Huygens Institute - Royal Netherlands Academy of Arts and Sciences (KNAW)
Citation:
C.E.B. Bremekamp, On the mutual influence of phototropic and geotropic reactions in plants, in: KNAW, Proceedings, 17 III, 1914-1915, Amsterdam, 1915, pp. 1278-1291
This PDF was made on 24 September 2010, from the 'Digital Library' of the Dutch History of Science Web Center (www.dwc.knaw.nl) > 'Digital Library > Proceedings of the Royal Netherlands Academy of Arts and Sciences (KNAW), http://www.digitallibrary.nl'

Botany. — "On the mutual influence of phototropic and geotropic reactions in plants." By Dr. C. E. B. Bremekamp. (Communicated by Prof. F. A. F. C. Went).

(Communicated in the meeting of March 27, 1915).

## § 1. Introduction.

It is conceivable that part of the quantity of unilaterally incident light which is just sufficient to cause a naked eye curvature in etiolated Avena coleoptiles, might be replaceable by a geotropic induction of shorter duration than the presentation time. Starting from this supposition Mrs. C. J. Rutten—Pekelharing 1) has carried out a number of experiments in which the seedling received both a light- and a gravitational stimulus, either simultaneously or in rapid succession and both lasting about two-thirds of what had been found to be the phototropic and the geotropic presentation time. These experiments gave uniformly negative results. Macroscopic curvatures were never observed.

Experiments of Mad. Polowzow 2) and of Maillefer 3) on geotropic curvatures and of Arisz 4) on phototropic ones, have shown that after a stimulus which had no macroscopic effect, deviations from the original position could nevertheless be demonstrated with suitable apparatus. In this connection the results of Mrs. Rutten's experiments are somewhat puzzling. An obvious deduction from them would be that light exercises an unfavourable influence on the gravitational reaction or, alternatively, gravity on the phototropic curvature. Before abiding by this conclusion, however, it is necessary to take another possibility into consideration.

Statements in the literature show, that in many cases a marked difference may be observed between the rates at which the phototropic and the geotropic reaction processes proceed. The gravitational curvature is generally visible sooner and reaches its maximum more quickly. When therefore the two stimuli are applied simultaneously or immediately after one another, there is every chance that the phototropic curvature will only have reached a very small value when the geotropic one has already passed its maximum and that, when

<sup>1)</sup> C. J. Rutten—Pekelharing. Untersuchungen über die Perzeption des Schwerkraftreizes. Recueil des Trav. Botan. Néerl. Vol. VII. 1910.

<sup>&</sup>lt;sup>2</sup>) W. Polowzow. Untersuchungen über Reizerscheinungen bei den Pflanzen. Jena 1909.

s) A. Maillefer. Etude sur la réaction géotropique. Bull. Soc. Vaud. Sc. Nat. XLVI. 1910. Nouvelle étude experimentale sur le géotropisme. ibidem XLVIII. 1912.

b) W. H. Arisz. Proceedings K. Akad. v. Wet. Amsterdam. 1911.

thereupon the light curvature begins to approach its maximum, there remain only traces of the other. There can in this case be no question of a clear reinforcement of the first reaction by the second. On the other hand, this reinforcement may be expected to be very pronounced, when so much time elapses between the stimuli that both curvatures reach their maxima at the same time.

It is convincingly proved by experiments which are described in the following section, that a complete summation does indeed take place in this last case. Moreover the surmise was confirmed that, when a small light-stimulus and a geotropic induction are applied simultaneously or in rapid succession, the geotropic curvature reaches its maximum before the phototropic one is clearly visible and has more or less disappeared again, when the latter has attained its greatest value. Mrs. Rutten's results thus find a simple explanation.

We must, however, guard against concluding from these data that there is no modification of the phototropic reaction, due to gravity, or of the geotropic curvature under the influence of light.

