoptiles were decapitated immediately after stimulation, the others 60 minutes later.

No. of coleoptiles	Time decapitated in minutes after stimulation	Time photographed	Curvature	Difference
11	0	135	26.7	5.1
11	60	135	31.8	
10	0	120	29.1	11.6
9	60	120	40.7	
8	0	150	19.6	6.2
8	60	150	25.8	
15	0	120	16.8	14.3
12	60	120	31.1	
3	0	145	16.0	8.7
3	60	145	24.7	

plants vertical after stimulation, since the curvature will have already begun in the 60 minutes and an opposing geo-induction will have consequently set in.

What is the explanation for the curvatures of coleoptiles which have been decapitated immediately after stimulation? It is possible that, while in the horizontal position, the unequal distribution of g.s. in the tip has already reached the base. If this is the case, then decapitated coleoptiles should show no curvature when the stimulation time is short, and there should be a corresponding quantitative relation between curvature and the distribution of g.s. in the tip. Coleoptiles of *Avena* and *Zea Mais* were therefore stimulated for short times on the centrifuge, using 1—5 minutes at 5 tot 10 times gravity. Immediately after stimulation the plants were decapitated. The stumps still showed distinct curvatures. In this case conduction of the stimulus from the tip is almost certainly excluded, so that these curvatures must be due to a perception by the base itself. It was even possible, by the method described on p. 526, to prove a distinct deviation from equal distribution of g.s. in these stumps. Further study of the distribution of geotropic sensitivity in the coleoptile was therefore needed.

B. *Survey of the literature.*

The distribution of geotropic sensitivity is more difficult to study than that of phototropic sensitivity because gravity cannot be made to act upon specified zones. The two methods which have been principally used are; (a) decapitation, and (b) rotation of the plant in such a way that the centrifugal force acts in opposite directions on the top and on the base, (Piccard's method).

Both Darwin (1880) and Rothert (1896) found a difference between the sensitivities for light and gravity in the coleoptiles of grasses. Rothert's experiments, which showed that the sensitivity to light and gravity was lost on decapitation but reappeared later, were, as he himself admits, extended over too long a time to give satisfactory data, since after regeneration of the new tip the sensitivity of that zone is also changed. I have also found (1926) that the phototropic sensitivity of any specified zone of a decapitated coleoptile is increased after regeneration of the g.s. Many of the regeneration experiments in the literature are on this account inconclusive. Rothert concluded that while geotropic sensitivity is located principally in the tip, since this portion curves the earliest, the region of maximum growth is located somewhat lower down. Tröndle (1913) attempted, from following the course of geotropic curvatures, to draw conclusions as to the distribution of sensitivity. Since he takes no account of the conduction of the stimulus, this method is invalid, for curvature in any zone does not necessarily arise from perception in that zone. The presentation time of such a zone can therefore not be determined from a study of the time required for minimum response of that zone.

F. Darwin (1899) showed that coleoptiles of *Phalaris*, *Setaria* and *Sorghum* placed horizontally with their tips fixed and their bases free to curve, reach no equilibrium but continue curving until the plant is rolled up. Massart (1902) repeated these experiments with coleoptiles of *Avena*, and found that although curvature proceeds beyond the vertical position, it at length reaches an equilibrium, indicating that the base also possesses some geotropic sensitivity. On account of the criticism of Miehe (1902) and Jost (1903), Darwin (1908) repeated the experiments on *Sorghum* with the method of Piccard and concluded that only the coleoptile is sensitive, but that the mesocotyl is not.

With the same method, von Guttenberg (1911) carried out extensive investigations upon various grasses, and found the sensitive zones to be of different lengths in different species. Herzog (1925) found that in seedlings of *Vicia sativa*, *Brassica Napus*, *Linum usitatissimum* and *Lepidium sativum*, the sensitivity was equally distributed over rather a large zone. In flower-stalks of *Bellis perennis*, however, the apical zones are distinctly more sensitive than the base, a situation similar to that which holds in the coleoptiles of *Avena*.

The method of Piccard can thus give valuable information as to whether any localisation of sensitivity is present, but it can give no further analysis of its distribution. One can only determine about which point the plant must be rotated in order that the stimulus shall be equal on either side; the method indicates nothing as to the sensitivity within these parts, especially since the length of the sensitive zone is unknown. On this account a number of different theories of the distribution of sensitivity could be put forward, any one of which would be capable of explaining the facts. This has been pointed out by many writers, including Jost (1912). A number of investigators have attempted to determine the length of the sensitive zones, using decapitation, but since this disturbs the normal correlation of the plant, and since the plants react generally only after regeneration, such experiments are in no way conclusive. Thus the data of Herzog, (1925), for instance, are of very doubtful significance.

Finally Dewers (1914) found that in the Piccard method the position of balance varies with the velocity of rotation. This makes interpretation of the results still more difficult.

C. *Experimental.*

The analysis of the distribution of sensitivity to geotropism was carried out by means of experimental decapitations. Brauner (1923), Seubert (1925), and Went Jr. (1926), have shown that stumps of coleoptiles would undergo geotropic curvature if growth substance was applied to them. Coleoptiles were decapitated at different lengths and the presentation time of the stumps determined. An advantage of determining the presentation time is that the product law holds for it; a disadvantage is, however, that the determination has a subjective character, the limit of the just visible curvature being never sharp. The data are reasonably comparative, nevertheless, and this was sufficient for the purpose.

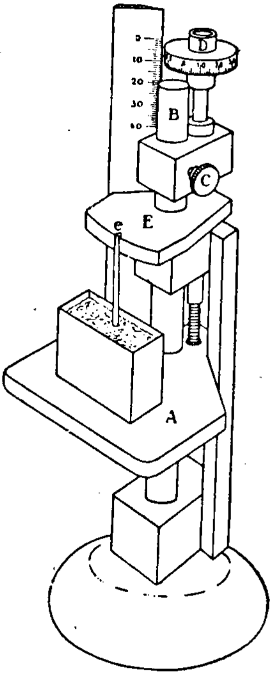


Fig. 7. Explanation in text.

The coleoptiles were grown in earth in the usual way. When they had reached a length of about 3 cm, the tip was removed to a definite length. For this purpose the following instrument was used (Fig. 7). The container with coleoptiles is placed on a brass plate, A, which can be moved along its vertical axis, B, by means of a screw, D, clamped to the axis by another screw, C. One turn of D moves the plate 1 mm, and each turn was divided into 100 parts so that each division = 10 μ. When C is unscrewed, the plate A and screw D can slide along the axis. The top plate, E, the edge of which has a semicircular opening in it, is fixed to the axis B. Plate A is adjusted so that the tip of the coleoptile makes contact with a razor blade lying on the upper plane E; screw C is tightened and the position of D is read off. The coleoptile is then raised through the required distance by turning D, and decapitated with the razor blade. In this way a number of coleoptiles can be decapitated to a given length in a short time. It is necessary to pull the shoot out of the coleoptile before putting on the blocks of agar. To do this it is ordinarily necessary to take off 3 or 4 mm of the tip but, to avoid removing so much, use was made of the method of Cholodny. A unilateral slit was made in the base, and by bending slightly to one side the coleoptile was broken off. The shoot remained intact at this point and usually broke off lower down, so that it could be pulled out. If the shoot broke in the pulling, it was pushed out by means of a glass capillary. The coleoptile cylinders so obtained were placed on long paraffin blocks, by fitting them over small glass rods fixed in the block. The rods were centred in holes filled with water, so the coleoptiles were thus held in position, dipping in water. Eight coleoptiles were decapitated to the same height and fixed in the blocks, and blocks of agar containing growth substance were fixed to the top surface of the coleoptile cylinders with 10% gelatin. The growth substance was obtained from Mais coleoptiles, the amount used being sufficient to produce a strong geotropic curvature. The experiments were carried out at 24° and 90% relative humidity. The paraffin blocks were placed vertical, the coleoptile cylinders being thus horizontal, under a bell-jar which was covered with moist filter-paper. The water remained in the holes by capillarity. After 30—45 minutes the curvatures were photographed, and later measured. With some practice these experiments can be carried out without causing any traumatotropic curvatures.

Preliminary experiments were carried out to determine whether the treatment reduced the sensitivity of the coleoptiles to gravity.

TABLE IX.

Geotropic curvature of decapitated coleoptiles placed horizontal for various times.

Length of tip in mm.	Time placed horizontal in minutes after decapitation	Time left horizontal in minutes	Curvature 25 minutes later
1	10	60	14.5
1	20	60	11.3
1	45	60	7.0
1	50	60	5.4
1	5	45	10.1
1	30	45	7.0
1	45	45	3.2

In these experiments (Table IX) the coleoptile cylinders were exposed to gravity at various intervals after placing in the blocks. The greatest curvatures were obtained when the coleoptiles were put horizontally immediately after decapitation. Traumatotropic action did not occur, and the data to the contrary in the literature must be ascribed to disturbances in correlation, which cease on the formation of new growth substance. These experiments show that it is desirable to place the plants horizontal as soon as possible after decapitation. The manipulations, however, occupied about 10 minutes.

The presentation time of stumps from which tips 1 mm long were removed is given in table X. The first column gives the time of stimulation, the 2nd the number of curved and the 3rd the number of uncurved plants. The degree of curvature, given in the last column, is purely subjective, — indicating no

TABLE X.

Geotropic curvature of coleoptiles decapitated 1 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
5	2	7	—
5	2	5	—
10	6	2	+ +
10	4	4	±
10	5	2	+
15	5	2	+ +
15	7	0	+ + +
20	6	1	+ + +
20	6	1	+ + +
25	6	1	+ + +
30	8	0	+ + +

reaction, ± indicating a just visible curvature in about half of the plants, + a clearly visible curvature, + + a strong and + + + a very strong reaction (25°). Before considering the results of these experiments it must be borne in mind that plants treated in this manner do not behave as regularly as do normal plants. Furthermore the number of plants is small, since these experiments take a long time, the utmost care being necessary for the decapitations. However, it was intended only to determine the order of the presentation time, rather than its exact value. For the same reason the times were chosen only with 5 minute intervals. Table X shows that 5 minutes' stimulation gives no reaction, 10 minutes a distinct reaction; the presentation time is therefore between 5 and 10 mins. In table XI, in which tips 2 mm long were taken off, the presentation time is between 15 and 20 minutes. Table XII, which gives the results for 3 mm tips, shows that the geotropic sensitivity has not greatly decreased, since the presentation time is also about 20 minutes. Similarly 4 mm decapitation gives a presentation time between 20 and 25 minutes (table XIII). Decapitation of 5 mm (table XIV), however, greatly increases the presentation time, since only in 2 plants

TABLE XI.

Geotropic curvature of coleoptiles decapitated 2 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
15	2	4	—
15	3	5	—
15	4	4	±
20	3	4	±
20	4	5	±
20	5	3	±
20	4	4	±
20	5	4	±
20	5	4	±
25	6	3	+
25	4	2	+
25	7	2	+ +
25	6	1	+ +
25	5	2	+ +
30	5	2	+ +
30	8	1	+ + +
30	7	2	+ +
45	5	1	+ + +
45	9	0	+ + +

TABLE XII.

Geotropic curvature of coleoptiles decapitated 3 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
15	2	5	—
15	2	5	—
15	4	4	±
15	1	6	—
20	6	3	+
20	4	5	±
20	5	3	±
25	4	3	+
25	6	2	+
25	6	3	+
30	3	2	±
30	7	4	+ +
30	8	1	+ +
30	5	2	+ +
35	7	4	+
40	7	1	+ +
45	7	1	+ + +

is a curvature visible after 30 minutes and reactions were still quite weak after 35 minutes. The presentation time is thus here 35 minutes, for 6 mm decapitation 35-40 minutes (table XV), for 7 mm about 60 minutes, (table XVI), for 8 mm 70 minutes, (table XVII), for 9 mm 80 minutes (table XVIII), and for 10 mm 100—110 minutes (table XIX)). The lower zones were not further investigated, since the presentation time is long enough to allow regenerative processes to enter in.

TABLE XIII.

Geotropic curvature of coleoptiles decapitated 4 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
20	4	4	±
20	4	5	±
20	1	7	—
25	6	2	+
25	4	2	+
25	7	2	+
30	7	2	+ +
30	4	1	+ +
30	5	2	+ +

TABLE XIV.