PFEFFER 1) has already pointed out the possibility of such changes. Excepting, however, certain special cases relating to plagiotropic organs (e.g. rhizomes of Adoxa, in which case STAHL first showed a change in the geotropic reaction under the influence of light) this phenomenon has not been completely demonstrated. (Compare Guttenberg 2)). I have succeeded in finding several examples of this in Avena seedlings. The reversal of the geotropic reaction after omnilateral illumination of certain duration may be put forward as a striking case. Details and discussion relating to these phenomena are embodied in sections 3 and 4.

## § 2. Summation of phototropic and geotropic curvatures.

After it had been found, in a number of preliminary experiments of which details may here be omitted, in what time light- and gravitational curvatures, as reactions to stimuli of definite strength, reached their maxima, I arranged the experiments in the following way.

I used for illumination a 10 candle-power Osram-lamp fed by an storage battery, which I kept constant at 10 volts. Since this had however drawbacks, the battery was strengthened later and the current was kept at the desired strength by the use of an adjustable

<sup>1)</sup> W. Pfeffer. Planzenphysiologie. 1 Aufl. 1881, Bd. 2, p. 338.

<sup>2)</sup> H. RITTER VON GUTTENBERG. Ueber das Zusammenwirken von Geotropismus und Heliotropismus in parallelotropen Pflanzenteilen. Pringsheim's Jhrb. XLV. 1908.

resistance. At a certain distance from the lamp were placed boxes of Avena seedlings which were always put in such a position that their longitudinal axis made a small angle with the direction of the rays of light, so that the seedlings which to the number of 17 to 20 stood in each box in one row, did not shade each other. For the geotropic stimulation the boxes were put upright on one of the narrow sides. For further details reference must be made to the fuller communication, which will appear later.

The apparatus was placed in a part of the laboratory greenhouse at Utrecht fitted up as dark room, where arrangements for ventilation and warming make it possible to carry out experiments at constant temperature and in pure air. In this case the temperature was kept at 21° C.

A series of experiments was generally carried out with six boxes. Nos. 1, 2, 3, and 4 were stimulated phototropically for six or ten seconds; No. 1 at a distance of 70 cm. from the lamp, the other ones at one metre. The geotropic stimulation of boxes 3, 4, and 5 began 50 minutes after the illumination and lasted 20 minutes (in some series 15 min.). Box 3 was placed upright in such a way that the side which during illumination had been in front, was now underneath, whilst with box 4 the front of the illumination came uppermost; 6 had already been placed upright 20 (in other cases 15) minutes earlier and remained 40 (or 30) in this position. Two hours after illumination, i.e. 50 minutes after the end of the geotropic stimulation, the light as well as the gravitational curvature had reached its maximum; at that moment their magnitude was noted. For this I used a method recommended by LINDNER<sup>1</sup>), in which a lamp, placed at a sufficient distance, throws a shadow of the box on a strip of bromide paper, stretched immediately behind. This was later developed and preserved as protocol of the experiment. The horizontal deviation from the apex in mm. served as a measure of the curvature.

In order to ascertain how far the average deviation of the 17—20 seedlings in one box furnished a sufficiently reliable value, five boxes were stimulated in the same way phototropically and geotropically: first illuminated unilaterally for six seconds with an intensity of 10 M.C. and then 50 minutes afterwards placed upright and left for 20 minutes in this position. After  $2^1/4$  hours the deviations in m.m. amounted to:

3.2, 3.2, 3.3 and 3.3.

<sup>1)</sup> P. LINDNER, Ber. d.d. Bot. Ges. XXXII, 4. 1914.

The values found in the experiments are collected in the following table. Each horizontal line represents a separate series. The figures in brackets indicate the magnitude of the light stimulus in metre candle seconds (MCS) and the duration of the gravitational stimulus in minutes.

	1	2	3	4	5	6
I	2.8 (200)	2.6 (100)	_	3 6 (100 + 15 mm)	0.8 (15 min.)	1.3 (30 min.)
II	2.5 (120)	1.9 (60)	1 O (60—15 min.)	2.2 (60+15 ")	0.4 (15 ")	1.6 (30 ")
III	2.3 (120)	2.1 (60)	_	3.2 (60+15 ,, )	1.0 (15 ")	1.6 (30 ")
IV	2.7 (120)	2.5 (60)	0.5 (60—20 ")	3.1 (60+20 ,, )	1.7 (20',, )	2.9 (40 ")
V	2.2 (120)	1.6 (60)	-0.2 (60-20 ")	2.5 (60+20 ,, )	1.4 (20 ")	2.1 (40 ")
VI	2.4 (120)	2.1 (60)	1.2 (60-20 ")	3.4 (60+20 ,,)	1.2 (20 ")	2.6 (40 ")
VII	2.0 (120)	1.4 (60)	-0.2 (60-20 ,, )	2.6 (60+20 ,, )	1.2 (20 ")	2.0 (40 ")

The fairly considerable divergence which sometimes occurs between the series, is explained by the difference in length of the seedlings used; thus those of IV were very tall, those of VII very short: in connection with this comparison should be made with Arisz' data 1) for phototropic curvatures and with Maillefer's detailed tables for geotropic ones (1912 l.c.).

When the experiments were taking place it could be noted that the phototropic curvatures were often already visible before the end of the gravitational stimulation. In those seedlings in which light-and gravitational curvatures acted in opposite direction, the phototropic one extended already lower down, at the moment when the geotropic one became visible at the apex, so that the coleoptile temporarily acquired a weak S-shaped bend.

As the figures show, the curvature which arises when light and gravity bring about deviations in the same direction, more or less equals the sum of the curvatures which each stimulus calls forth, when acting separately. When they act in opposition to one another, then the resulting deviation is approximately the same as the difference of the separate deviations. In the following table the relative figures are once more placed side by side with the sums and differences calculated from 2 and 5 placed between brackets after those found.

<sup>1)</sup> W. H. Arisz. Onderzoekingen over fototropie. Diss. Utrecht. 1914,

2	5	4	3
2.6	0.8	3.6 (3.4)	
1.9	0.4	2.2 (2.3)	1.0 (1.5)
<b>2</b> .1	1.0	3.2 (3.1)	
2.5	1.7	3.1 (4.2)	0.5 (0.8)
1.6	1.4	2.5 (3.0)	-0.2(0.2)
2.1	1.2	3.4 (3.3)	1.2 (0.9)
1.4	1.2	2.6 (2.6)	-0.2(0.2)
	2.6 1.9 2.1 2.5 1.6 2.1	2.6 0.8 1.9 0.4 2.1 1.0 2.5 1.7 1.6 1.4 2.1 1.2	2.6 0.8 3.6 (3.4) 1.9 0.4 2.2 (2.3) _ 2.1 1.0 3.2 (3.1) 2.5 1.7 3.1 (4.2) 1.6 1.4 2.5 (3.0) 2.1 1.2 3.4 (3.3)

This complete summation is all the more remarkable when the figures are compared with those of the illumination with the double amount of energy. These remain everywhere behind the summation curvatures. We find here a confirmation of the surmise that the phototropic curvature does not remain below a certain maximum in consequence of increased mechanical resistance, but that in reality under the influence of the illumination there occurs a change of condition in the plant, whereby the phototropic curvature with increase of the stimulus finally again diminishes and may even attain negative values, as CLARK 1) and ARISZ 2) have shown for Avena.

If the gravitational stimulus is applied immediately after illumination, then the geotropic curvature has almost completely disappeared when the phototropic one reaches its maximum. A single example will suffice to show this.

Deviations in mm.  $2^{1}/_{4}$  hours after the beginning of the experiment:

2	3	4	5
1.6 (40)	1.3 (40 –20 min.)	1.9(40+20 min.)	0.4 (20 min.)

The maximal geotropic curvature 50 minutes after the cessation of stimulation amounted in this case to about 1.5 mm. The small deviation which still remains after  $2^{1}/_{4}$  hours, shows itself clearly however in the figures of 3 and 4.