Geotropic curvature of coleoptiles decapitated 5 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
25	2	6	—
25	0	6	—
30	2	5	—
30	2	5	—
30	3	4	±
30	4	4	±
35	3	5	±
35	4	5	±
35	4	4	±
35	4	4	±
35	5	4	+
35	4	3	±
40	5	2	+
40	4	4	+
40	3	4	±
45	7	2	+ +
45	6	2	+ +
47	7	0	+ + +
45	5	3	+
45	5	0	+ +
50	6	1	+ + +
60	6	1	+ + +

TABLE XV.

Geotropic curvature of coleoptiles decapitated 6 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
35	2	7	—
35	4	3	±
40	5	3	+
40	5	3	+
45	3	4	±
45	4	3	+
45	7	1	+ +
45	3	4	±
50	6	2	+
50	5	4	+
60	3	1	+

TABLE XVI.

Geotropic curvature of coleoptiles decapitated 7 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
40	3	4	—
45	3	5	—
50	3	6	—
50	5	4	±
55	4	4	±
55	4	4	±
60	3	4	—
60	4	4	±
65	3	5	—
65	3	3	±
65	4	3	±
70	6	3	+
70	5	2	+
75	4	3	+
75	4	2	+

TABLE XVII.

Geotropic curvature of coleoptiles decapitated 8 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
45	0	6	—
50	2	5	—
55	1	4	—
55	2	4	—
60	3	4	—
65	3	4	—
70	5	5	±
70	3	3	±
80	6	2	+ +
80	5	3	+
90	7	2	+ +
90	7	0	+ +
100	5	3	+
100	6	1	+ +

TABLE XVIII.
Geotropic curvature of coleoptiles decapitated 9 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
60	1	7	—
70	2	7	—
70	2	6	—
70	3	4	—
80	4	3	±
80	4	3	±
80	4	3	±
90	4	3	±
90	4	2	+
100	3	4	±
100	6	1	+ +
100	7	0	+ + +

TABLE XIX.
Geotropic curvature of coleoptiles decapitated 10 mm from the top.

Time horizontal in minutes	Number curved	Number not curved	Result
80	2	5	—
90	1	5	—
90	2	4	—
100	4	4	±
100	3	3	±
110	2	2	±
110	3	3	±

D. *Comparison of results with those in the literature.*

Table XX summarizes the above experiments, showing that the geotropic sensitivity is greatest at the top and decreases towards the base. Control experiments, in which the base was severed as before, but the decapitated tip was glued on again, showed a remarkably short presentation time, about 4 minutes. The geotropic sensitivity of these coleoptiles is therefore not markedly affected by the various injuries inflicted, since Rutten-Pekelharing (1910) and Rutgers (1912) found the presentation time of normal coleoptiles to be 2-3 minutes. The whole zone studied, 10 mm, was apparently sensitive to gravity and there is no question of strict localisation in the tip. If the theory of Went

TABLE XX.

Presentation time of coleoptiles decapitated at different distances from the top.

Length of tip removed in mm.	Presentation time in minutes
Control =	4
1	5—10
2	15—20
3	20
4	20—25
5	35
6	35—40
7	60
8	70
9	80
10	100—110

and Cholodny is correct, polar transport of growth substance must take place in the base, as was in fact shown in section III C. In general the results are in accord with the literature.

In the first place it is easy to explain the results of Massart, in which the coleoptiles of *Avena* do not roll up into a spiral while those of *Setaria* and *Sorghum* do. They are in accordance with the results of von Guttenberg, who finds a comparatively long zone able to perceive gravity. He gives a length of about 5 mm, and claims that the uppermost 2,8 mm is 6 times as sensitive as the lower part. This is not in exact agreement with my experiments, but von Guttenberg points out that his experiments have only a limited significance. The conclusions of Tröndle, however, are at variance with mine, but his views have been shown above to be unjustified.

Comparison of the results with what is known about the phototropic sensitivity of *Avena* coleoptiles shows a considerable difference. Both Sierp and Seybold (1926) and Lange (1927) have shown the phototropic sensitivity to be strictly localised in the tip. Thus Sierp and Seybold found that by excluding the uppermost 2 mm from the light the presentation time was 360 times as long. Lange obtained similar values. Presentation time in geotropism under the same conditions is increased only 4 times. Sierp and Seybold and Lange point out that the phototropic stimulus is perceived only in the zone in which growth substance is produced; the geotropic stimulus, however, is also perceived in the growing zones. This difference is also seen in the coures of the curvature, as will be shown in the next section. With strong illumination, the basal zones also perceive, but while Lange assumes these basal curvatures to be due to scattering of light inside the coleoptile, they are, in my view, probably due to a true perception by these zones, as many investigators have believed. Sierp and Seybold also distinguish between the influence of light on a zone of tip action and that on a zone of growth. It was therefore important to determine how far the difference between the distribution of geotropic and phototropic sensitivities could be observed by following the course of the reaction.

Section V.

THE COURSE OF THE CURVATURES.

A. *Literature.*

The course of geotropic curvatures in *Avena* coleoptiles has been little studied, most investigators describing it in general terms only. Maillefer (1912 and 1915) determined the displacement of the top of the coleoptile, taking this as a measure of the geotropic curvature. He concluded that the curvature begins slowly and then becomes more rapid. The process of curvature thus would follow the same laws as the acceleration of free fall by gravity. The displacement of the top was also measured by Weber (1927) and by Polowzow (1909). Tröndle (1913) correctly realised that the displacement of the top indicates little about the curving process, since the amount of displacement is entirely dependent on the zone in which curvature is taking place. A small curvature in the base displaces the tip considerably, while curvatures in the tip itself have little influence. Also the basal zones curve while the apical zones are already straightening. A more accurate procedure is to measure the curvature of single zones, as was done by Tröndle. If one examines his data, rough as they are, the curvature appears irregular, starting slowly, accelerating, and finally decreasing again. The same thing was shown by Jost (1923). Lundegardh, (1926), using a cinematographic method, followed the process of curvature in several plant organs, particularly in the roots of *Pisum.* However, only the total reaction and not the reaction of each individual part is given, so that one cannot get a complete picture of the reaction. He divides the course of the reaction into 3 phases, slow, accelerating, and slow again. The intermediate stage between the second and third phases is called the reaction optimum. From his data, the phases are not sharply distinguishable from one another, and on this account it is doubtful whether any such generalisations can be deduced, as Jost (1926) has already pointed out. In order to determine whether geotropic curvature can really be explained by the Cholodny-Went theory, it is necessary to follow the course of the curvatures in different zones. This was done by F. W. Went (1928, b) for a single case of phototropic curvature and it was therefore desirable to repeat it on geotropic curvature.

B. *Method.*

The coleoptiles were first stimulated horizontally for a definite time, and thereafter the progress of the curvature was registered cinematographically. The method was essentially that of F. W. Went, except that during registration the plants were continuously rotated on the horizontal axis of the de Bouter intermittent clinostat. (F. A. F. C. Went, 1929). A „Universal Kinamo" with a Zeiss Ikon lens and Agfa „Pankine" film were used. The camera was connected with the clinostat by a flexible cable. Pictures were taken every 4 minutes with an exposure time of 2 minutes in red light, during which the plants remained horizontal. During the other 2 minutes the camera was closed and the clinostat axis turned through 180°. The distance was selected so that the plants were reduced 2 to 3 times in size, and 4 could thus be photographed together. The plants were planted in earth in long zinc boxes which stood vertical to the axis during the rotation.

Measurement of the pictures proved to be rather difficult. Went's method of projecting the image on paper and tracing it was not satisfactory, since great enlargements could not be obtained. The pictures were therefore projected on to a ground glass plate, using a Zeiss micro-projection lamp. The total enlargement of the coleoptiles was exactly 20 times. The projected picture was then divided into zones 4 cm in lenght (2 mm actual size) and the radius of the concave side was determined by fitting circles of cardboard on to it. After some practice the radii of curvature of single zones could thus be measured rather accurately. The difference in growth between the two sides is t/r, where t is the thickness of the coleoptile, 1.2 mm, and r the radius. The radii of the cardboard circles were chosen as $\frac{1.2 \times 20}{1 \times 0.005}$, $\frac{1.2 \times 20}{2 \times 0.005}$,

$\frac{1.2 \times 20,}{3 \times 0.005}$ etc., i.e. to correspond with successive increase in the growth difference of 5 μ per mm.

There are disadvantages to this method. The length of each zone was kept constant at 4 cm, so that no allowance was made for growth occurring during the registration. Since the registration lasted only a short time and the total growth was only 2 mm, however, this factor is not serious. Another disadvantage is that the difference in growth between the two sides is measured only indirectly, and it is impossible to tell whether it is due to acceleration of the upper side or retardation of the lower, or both. The method of Du Buy and Nuernbergk (1929 a), in which the growth of each side is measured separately, is preferable, but cannot be adopted here since my pictures cannot be sufficiently enlarged. Furthermore, absolute measurement of the amount of growth introduces new difficulties, because variations in growth due to slow reactions such as that of phototropism are difficult to distinguish from variations in the normal growth. To know whether a given amount of growth represents a true acceleration or retardation it would be necessary to know the normal growth curve of each zone. For this reason, as well as for the technical objection above, the method of du Buy and Nuernbergk was unsuitable, while that here employed was quite satisfactory for following the general progress of the curvature. The regularity found in the reaction shows that the errors of measurement must have been very slight.

C. *Experiments.*

1. *Normal geotropic curvature.*

The progress of the curvature after a stimulation time of 30 minutes is given in Fig. 8 which is the derived from the mean of 5 plants. The reactions of the plants were closely similar; a few obscuring nutations occurred, but data from these plants were not used.

Only the first 30 exposures were measured, and thereafter one in five only, since the curvature slows up after 120 minutes. The uppermost 2 mm, zone 0, could not be measured owing to its parabolic shape.

Possible variation in thickness of the coleoptiles deprives the data of any absolute value, but only comparative measurements were desired.

The absissae are the times, the ordinates the difference between

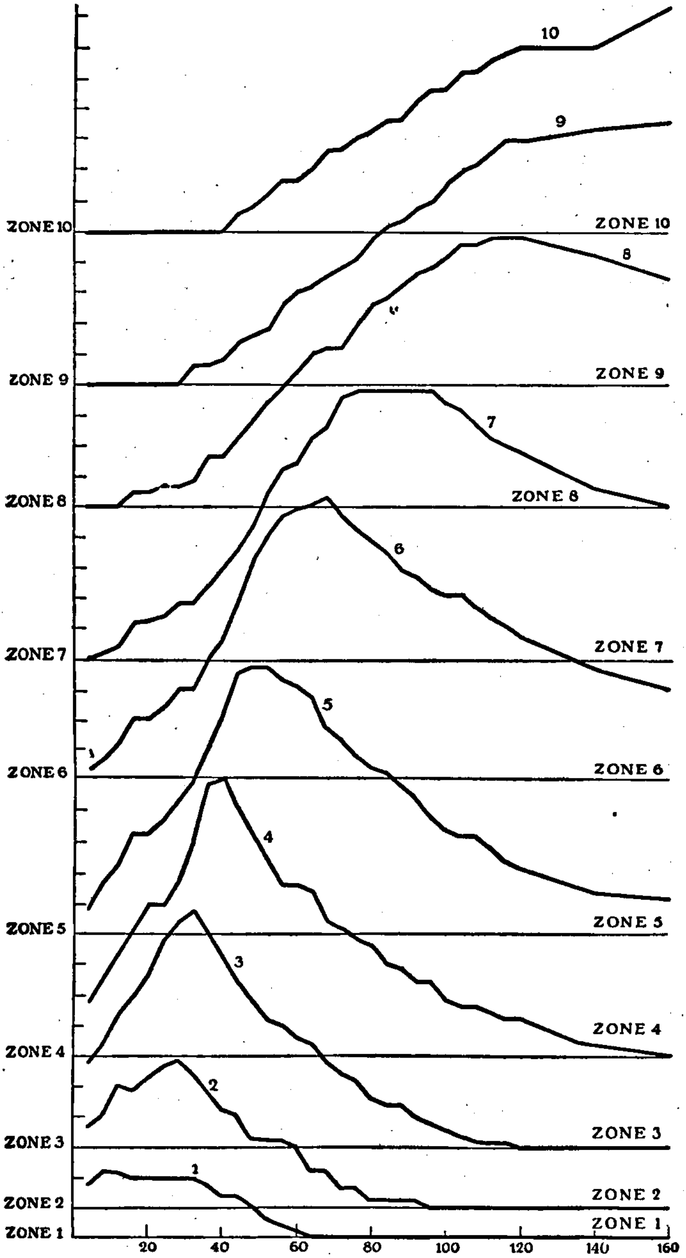


Fig. 8. Course of the geotropic curvature in the single zones of a coleoptile. Abscissae, time in minutes; ordinates, difference of the growth of the two sides in 5 μ units. Mean of 5 curvatures. Stimulated horizontally for 30 minutes.

the growth of the 2 sides, in 5 μ units. The first zones are already curved at the beginning of registration; zone 1 does not curve further and soon straightens out, being completely straight after 64 minutes. Zone 2 curves further, reaching a maximum after 28 minutes, and finally becomes straight again after 96 minutes. Zone 3 reaches its maximum at 32 minutes, zone 4 at 40, zone 5 at 50, 6 at 68, 7 at 84 and 8 at 116; in zones 9 and 10 no maximum is reached during the time of registration. Zone 4 is completely straight after 160 minutes, while the lower zones do not reach straightness. Since the curvature decreases so rapidly in the apical zones it is always localised in a rather small region.