In some experimental series the boxes were placed on the clinostation before and after stimulation in order to eliminate the opposing

<sup>1)</sup> O. L. Clark, Über negativen Phototropismus bei Avena sativa. Zeitschr. f. Bot. V. 1913.

<sup>2)</sup> W. H. Arisz. Proceedings K. Akad. v. Wet. Amsterdam. October 1913.

effect of gravity. 1) It is of little importance in this case whether the stimuli are applied immediately after one another or with a certain interval between them. The speedy falling off of the curvature as soon as it has reached its maximum, is not observable in plants which turn on a horizontal axis. On the other hand the phototropic reaction goes on for so much longer than the geotropic one (a difference of hours) that it is experimentally impossible to make the maxima coincide. We must in this case therefore limit ourselves to establishing that the curvature of seedlings to which both stimuli have been applied, according as they have acted to reinforce or counteract each other, equals the sum or the difference of the curvatures which are shown by two groups of controls of which one is only illuminated and the other only stimulated geotropically. This is found to be possible at any moment, chosen arbitrarily. In the following example the geotropic stimulation was administered 50 minutes after the phototropic and the record was made 5 hours after the commencement of the experiment.

2	3	4	5
7.7 (100)	5 5(100 – 20 min.)	11.1 (100+20 min.)	3.3 (20 min.)

Since it might be considered objectionable when dealing with such marked curvatures to take the horizontal deviation of the apex as a measure, I have in addition determined the angle of the curvature. For the sake of simplicity I considered the curvature as a circular arc, to which the lines bisecting the base and the apex — which latter at this moment has become straight again, — are tangents. The supplement of this arc gives an idea of the distance travelled. This amounts to:

2	3	4	5
470	35°	66°	15°

There is here therefore also a complete summation.

The experiments which are described in this section, lead to the following conclusion:

85

Proceedings Royal Acad. Amsterdam. Vol. XVII.

<sup>1)</sup> In very small carvatures, it is principally the longitudinal component which opposes the reaction. Cf. § 4.

The reactions to small light and gravitational stimuli do not noticeably influence each other.

§ 3. Changes in the phototropic and geotropic reactions under the influence of light.

Up to this point we only used unilateral illumination of fairly slight intensity. The question now is whether other results are obtained by the application of greater quantities of light. By changing the duration of illumination as well as its intensity it is possible to bring about modifications in the phototropic reaction which for our purpose we may arrange in two different categories: 1. reversal of the direction of the curvature and 2. change in the rate of reaction. If we wish to know how a definite phototropic curve at its maximum extent is combined with a maximal geotropic deviation, we have only to determine the length of time after which the maximal light-curve is reached and then to administer the two stimuli with such an interval that the curvature maxima coincide.

In carrying out these experiments it is found to be quite immaterial whether we are concerned with a positive phototropic curvature or one in the opposite direction and whether the maximum is reached after a shorter or longer time. Summation always takes place.

This is, however, not the end of the process. If, after stimulation, the seedlings are placed on the clinostat and observation is continued for a considerable time, then one begins to note deviations, at least when there has not been too great an interval of time between the two stimulations. By summation of curvatures of the same direction apex curvatures finally occur in opposite direction and seedlings in which opposite curvatures have been induced, sometimes show stronger curvatures.

The same phenomenon was to be observed when unilateral was replaced by\_omnilateral illumination.

During illumination which in different experiments was varied in strength as well as in duration, the seedlings were rotated at constant velocity round their axis. When illumination ceased, they were immediately placed in a horizontal position and stimulated geotropically for some time.

Already in the first series of experiments differences were obvious. The distance from the Osram lamp- of 10 candle power amounted in this case to 2 metres. The times of illumination are in the following table placed in the top line, with the product of intensity and duration in metre-candle-seconds (M.C.S.) placed between brackets. The last box was not illuminated beforehand. The geotropic induction lasted

1285

20 minutes. Examination took place 55 minutes after its end. As in the former section the horizontal deviation of the apex in mm. is given as a measure of the curvature.

20 min. (3000)	10 min. (1500)	5 min. (750)	2.5 min. (3 <b>7</b> 5)	1 min. (150)	30 sec (75)	_
0.5	0.7	0.8	0.7	0.9	1.4	1.4

These figures were confirmed in different series of experiments. In these it was further noticed that the curvatures arose everywhere at the same time and at first also increased at the same rate.

Thus further observations were suggested with the object of seeing to what these differences arising in the course of the curvature-process might lead.

In the following table the magnitude of curvature after 40 minutes and after 2 hours are placed side by side.

Duration of	Strength of	Product M.C.S.	Cı	urvature
illumination	illumination	Product M.C.S.	After 40 min.	After 2 hours
300 sec.	2.5 MC	750	0.8	-0.9 (0.1)
150 "	2.5 MC	375	1.5	-0.4 (1.1)
180 "	1/8 MC	<b>2</b> 2.5	2.0	
90 "	1/8 MC	11.25	2.1	_
Not illuminated			2.0	-0.0 (1.4)

The duration of the geotropic stimulation amounted to 30 min. Seedlings which were illuminated beforehand with 750 and 375 M.C.S., showed a clear S-shape after 2 hours. The apex of those that were not illuminated, was quite straight. The figures given are the apex-curvatures. Placed after in brackets are the figures which indicate the amount of the remainder of the original curvature, calculated on the assumption—that the apex was straight. The antagonistic geotropic curvature was not yet measurable as is shown by the last line. The curvatures of the previously illuminated seedlings cannot therefore be ascribed to this cause. Experiments in which, after the cessation of geotropic stimulations, plants were placed on the clinostat, have indeed convincingly proved that without

the unilateral opposition of gravity, curvatures arise in a contrary direction in plants previously illuminated omnilaterally.

These experiments can be simplified by illuminating the seedlings from above instead of making them perform a certain number of revolutions during illumination. This has been done in all subsequent experiments. The quantity of light is again given in M.C.S.; in connection with this it should be remembered that it of course makes a difference to the plant whether the uppermost part of the apex only is constantly exposed to the light or whether successively the whole surface. Further, another sort of incandescent lamp was used in these experiments.

Geotropic stimulation lasted 30 minutes. After this removal to the clinostat. Examination  $3^{1}/_{2}$  hours after the completion of stimulation.

_				
3	Duration of illumination	Strength of illumination	Product MCS	Curvature
_	16 min.	8 MC	4000	- 1.0
	4 "	8 MC	1000	- 1.1
	1 "	8 MC	250	+ 0.7
	15 sec.	8 MC	60	+ 1.6
		_	-	+ 1.6

In other experiments the duration of the geotropic stimulation was changed, e. g.:

Time of illumination 20 min., strength 8 M.C., product 5000 M.C.S. Horizontal during

40 min.	20 min.	10 min.	5 min.	_
- 0.9	- 2.5	- 2.0	- 1.8	(3 hours on the cli- nostat).

As is seen, the result is only slightly dependent on the duration of the geotropic stimulation.

The fact that in 40 min. a great deviation is observed, is undoubtedly connected with the fairly rapid cessation of the influence of preliminary illumination. When half-an-hour is allowed to elapse between illumination and geotropic stimulation, the influence of the first factor can no longer be demonstrated with certainty. This result is in remarkable agreement with the rapid disappearance of the

phototropic change of sensitiveness after preliminary illumination (Arisz 1914 l. c. "fading of the excitation").

CLARK I. c. has described experiments in which a unilateral geotropic stimulation was followed by omnilateral illumination. Under these conditions also there occurs a curvature in contrary direction. With regard to the nature of the curvature which arises, it is difficult to form a definite judgment by this method of experimentation, because the geotropic stimulation induces a dorsiventrality (as yet not outwardly visible). A dorsiventral organ can, however, quite easily react to an omnilaterally symmetrical stimulus with a curvature of definite direction. In connection with the experiments described above it is however indeed probable that the curvatures mentioned by Clark correspond to those observed in the present investigation.