The distribution of curvature can be better seen when the data of Fig. 8 are replotted as in Fig. 9, the zones being now the abscissae and the growth differences the ordinates; zone 0 is not included. The curves then show the distribution of curvature over the coleoptile at a definite time, the interval between successive curves being 20 minutes. This figure shows clearly that the curvature begins in the tip and migrates rapidly towards the base; at the beginning of registration its maximum is in zone 3, and so on. The narrowness of localisation of the maximal curvature is also clearly seen.

Using a stimulation time of 15 minutes, the curvature was registered in exactly the same way, the results being given in Figs. 10 and 11, which have the same significance as before. The progress of curvature in the various zones takes place much as with the 30-minute stimulation time. Curvature begins in the apical zones, reaching its maximum in zone 1 after 24 minutes, in zone 2 after 32 minutes; straightening out begins soon after the maximum is reached, and the first three zones have straightened completely in the registration period. The quantitative relations are also the same in the first two zones; in the more basal zones, however, the reaction is weaker, and in the last two zones has only half the value of the reaction in the first experiment. The distribution of curvature over the coleoptile, (Fig. 10) is similar to that of the first experiment, but since the basal zones react so much more weakly the curvature is not so sharply localised. These differences are even more noticeable in coleoptiles stimulated for 7.5 minutes, as shown in figs. 12 and 13, which again give the mean results of 5 plants. The first zones here begin curving 16 minutes after stimulation and rapidly increase to a maximum. The decrease of curvature is, however, slower, so that it is often difficult to determine the time of maximum curvature. Zones 7 to 10 show no maximum at all, and it is remarkable that while

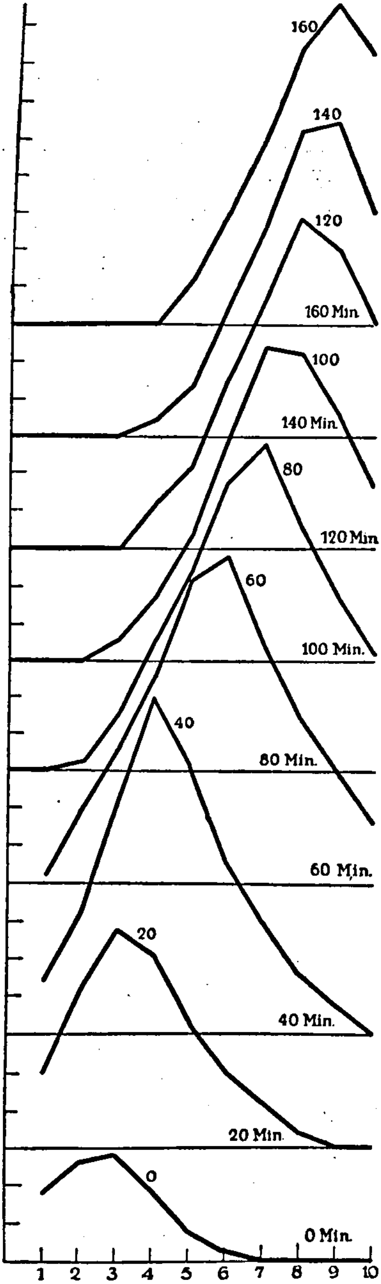


Fig. 9. Distribution of curvature over the coleoptile. Each curve shows the distribution at one time; they are plotted every twenty minutes. Abscissae, the zones; ordinates, difference between the growth of the two sides, in 5 μ units. Stimulated 30 minutes; mean of 5 curvatures.

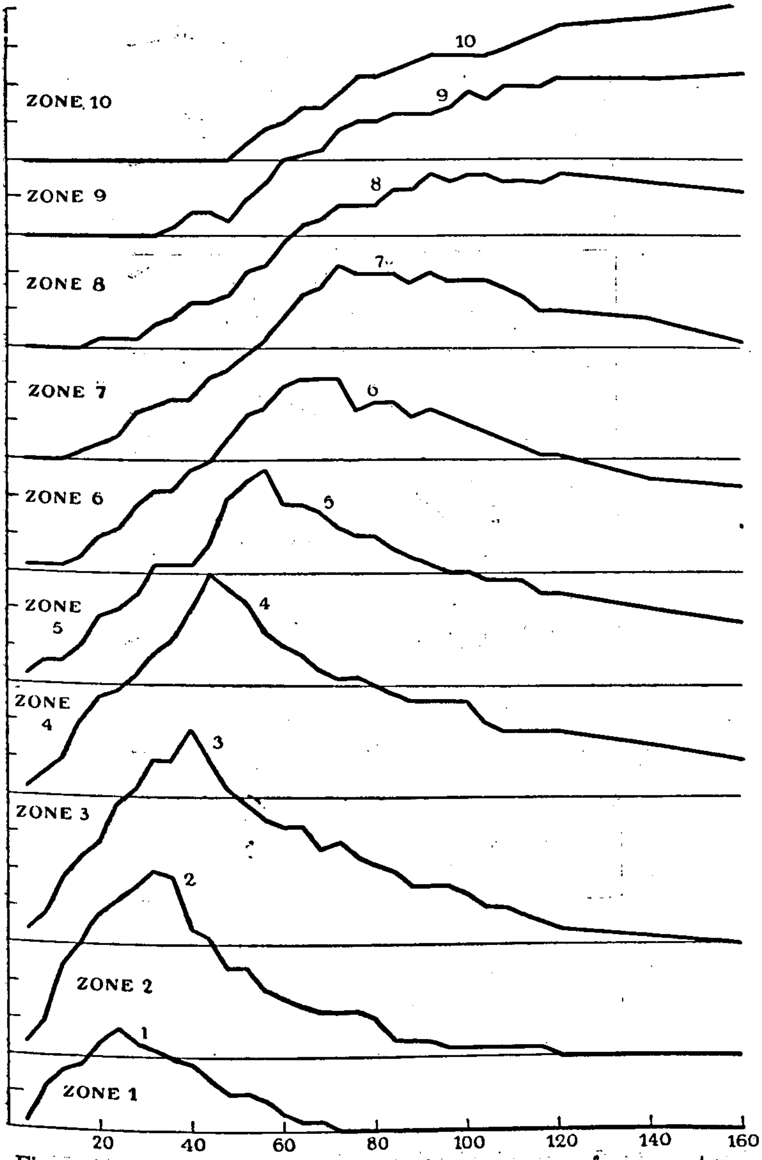


Fig. 10. As Fig. 8; stimulated 15 minutes; mean of 5 curvatures.

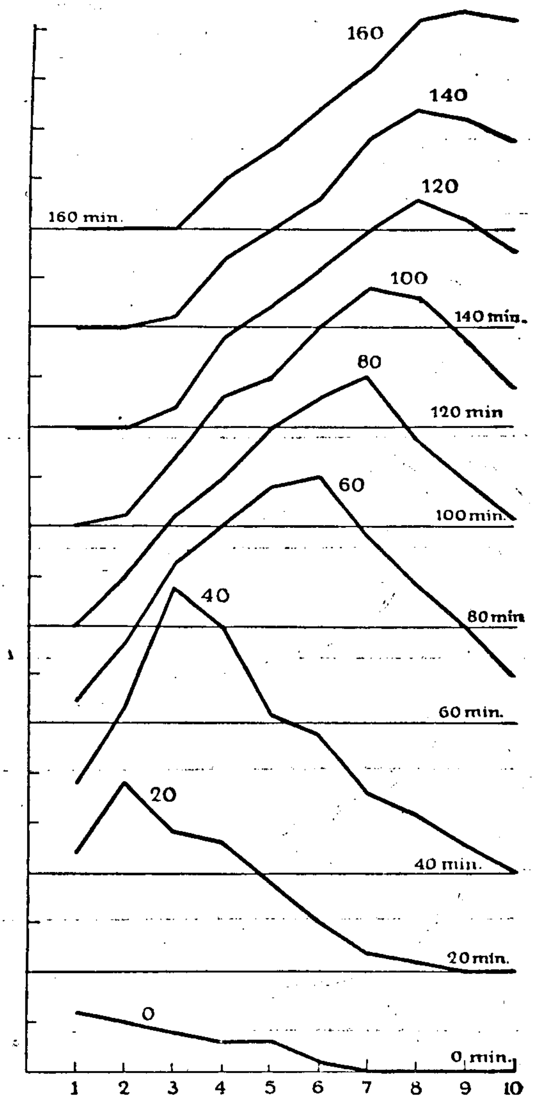


Fig. 11. As Fig. 9; stimulated 15 minutes; mean of 5 curvatures.

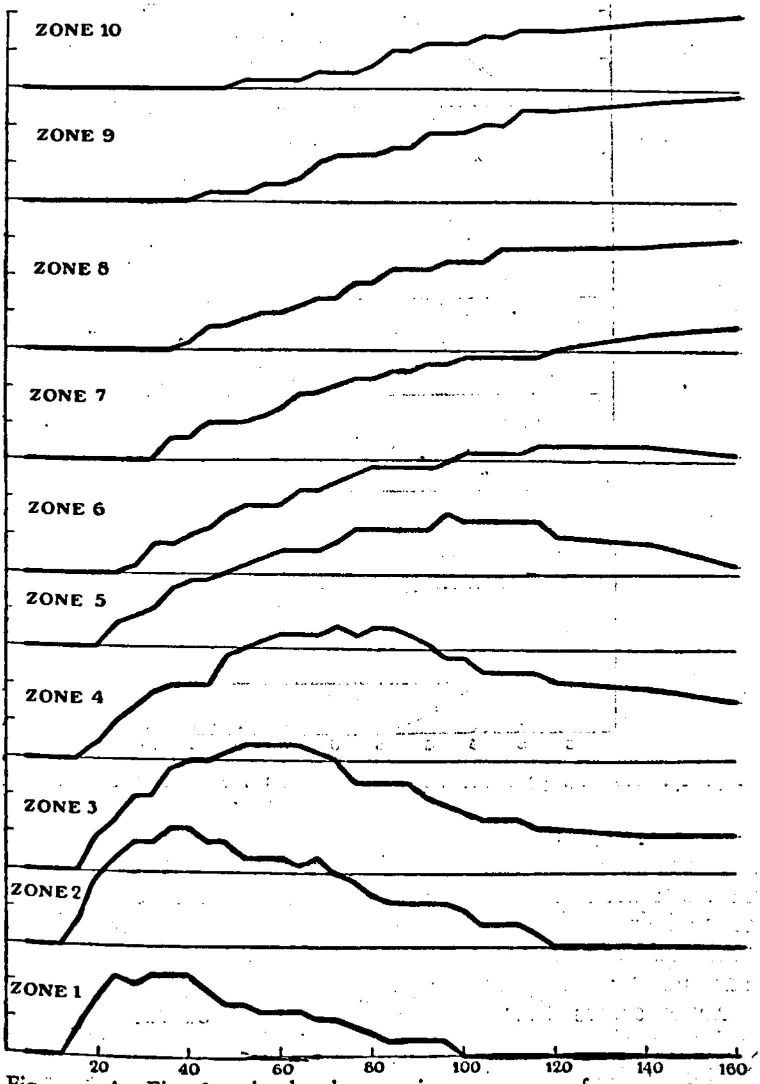


Fig. 12. As Fig. 8; stimulated 7.5 minutes; mean of 5 curvatures.

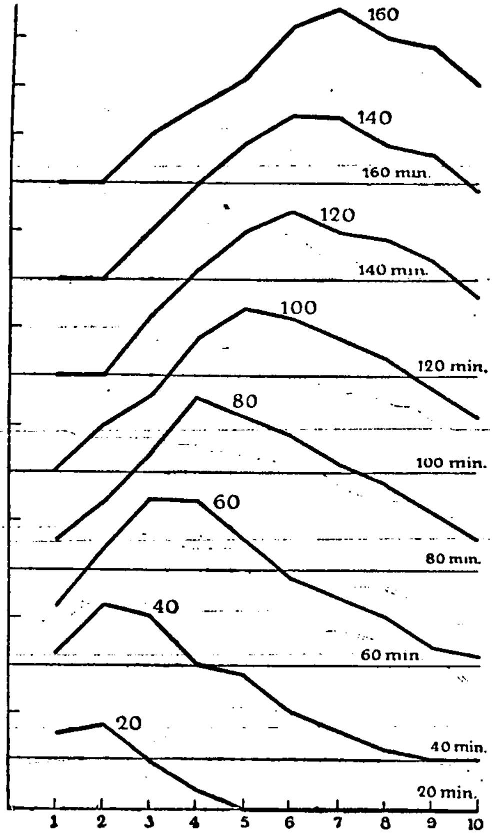


Fig. 13. As Fig. 9; stimulated 7.5 minutes; mean of 5 curvatures.

the first zone reacts just as strongly as in the first experiment, the more basal zones are weaker still, the strength of the reaction in zone 10 being only one quarter of that of the plants stimulated 30 minutes. During the migration of the curvature from apex to base its localisation is also less marked than before. Comparison of graphs shows that at 160 minutes the curvature following 30 minutes stimulation is mainly localised in zone 9, while following 7.5 minutes' stimulation it is evenly distributed over zones 6 to 9. The longer the stimulation, the quicker is the migration towards the base. The results of Tröndle (1913) also show that the curvature decreases rapidly in the upper zones; his data cannot be closely compared to these, however, for his coleoptiles were kept horizontal.

It is very unfortunate that the uppermost zone had to be omitted, but with this method no quantitative measurements of it could be obtained.

The experiments show, then, that the curvature often, but not always, starts in the extreme tip, which becomes asymmetrical. The curvature is, however, never very strong here, and even zone 1 is not strongly curved. For phototropic curvature, F. W. Went (1928 a) denied any asymmetry in the tip itself, but he later agreed that it might occur (1928 b). In geotropic curvatures it is certain that asymmetry of the tip may, but does not always, occur, — a fact which was observed by Weber (1927).

How far it is possible to relate the curvature reaction to what is known of the distribution of growth substance will be considered after the other curves have first been discussed.

2. *Geotropic curvature in decapitated coleoptiles.*

In order to eliminate the influence of the tip after stimulation, coleoptiles were decapitated immediately after exposure to gravity. Three series of experiments were again carried out, using stimulation times of 30, 15, and 7.5 minutes respectively. In Figs. 14 and 15 are given the means of 5 coleoptiles stimulated for 30 minutes and at once decapitated 2—2.5 mm from the top. Zone 0 and part of zone 1 were thus removed. Some of the coleoptiles were also somewhat shorter, so that only 8 zones instead of 10 could be made. The curvature in the various zones proved to be completely different from that in normal coleoptiles. At the beginning of registration the apical zones are already noticeably curved; this curvature increases, as was found before, but does not decrease, maintaining a constant value for some time. Only after 120—140 minutes (time from decapitation) do the apical zones begin to straighten out; on this account registration was continued to 200 minutes. The basal zones do not straighten appreciably in this time.

Comparison of Fig. 14 with Fig. 8 shows the difference in behaviour clearly. The distribution of curvature is also completely different from that in intact coleoptiles, (Figs. 15 and 9). The curvature is at first strongest in the apical zones, as normally, but later, when the basal zones also start tot curve, the apical zones do not straighten, and in consequence the coleoptile soon becomes curved almost evenly throughout its entire length. Localisation of curvature in the base appears only after 140 minutes.

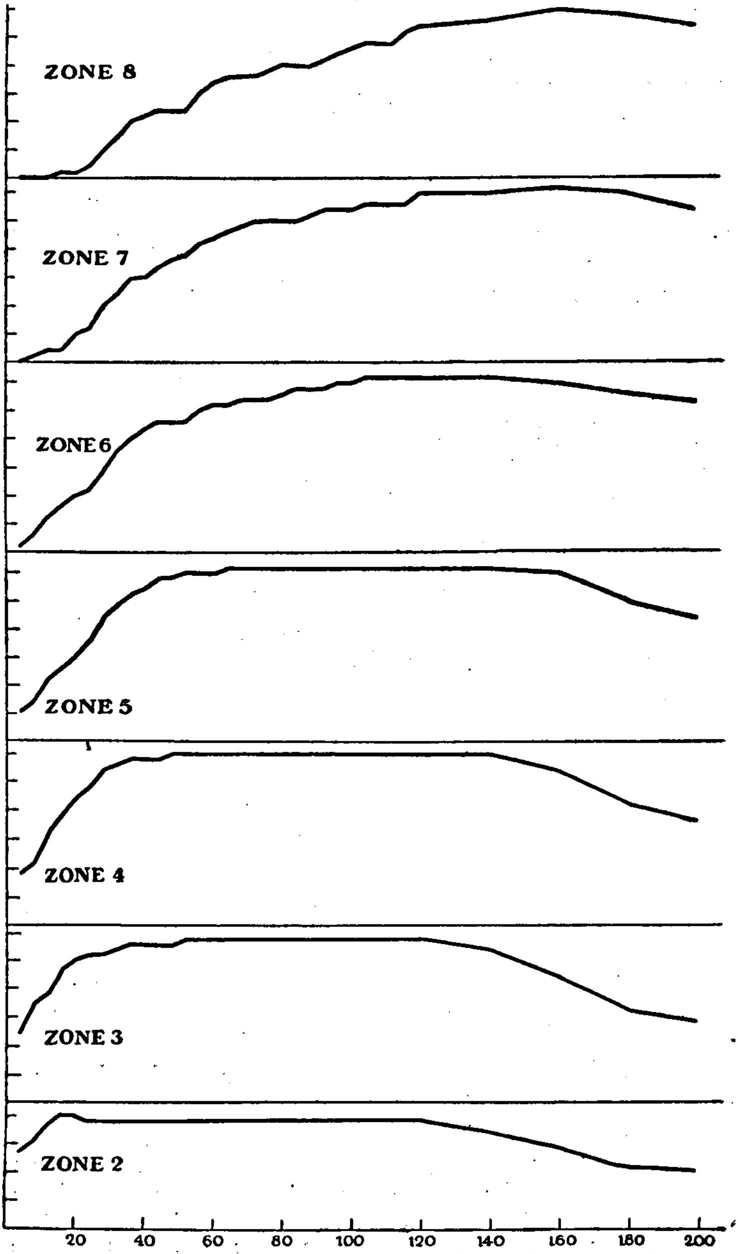


Fig. 14. Course of the geotropic curvature in the single zones of decapitated coleoptiles. Abscissae, time in minutes; ordinates, difference between the growth of the two sides in 5 μ units. Mean of 5 curvatures. Stimulated 30 minutes and then decapitated.

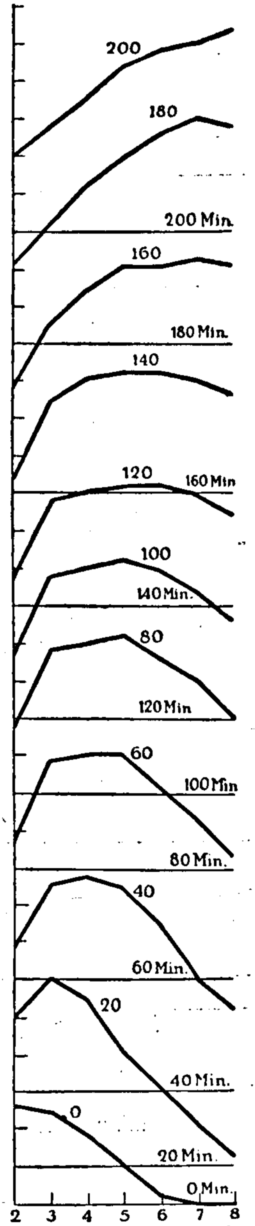


Fig. 15. As Fig. 9; stimulated 30 minutes and then decapitated. Mean of 5 curvatures.

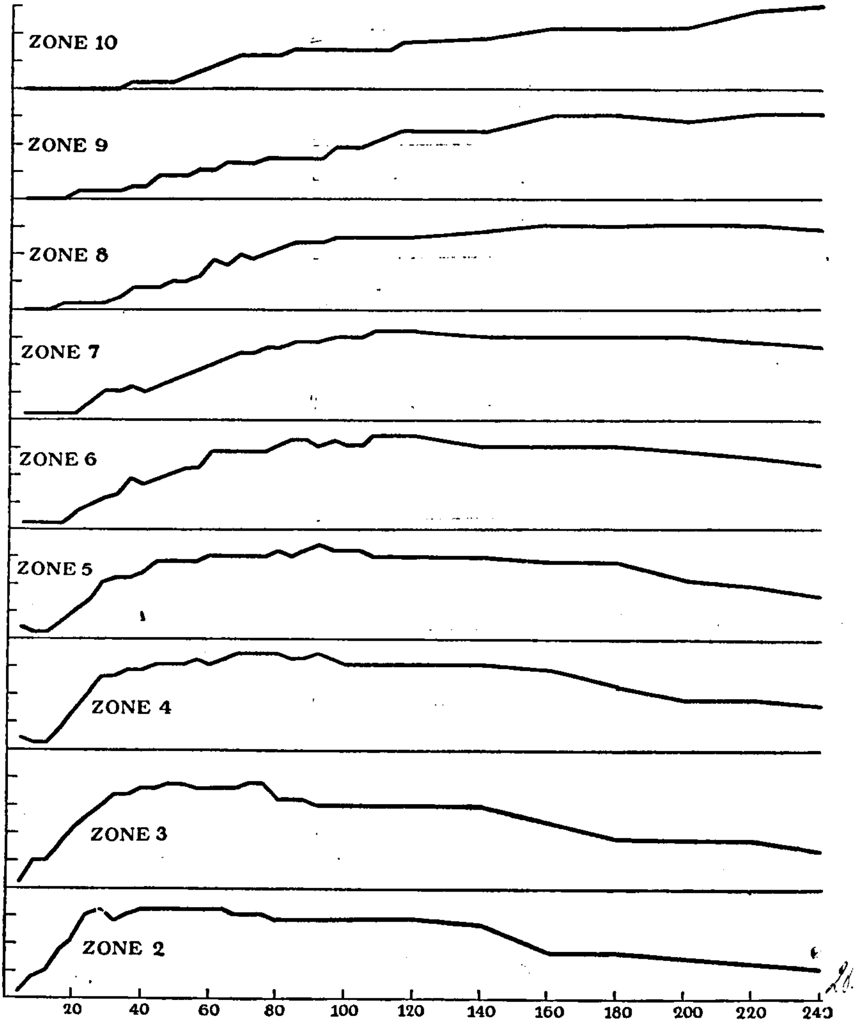


Fig. 16. As Fig. 14; stimulated 15 minutes and then decapitated. Mean of 5 curvatures.

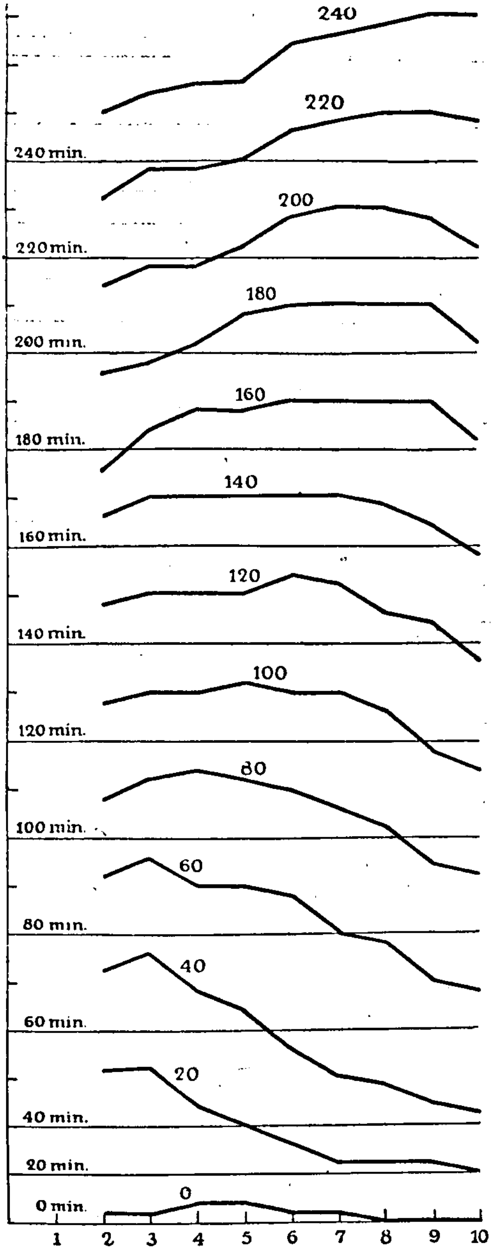


Fig. 17. As Fig. 9; stimulated 15 minutes and then decapitated. Mean of 5 curvatures.

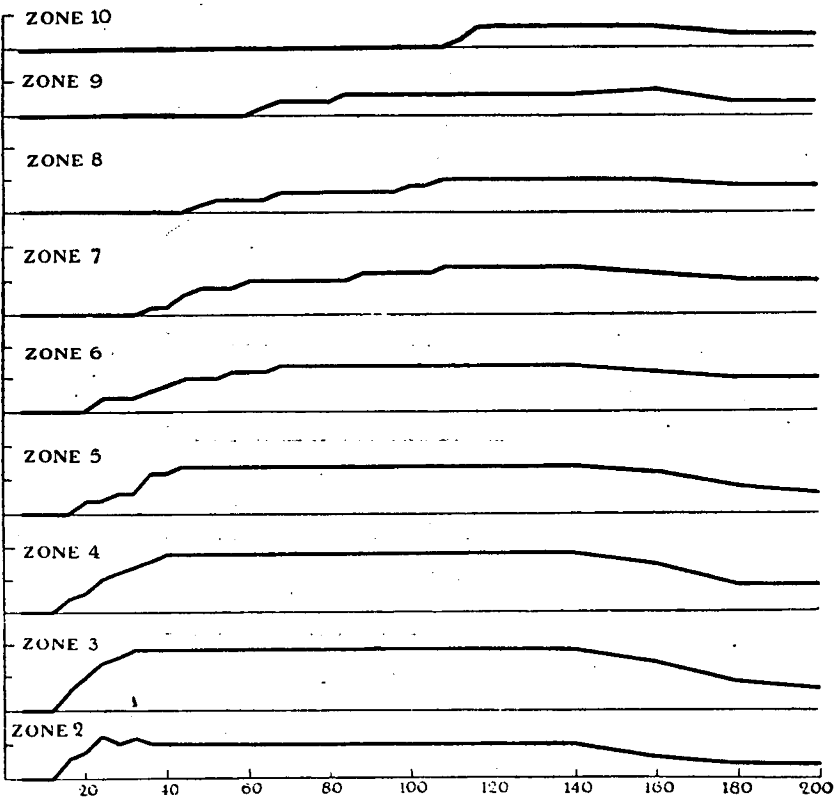


Fig. 18. As Fig. 14. Stimulated 7.5 minutes and then decapitated. Mean of 5 curvatures.

when some straightening begins. After 180 minutes the distribution of curvature is somewhat like that in the intact coleoptile. Stimulation for 15 minutes, followed by decapitation, leads to an almost identical reaction, (Figs. 16 and 17). The only difference is that the curvature in the base is much weaker. Stimulation for 7.5 minutes gives a curvature very weak but otherwise similar. Because the basal zones react so weakly, localisation is not visible after 200 minutes, (Figs. 18 and 19). These experiments show plainly the importance of the tip in geotropic curvature, and they indicate its role in the straightening out of the apical zones. (See discussion in section VI).

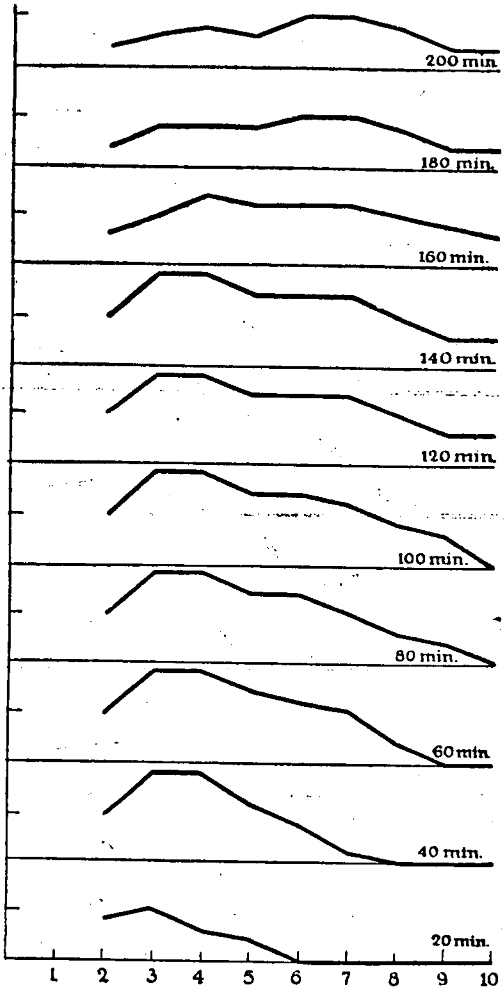


Fig. 19. As Fig. 9. Stimulated 7.5 minutes and then decapitated. Mean of 5 curvatures.

3. *Phototropic curvature.*

The progress of phototropic curvature was investigated in one case by Went (1928 b), but since the influence of gravity was not excluded the results cannot be compared with the above, and a further study was therefore carried out. The coleoptiles were illuminated unilaterally with 50 meter-candles for 10 seconds,

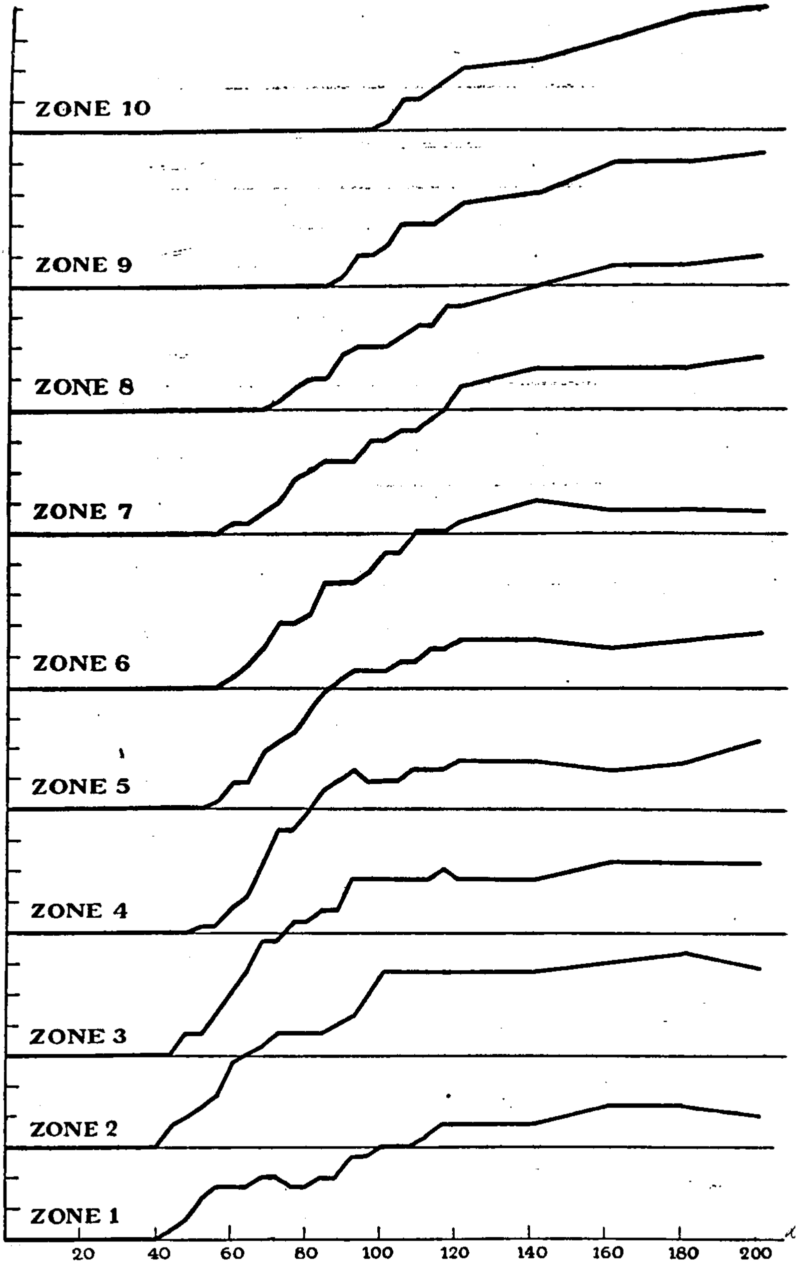


Fig. 20. Course of the phototropic curvature in the single zones. Unilateral illumination with 50 meter-candles for 10 seconds. Mean of 3 curvatures.

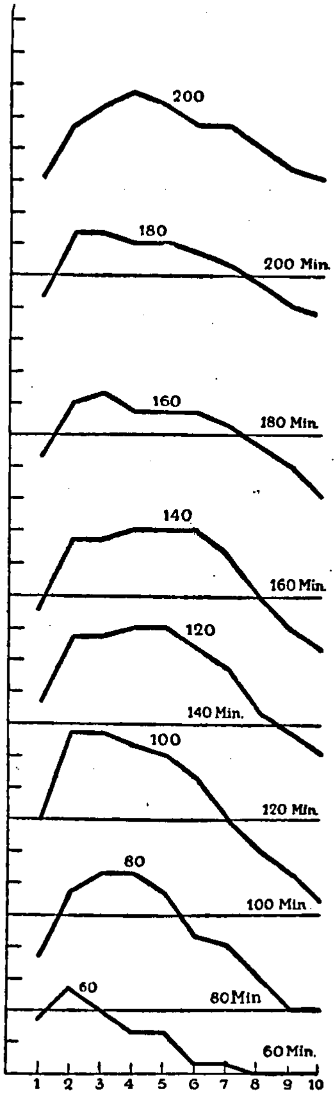


Fig. 21. Distribution of phototropic curvature in the single zones. Unilateral illumination with 50 meter-candles for 10 seconds. Mean of 3 curvatures.

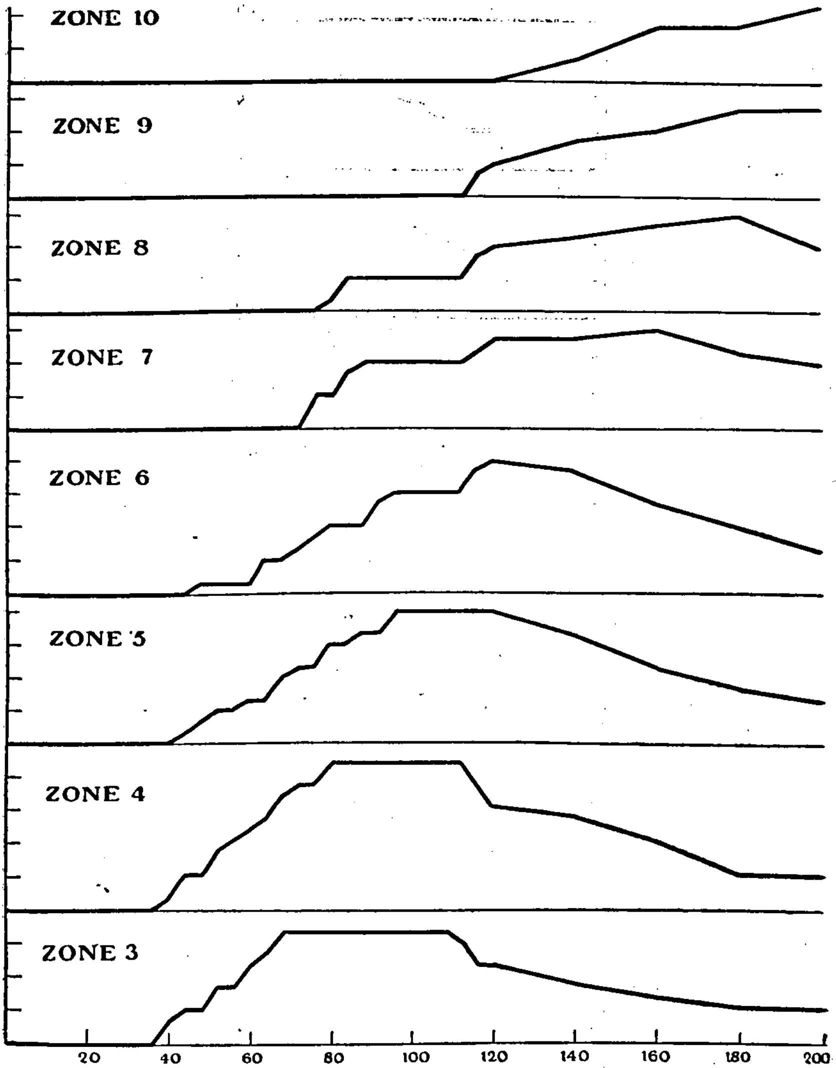
so that, according to Arisz (1915) a strong first positive curvature can be expected. The first positive curvature seemed better for study since the second might involve complications, such as basal reactions. Immediately after illumination the coleoptiles were placed on the intermittent clinostat and registration begun. Fig. 20 gives the mean of 3 plants. Comparison of the single zones shows that the reaction proceeds quite differently from that of geotropism.

Firstly, the zones all begin curving much later, (as has been pointed out by several investigators). Secondly the maxima are reached much later. Thus only zones 1 and 2 reach a maximum and even this is very indistinct. There is no sign of any rapid decrease in curvature in the apical zones. Zone 1 again gives the weakest reaction, but now the most basal zones are also weak. If registration had been continued, however, the curvature would no doubt have increased somewhat in the base.

Since the curvature decreases so little in the apical zone, there is no sharp localisation; Fig. 21 shows the curvature starting in the apex and migrating slowly towards the base. After 200 minutes the maximum curvature is still only in zone 4, and the zones are all nearly equally curved. The great difference between the distribution of curvature in geotropic and phototropic response can be seen by comparing Fig. 21 with Fig. 9. The results agree with those of F. W. Went, since his figures also show very slow migration of the curvature; the decrease in curvature in the upper part is somewhat more rapid, but this is doubtless due to the opposing action of gravity. The results are also in general agreement with those of du Buy and Nuernbergk, in that they also found the curvatures to decrease very slowly in the apical zones.

4. *Curvatures caused by the unilateral application of growth substance.*

Lastly, records were made of the curvatures which result when growth substance is applied unilaterally to decapitated coleoptiles. This is, of course, the simplest type of curvature, since its cause is precisely known. The technique used was the same as in the determination of growth substance, the plants being decapitated and the growth substance applied on one side 40 minutes later. The growth substance was obtained from coleoptiles of *Mais*, and two series of experiments were made using different amounts of growth substance. In these experiments the plants were not rotated since this was found to cause rapid drying out, and even falling



Fg. 22. Course of the curvature resulting from the unilateral application of growth substance to decapitated coleoptiles. Each coleoptile received 15 top-minutes of g.s. Mean of 3 curvatures.

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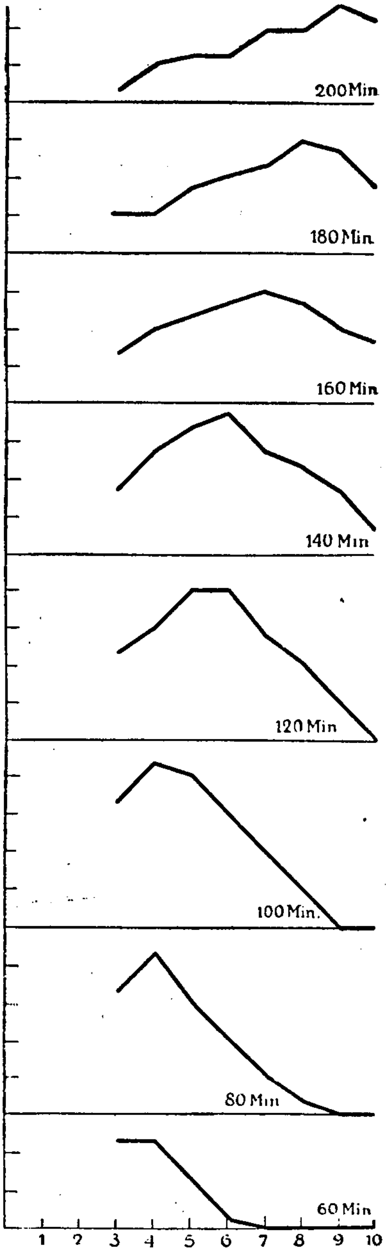

Fig. 23. Distribution of the curvature resulting from the unilateral application of growth-substance to decaptitated coleoptiles. Each coleoptile received 15 top-minutes of g.s. Mean of 3 curvatures.

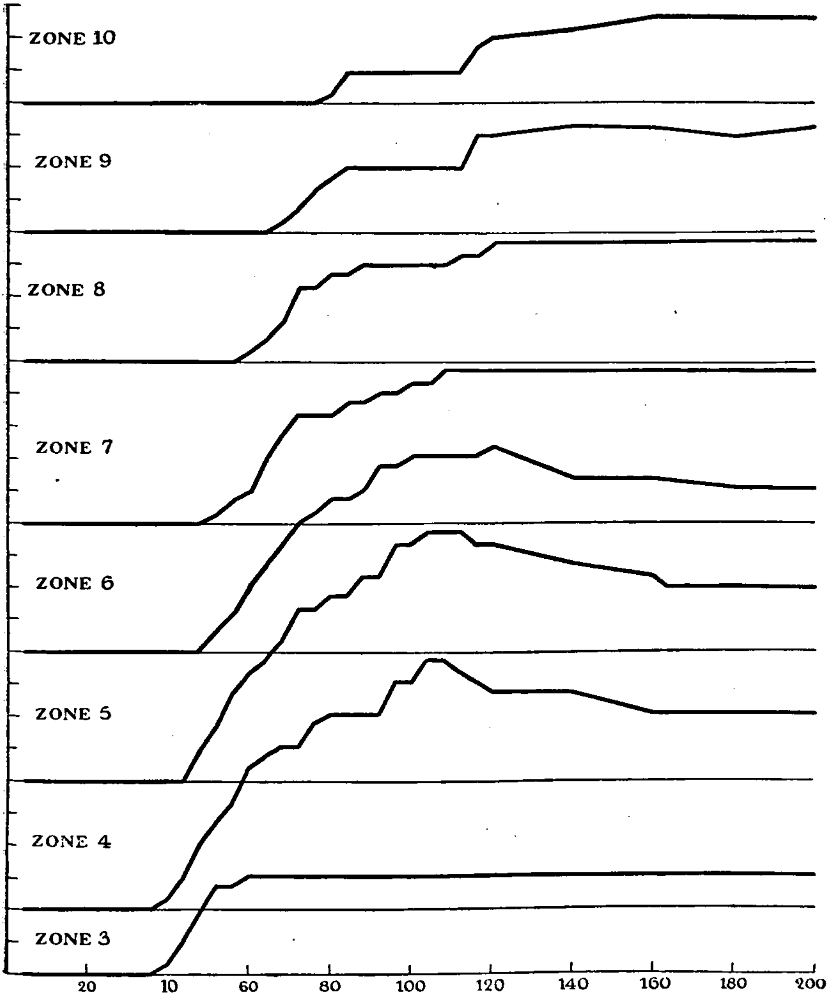

Fig. 24. As Fig. 22. 60 top-minutes of g.s. Mean of 3 curvatures.

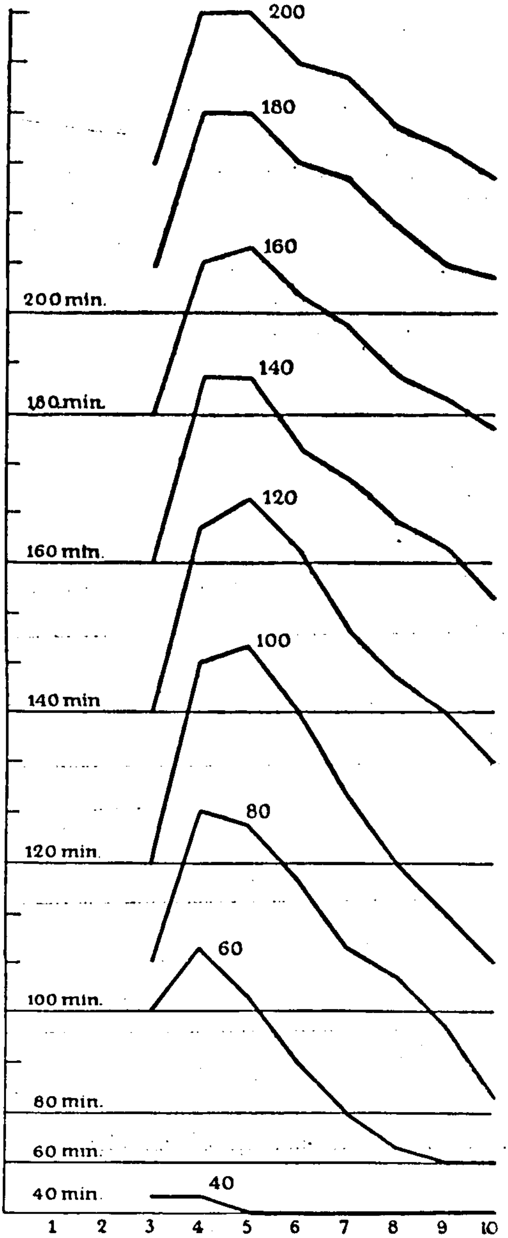

Fig. 25. As Fig. 23. 60 top-minutes of g.s. Mean of 3 curvatures.

off, of the agar blocks. The influence of gravity was thus, unfortunately, not ruled out. In the first experiment, the amount of growth substance which diffuses from 1 *Mais* tip in 15 minutes was used for each plant. The mean data for three curvatures are given in Figs. 22 and 23. The curvature is seen to begin in the apical zones only after 40 minutes, but it increases rapidly, reaching a maximum first in zone 3 and then in zone 4. Straightening out of the apical zones does not begin for 112 minutes, i.e. 152 minutes after decapitation; at the same time the basal zones curve more strongly, so that the curvature migrates towards the base. In Fig. 23 it can be clearly seen that the curvature remains localised in zone 4 for 100 minutes, after which it moves towards the base, the maximum curvature being in zone 9 after 200 minutes. In general the process is similar to that in coleoptiles decapitated after geotropic stimulation, except that in the basal zones the curvature appears much later.

In the second series of experiments the growth substance which diffuses from 1 *Mais* tip in 60 minutes was used. Figs. 24 and 25 give the results. The progress of the curvature is here somewhat different, since is begins in a normal way in the apical zones, but reaches a maximum which does not decrease; even after 122 minutes the decrease of curvature in the apical zones is only slight compared to that in the first series of experiments, while the basal zones are still curving. The distribution of curvature in the coleoptile is therefore not quite the same, since it remains more localised in the apical zones. This type of curvature resembles more that of phototropism, (cf. Figs. 24 and 25 with 20 and 21), in which also an increase in curvature without any straightening in the apical zones can be observed. These experiments show that the curvature proceeds as described by Went Jr. (1928 a), the maximum, reached after 110 minutes, being followed rapidly by a decrease of curvature. The time at which the curvatures are photographed in Went's method is also 110 minutes, so that the maximal curvature is always registered.

Section VI.

THEORETICAL DISCUSSION.

A. *The relation between curvature and growth.*

At the beginning of the introductory section it was pointed out that tropisms can only be explained in relation to the growth process, so that before discussing the curvatures in greater detail the normal growth process in *Avena* coleoptiles must be considered. For this purpose I will take the synthesis of growth as described bij Went (1928 a). According to this, the growth of the coleoptile is conditioned by various factors. If growth substance is applied to a decapitated coleoptile the growth increases proportionately to the amount of growth substance applied. This increase cannot go on indefinitely, and Went found that at a certain limit an increase in the amount of growth substance brought about no increase in growth. At that point the growth should be limited by another factor, the amount of cell-elongation material which is available. This material is still somewhat hypothetical in nature, and further analysis might reveal it to consist of several factors. In the absence of further analysis, however, we will consider it simply as the cell-elongation material, („Zellstreckungsmaterial", Z.S.M.). The distribution of growth along the coleoptile can be explained, according to Went, by these two factors, the growth substance and the cell-elongation material.

The Z.S.M. factor must be present in largest amount in the base and decrease towards the tip, while the distribution of growth substance is exactly the reverse. In the tip the growth will be limited by the Z.S.M., and in the base by the growth substance. According to Went, the limitation of growth by these two factors should follow an ideal Blackman scheme, the amounts of growth substance in the tip, and of Z.S.M. in the base, having no influence whatever on the growth. This conclusion was drawn from the curve relating quantity of growth substance supplied with increase in growth. This curve has indeed the appearance of a Blackman diagram, but one cannot safely deduce from it that the limitation by growth substance or by Z.S.M. must be complete immediately, especially since even in this curve a transitional region exists; (cf. Boresch, 1928, Romell, 1926, and van den Honert, 1928). If in the extreme tip the growth substance had no influence it would be exceedingly difficult to explain the occurrence of an asymmetry of the tip at the beginning of a phototropic or geotropic curvature. The existence of this asymmetry was at first denied by Went (1928 a), but later (1928 b) he partially changed his view. The curvatures which arise from a unilateral cut in the base of the coleoptile, as in the experiments of Beyer (1925), are also very difficult to explain if limitation by the Z.S.M. factor was strictly in accordance with the Blackman diagram. The curvatures in the experiments of Beyer show that even in the base the Z.S.M. has some effect.

I propose, therefore, to follow Went's description of the growth process, as a basis for discussion, but with the reservation that the two factors exert only a relative and not an absolute limitation on the growth. In the whole coleoptile, then, the growth depends on both factors, but their influence is quantitatively different. Thus, in the tip, a change in the Z.S.M. factor will cause a marked difference in growth, while a change in the amount of growth substance will have only a rather slight effect. In the base the reverse is the case. How far can now the curvatures which I have measured be explained with this hypothesis, together with the facts obtained in regard to the growth-substance distribution?

Examination of the curvatures produced in intact coleoptiles which have been placed horizontally for different times, makes clear that the total curvature is greater the longer the coleoptiles have been horizontal, (Figs. 8, 10 and 12; 9, 11 and 13). However, the records of the curvature in single zones show that the apical zones react to almost the same extent in all cases, while in the basal zones there is a great difference in the intensity of the curvature. It was shown in section III that under the lateral influence of gravity the growth substance becomes unequally distributed in the two halves of the coleoptile. The growth of the 2 halves is thus unequal. In the apical zones the difference in growth is not proportional to the amount of growth substance, and the unequal distribution in the growth substance will here have only a slight effect. If the geotropic curvature is exclusively the result of a change in the amounts of growth substance in the two sides, then the apical zones can only curve to a slight extent, but the basal zones should show a curvature proportional to the difference in the amounts of growth substance.

If now one examines the distribution of curvature over the coleoptile, it appears that the longer the plants have been kept horizontal the more rapidly does the curvature migrate towards the base, (see Figs. 9, 11 and 13). Thus, with a stimulation time of 7.5 minutes, the maximum curvature after 100 minutes is in zone 5; when the stimulation time is 15 or 30 minutes, it is in zone 7. This can be explained from the results in sections III and IV, in which it was shown that the change in the direction of transport of growth substance is not limited to the tip, but occurs also lower down. The presentation time of the lower zones is indeed longer, so that with a short stimulation time the perception of the tip is the dominant factor, but with longer stimulation other zones also begin to perceive.

A point of importance is that the curvature of each zone reaches a maximum and then falls off, the apical zones eventually becoming straight. This is the phenomenon known as autotropism.

Autotropism, unlike curvature, has been remarkably little studied, and different workers on the subject have held widely differing opinions. According to Sierp (1918) and van de Sande Bakhuyzen (1920), the autotropism which follows phototropic curvature is the result of the „dark growth reaction". On the other hand Koningsberger (1923) believes autotropism to be the result of internal factors, the photogrowth reaction consisting of 2 parts; (a) the true growth reaction, and (b) the antireaction, completely independent of the former, and causing the autotropic straightening. Pisek (1926) points out that autotropic straightening starts much later than the acceleration which constitutes the light growth reaction in bilaterally illuminated plants; he therefore does not consider straightening can be due to the light growth reaction itself. In contradiction to the above authors, Pisek considers further that the light growth reaction does not explain phototropic curvature either. Both Zollikofer and Weber have attempted to explain autotropism on the basis of the sinusoidal nature of growth reactions. Simon (1912) considers autotropism to be an autonomic anti-reaction to geotropism, while Lundegardh regards both as part of the curvature process, which is a resultant of several actions and antireactions.

In spite of the wide diversity of opinion, illustrated in the above paragraph, it is possible to relate the phenomenon of autotropism directly with the curvature which precedes it. An indication of this was given in the experiments on coleoptiles which were decapitated after geotropic stimulation, (Figs. 14—19). As mentioned in that section, no straightening occurs in this case until after the lapse of 2.5 hours, which is the time required for regeneration of the growth substance. The straightening of the apical zones is therefore influenced by the tip. This can be explained as follows:

In a coleoptile which has been horizontal for some time, the g.s. has been redistributed under the influence of gravity, so that the amount in the lower side, a_1b_1, is greater and in the upper side, a b, less (Fig. 26). The Z.S.M. factor will thus be more rapidly used up in the lower side and will soon reach a minimum. On the upper side less will be used. If, after cessation of the stimulus, the coleoptiles are rotated on the horizontal clinostat, the g.s. transport will soon become normal, (see Section III, table VI). On both sides of the coleoptile the same amount of g.s. will thus be transported to the base. Thus a b and a_1b_1 now both contain

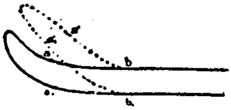

Fig. 26.

the same amount of g.s., but their growth will not be the same, since the distribution of Z.S.M. is now unequal. The growth of a b will be the greater, and this will continue until the zone is straightened out. During this time more g.s. was used at a than at a_1, so that the next zone b receives less g.s. than b_1. The growth at b is thus less than at b_1, and the curvature becomes intensified in this zone. In this way the curvature migrates towards the base, while the apical zones straighten out. Finally the curvature becomes fixed in the basal zones (Went, 1928 a) which do not straighten out (Pisek, 1926, Arisz, 1915).

Such an explanation is only valid for coleoptiles. In roots the process is doubtless more complex, since here, as was shown by Lundegardh (1918), strong anti-curvatures occur, the whole root sometimes curving in the opposite direction. So little, however, is known about the growth of roots, and particularly about the influence of the tip upon it, that further analysis of these curvatures is impossible.

This influence of the tip upon straightening appears not only in tropistic curvatures, but also in those caused by unilateral application of g.s. In these cases also the apical zones only begin to straighten 150 minutes after decapitation, (see Figs. 22—25). The same explanation as for geotropic curvature can here be applied. When larger amounts of growth substance are applied, it will not all have diffused out of the agar within 110 minutes, so that the difference in concentrations of g.s. on the 2 sides will persist for a longer time, and the apical zones will straighten less strongly. Even if the basal zones begin to curve, the curvature will thus remain localised in the apical zones, as in Fig. 25.

The course of phototropic curvature (Figs. 20 and 21) is most comparable with the latter case, for here the curvature of the base begins before any straightening of the apex. Went Jr. has shown that long after unilateral illumination the g.s. transport is still laterally polar, the difference between the amounts of g.s. in the two sides of the coleoptile being even larger during the second 75 minutes after illumination than during the first. The difference between the times during which transport remains laterally polar is clearly seen in the progress of the curvatures. That the curvature resulting from unilateral illumination begins so much later than that resulting from gravity is explained by the almost complete localisation of perception in the extreme tip in the first case, while in the second case the growing zones also perceive. It was pointed out above that the shorter the geotropic stimulation time the more dominant is the perception of the tip.

Summarising the above conclusions, it is shown that the explanation of geotropic curvature in *Avena* coleoptiles follows from the Cholodny-Went theory. Curvature arises from the influence of gravity on the correlation between tip and base, by which one of the factors controlling the growth process, namely the g.s., becomes temporarily unequally distributed and thus causes unequal growth on the 2 sides. The distribution of the other controlling factors is correspondingly shifted in the opposite direction, causing a subsequent straightening of the curved part. Since in phototropism the lateral polarity of g.s. transport lasts longer and is restricted to the tip, the course of the resulting curvature is different, but both are ultimately dependent on the same phenomenon.

The analysis of curvatures here given will no doubt prove in the future to be too simple, but a more complete knowledge of the growth process, and particularly of the hypothetical Z.S.M. factor, will be necessary before curvature can be completely explained. Furthermore, direct quantitative measurement of the differences between the growth of the two sides will need to be substituted for the indirect method used here.

B. *The perception of geotropism.*

The principal problem in connection with geotropism is that of how it is that the deviation from the normal g.s. transport occurs, and to this no solution has been offered. In the preceding it has been stated merely that gravity induces a polarity, which is only a restatement of the facts. The actual perception of gravity remains mysterious, and any mental picture of it that we can make rests on vague hypotheses. In the perception of light, photochemical processes probably play a part, and the light gradient across the coleoptile is in itself a kind of polarity. From the product law, it is probable that the influence of gravity is exerted on moving particles (Rutten—Pekelharing, 1910), but whether any part is played by statoliths has not yet been proved. That statoliths should cause pressure on part of the protoplast, resulting in geoperception, seems to me improbable. However the displacement of protoplasts may cause some movement of electric charges (Zollikofer 1921). Many investigators have adopted the view that movement of electric charges plays a role in geoperception, (Stoppel 1920, Cholodny 1923, Small 1920, Jost 1924). Brauner (1927, 1928) has shown a real difference in potential to occur under the lateral influence of gravity.

If geoperception depends on a displacement of charges, it may be possible to connect it with the polar transport of the g.s. Two possibilities are open; (a) the potential difference acts on the g.s., (b) the potential difference acts on the mechanism of the action of the g.s. If the g.s. is electrolytically dissociated, an E.M.F. could act upon it directly. Some experiments carried out to test this indicate that g.s. does not move in the electric field. For this, g.s. was isolated in agar in the usual way from *Mais* tips. Two pieces of agar containing the same amounts of g.s. were placed in contact between two platinum electrodes. A potential difference was applied, and after an hour the concentration of g.s. in the two pieces was determined. If the potential difference is large (e.g. 10 volts) then strong electro-endosmosis occurs, water being carried from one pole to the other. Under these circumstances any displacement of g.s. would not be significant. It must also be remembered that the current might inactivate the g.s. When 2 volts were used the electro-endosmosis was very slight, but the g.s. concentration remained the same in both blocks. Although these experiments are not conclusive, they indicate that g.s. does not move in an electric field. The method of Fürth (1929) i.e. use of a high tension discharge through poor conductors, would have avoided electrolysis and probably also electro-endosmosis, but the equipment was not available.

It is not, however, probable that there is any direct influence of a potential difference in geoperception. The potentials which would result from the influence of gravity are alle electrokinetic or ζ potentials. Unlike the true thermodynamic or ϵ potentials, the charges involved are of small capacity, so that the potentials can have only small energy. Since their forces are divided between all charged particles, the resulting deviation in transport of any one substance such as the g.s., can only be small.

The second possibility is that the potential difference acts on the transport mechanism. According to Brauner (1924) and Went (1928 a), protoplasmic streaming plays a part in g.s. transport. The potential difference, by making all cells polar, could so affect the streaming that it takes place in one direction only. If now in all cells the protoplasm streams in the same direction the whole tissue will be polarised and the g.s. will thus be transported in the new direction. Further, if the protoplasm in each cell, under the lateral influence of gravity, streams basipetally on the lower side and acropetally on the upper side, then the g.s. will be transported to the lower side of each cell. By passing through a number of cells the g.s. will thus become carried to the lower side of the coleoptile. Both polar transport and geoperception would find a place in this explanation. So long, however, as the mechanism of g.s. transport is unknown, the mechanism of geoperception will probably also remain unknown. A microscopic investigation of protoplasmic streaming under the influence of gravity might throw some further light on the problem.

Section VII.

THE INFLUENCE OF GRAVITY, ACTING LONGITUDINALLY, ON GEOTROPIC CURVATURE.

A. *Introduction.*

It was shown in section IV that it was not possible to calculate geotropic curvatures directly from the difference between the amounts of g.s. isolatable from the two sides of the tip after stimulation. In these experiments the coleoptile was placed vertically on agar, while for the registration of growth the plants were rotated horizontally, on the clinostat. It was therefore of interest to determine whether gravity, acting along the longitudinal axis of the coleoptile, has any effect on the geotropic curvature. The few experiments which could be carried out cannot be regarded as complete.

The investigations of Rutten—Pekelharing (1910), Fitting (1905), Tröndle (1913) Schneider (1925) and others have made it clear that the action of gravity varies with the sine of the angle of deviation from the vertical. At 90° it is therefore optimal. The force of gravity may therefore be resolved into 2 components, 1 acting perpendicular to the organ and the other along its longitudinal axis. Only the first of these was generally supposed to be active. In all these investigations either the presentation time was determined, or else the stimulation was intermittent. The stimulation time was thus very short. All these results differ from those of Czapek (1906) who found optimal action at an angle of 135° to the vertical, but he used long stimulation times.

It was later shown by various investigators that gravity acting in the longitudinal direction has, in fact, a real influence. Thus, acting longitudinally in the normal direction, it decreases the geotropic response, while in the inverse direction it increases it. Although all the experiments were carried out with roots, Bremekamp (1915) came to exactly the same conclusions with coleoptiles. The mechanism of this relation between *geotonic* influence and *geotropic* curvature is unknown. Koningsberger (1922), Nemecek (1924) and Weber (1927) have attempted to explain it by means of the geogrowth reaction which results from the longitudinal action of gravity. It was, however, shown in section II that the geogrowth reaction has no existence, so that this explanation is ruled out.

Nevertheless a true geotonic action was found, as will be described below.

An attempt to find a quantitative relation between the geotropic and geotonic effects was made by von Ubisch (1925). The geotonic effect was considered to be proportional to the cosine of the angle of deviation from the vertical, so that at a certain angle, whose value varied with the type of root used, the geotonic inhibition should become so great as to prevent the occurrence of any curvature. According to von Ubisch, the following relation then holds:

$g \sin \alpha = l \cos \alpha$, l being a measure of the geotonic factor. This formulation has been criticised by Rawitscher (1926) and by Zimmermann (1927 b). The latter considers it quite unproven that the cosine rule holds for geotonic action, so that it is not allowable either to divide gravity into two components or to calculate the value of the geotonic component by this means. He points out also that one side of the equation expresses a tendency to curve while the other expresses an inhibition, and it is very improbable that they can be connected in this way. Both these authors consider that the geotonic action is really proportional to the lateral stimulus, as I also suggested in my earlier publication (1929 a). After the conclusion of my experiments the same views were expressed in a detailed paper by Metzner (1929). Metzner gives the following equation:

$G = gt \sin \alpha - gt \sin \alpha \; k \cos \alpha = gt \sin \alpha \; (1 - k \cos \alpha)$, where G is the geotropic effect and t the stimulation time; the first term thus indicates induction and the second term inhibition. k is a constant for the geotonic effect. The inhibition would thus be proportional to the preceding induction. Metzner calls this the „Erweiterte Sinusgesetz".

How can it be explained that the geotonic effect did not appear in those experiments which proved the sine rule for geotropism? It has already been shown that the time factor is of considerable consequence. That component of gravity which acts in the lenghtwise direction can only influence the curvature impulse which precedes it, so that the geotonic effect can only appear when gravity acts, at a definite angle to the vertical, for a long time. In experiments on presentation time, the stimulus time is usually so short that the geotonic effect is not appreciable. If the equation of von Ubisch were true, on the other hand, the geotonic effect should appear even at small angles from the vertical, for the smaller the angle of deviation, the longer is it necessary to stimulate to get minimal curvature; the geotonic effect, since it follows the cosine rule, should thus be nearly maximal. From the equation of Metzner, however, the geotonic effect varies both with the sine and the cosine, hence it will not increase strongly at small deviation angles, for the increase in the cosine is accompanied by a decrease in the sine.

B. *Experimental.*

The first experiments were carried out to determine the effect of gravity, acting in the longitudinal direction, on the geoinduction which precedes it. Coleoptiles were stimulated for 10 minutes, then placed vertical, either normal or inverted, for 15 minutes,

TABLE XXI.

Geotropic curvature of coleoptiles stimulated for 10 minutes horizontally, placed vertically for 15 minutes in the normal or inverse position, and finally rotated for 45 minutes on the horizontal axis of the clinostat.

No. of plants	Geotropic curvature in degrees	
	Normal vertical position	Inverted vertical position
14	7.5	9.5
12	3.0	9.6
38	6.9	18.1
35	6.0	14.5
13	5.4	16.3
18	6.8	13.5
9	7.3	17.4
	42.9	98.9

and subsequently rotated on the horizontal axis of the clinostat. The data (table XXI) show that when gravity acts inversely the curvatures are much greater than when it acts in the normal direction. Control experiments, in which the coleoptiles were rotated horizontally immediately after stimulation, gave a value intermediate between the two.

To determine whether the geotonic effect depends *only* on the preceding geoinduction, coleoptiles were placed horizontal for varying times, and thereafter placed vertical either, normal or inverted, for a fixed time, 10 minutes. Finally they were rotated on the clinostat as before. If the geotonic effect is independent of the geo-induction, then with a small lateral stimulus it must appear proportionately more strongly than with a large stimulus. If, however, the geotonic effect depends on the amount of preceding geo-induction, then all stimuli will be affected in the same proportion. This is believed by Metzner to be the case. The results, given in tables XXII, XXIII and XXIV, show that with short stimulation time (5 minutes) the curvatures are nearly the same with coleoptiles placed normal or inverted, but with longer stimulation times the difference increases. For the equation of

TABLE XXII.

Geotropic curvature of coleoptiles stimulated for 5 minutes horizontally, placed vertically for 10 minutes in the normal or inverse position, and finally rotated for 30 or 45 minutes on the horizontal axis of the clinostat.

No. of plants	Period of rotation in minutes	Geotropic curvature in degrees	
		Normal vertical position	Inverted vertical position
12	45	5.8	5.3
12	45	5.4	5.7
15	45	4.7	4.8
12	45	4.2	4.6
18	30	3.9	3.9
21	45	2.1	2.2
23	30	4.1	7.0
17	30	5.4	4.5
21	30	4.3	5.7
16	30	4.5	5.8
24	30	4.0	6.5
25	30	4.8	5.3
13	30	4.6	5.1
		57.8	66.4

TABLE XXIII.

Geotropic curvature of coleoptiles stimulated for 10 minutes horizontally, placed vertically for 10 minutes in the normal or the inverse position, and finally rotated for 45 minutes on the horizontal axis of the clinostat.

No. of plants	Geotropic curvature in degrees	
	Normal vertical position	Inverted vertical position
16	11.1	16.0
13	10.1	15.8
13	5.0	11.4
15	4.6	7.4
15	6.4	7.9
15	6.6	7.3
14	4.4	5.2
11	3.2	5.5
11	2.3	7.0
11	6.1	6.8
24	5.6	8.6
24	5.4	9.4
23	4.5	11.0
12	6.4	9.6
14	5.0	7.5
	86.7	136.4

TABLE XXIV.

Geotropic curvature of coleoptiles stimulated for 15 minutes horizontally, placed vertically for 10 minutes in the normal or the inverse position, and finally rotated for 45 minutes on the horizontal axis of the clinostat.

No. of plants	Geotropic curvature in degrees	
	Normal vertical position	Inverted vertical position
12	6.5	8.3*
12	4.5	7.7*
11	5.8	9.3
11	8.8	11.4
28	8.5	11.8
29	5.7	14.4
24	8.5	13.1
9	4.8	8.0*
14	7.5	10.0
	60.6	94.0

(* Plants unusually long; less sensitive) von Ubisch, the differences should be greatest for small stimuli.

Following Metzner, the geotropic effect for inverted coleoptiles, is (the sine and the cosine always being 1):

$$G_1 = gt + gt\ k\ t'.$$

and for normal coleoptiles

$$G_2 = gt - gt\ k\ t',$$

where t is the stimulation time and t' the time during which the coleoptiles were either normal or inverted. The ratio:

$$\frac{G_1}{G_2} = \frac{1 + kt'}{1 - kt'}$$

and since t' is constant the fraction must be a constant. In the last two experiments this ratio was in fact constant (1.57 and 1.55) but in the first it was considerably smaller (1.15). It may be noticed that with stronger stimulation the response is no longer proportional to the amount of excitation (cf. Fitting, 1905).

The slighter tonic influence resulting from a smaller stimulation can be explained in two ways; (a) the geotonic effect is not proportional to the preceding geoinduction but to some power of it, or (b) a time factor is involved. In the above experiments the longitudinal action of gravity did not always start at the same moment, for the shorter the stimulation time used, the sooner the geotonic effect was allowed to begin, and consequently its effect might have been weaker. The experiments of Zimmermann point in this direction, and Metzner has indicated the same thing.

This phenomenon was not worked out completely, owing to lack of time. It is clear, however, that in the experiments of Rutten—Pekelharing and Schneider the apparent validity of the sine rule was due to the slightness of the stimulus, which made it impossible for the geotonic effect to be observed.

SUMMARY.

1. When all growth substance is removed from the *Avena* coleoptile, growth comes to a standstill, and only recommences when growth substance is again present.
2. Unter the influence of the lateral action of gravity the total amount of growth substance produced in the coleoptile does not change.

3. The growth of the *Avena* coleoptile is not affected by rotating on the horizontal axis of the klinostat and subsequently returning to the vertical position.

4. The lateral action of gravity changes the direction of transport of the growth substance, so that more goes to the lower side of the coleoptile, and less to the upper. This was proven both for *Avena sativa* and for *Zea Mays.*

5. Shortly after the termination of the stimulus, the growth substance transport is again normal.

6. The deviation from normal transport is not limited to the tip, but occurs also in the more basal zones.

7. The geotropic sensitivity of the coleoptile decreases only slowly from the tip to the base, a zone about 10 mm long being sensitive.

8. The course of the curvature was registered with a cinematographic camera, and compared with the curvatures resulting from phototropism and from the unilateral application of growth substance.

9. The curvature of geotropism was thus found to move down the coleoptile more rapidly than that due to phototropism. The apical zones begin to straighten out soon after the stimulation.

10. The course of the curvatures can be explained qualitatively, on the theory of Went and Cholodny, by the change in growth substance transport.

11. The presence of the tip is one of the factors controlling the autotropic straightening of the apical zones.

12. The geotropic curvature is due to the temporary deviation of the transport of growth substance to one side of the coleoptile over a considerable zone. This deviation leads to the using up of the other factors necessary for growth, and thus allows autotropic straightening to take place.

13. A possible mechanism whereby the perception of gravity results in a deviation from the normal growth substance transport is suggested.

14. The chain of reactions constituting geo-induction is influenced by the subsequent action of gravity in the longitudinal axis of the coleoptile.

15. The shorter is the geo-induction, the smaller is the subsequent influence of gravity acting longitudinally. This influence therefore does not appear in determinations of the presentation time.

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