May we now regard these curvatures as positively geotropic? Before answering this question, we may briefly examine the curvatures of opposite direction which arise in other cases and consider whether it is possible to form a simple conception of the way in which they arise. I have chosen Avena coleoptiles for a further analysis, because in their case inverse phototropic curvatures are very easily obtainable.

In Arisz' experiments (l. c. 1914), in which the seedlings were given an omnilateral preliminary illumination of varying duration, it was found that the sensitiveness rapidly diminished at the beginning, and after more prolonged illumination increased again somewhat.

If the intensity of illumination was also varied, then the initial decrease in sensitiveness was seen to take place more rapidly according as the seedlings were exposed to stronger light, whilst the return of sensitiveness was thereby slightly delayed. Since when illumination is unilateral the front absorbs part of the light, the back receives less light. The consequence of this is that there the sensitiveness during illumination declines less markedly than in the front. When therefore after some time the sensitiveness of the front has more or less disappeared, the reaction of the posterior side can predominate. The result must then be a curvature away from the source of light.

In order to find out whether the here postulated differences in sensitiveness of the anterior and posterior sides can actually be observed, I have made a series of experiments in which three groups of boxes were always compared. The first group consisted of one box, the other two of from four to eight. The experiment began with an equally long and equally strong unilateral illumination of all the boxes. Afterwards the box of the first group was placed in

the dark and those of the other two groups stimulated again with different quantities of light, one group from the same side as before, the other from the opposite side. Finally, the curvatures obtained were compared. In this way I succeeded in showing that after a unilateral illumination sometimes important differences in sensitiveness of the posterior and the anterior sides occur. These are greatest in the neighbourhood in which the negative curvature begins to arise. Further data on this point will be published later.

We arrive therefore at the conclusion that the curvature away from the source of light arises, because the sensitiveness of the anterior side diminishes more quickly than that of the posterior and consequently the reaction predominates at the back.

This leads us further to deny the possibility of any direct comparison of this curvature with the negative phototropic reaction of roots which is not preceded by a positive one 1) and remains on continued illumination. We ought therefore henceforth to distinguish the curvatures of contrary direction which occur in Avena coleoptiles by another name. They may be called *antiphototropic*.

Is it now possible to explain in the same way the contrary curvatures which arise when coleoptiles of Avena are stimulated geotropically after preliminary omnilateral illumination and the negative geotropic curvatures which Jost and Miss Stoppel. 2) were able to observe in roots of *Lupinus albus* which were exposed to high centrifugal forces? Evidently not. The difference of pressure must always be the same in the cells of the upper and lower side. A

<sup>1)</sup> K. Linsbauer and V. Vouk. (Zur Kenntnis des Heliotropismus der Wurzeln. Vorl Mitteilung. Ber. d. d. bot. Ges. Bd. 27. 1909) have stated that in roots of Sinapis alba and Raphanus sativa small intensities of light cause positive curvatures and greater intensities negative ones. Your has described these experiments somewhat more fully (Zur Kenntnis des Phototropismus der Wurzeln. Sitzungsber. d. K. K. Akad. d. Wiss. zu Wien Bd. 121. Abt. I. 1912). It results from this that the positive phototropic curvatures which these investigators observed in Sinapis alba, arose when there was illumination for 15 hours with an intensity of 064 M.C.; therefore by a quantity of light of 34.560 M.C.S. Your on page 503 gives a table, in which are found different examples of illumination with 128 M.C. during 5 minutes, by which means a quantity of light amounting to 38.400 M.C.S. was applied. The occurrence of a positive curvature is nowhere mentioned. Moreover with illumination lasting 2 minutes no positive curvature arose either. This discrepancy permits us to doubt the phototropic nature of the curvatures found. It is moreover quite unintelligible why even in the most favourable case not more than  $71^{\circ}/_{0}$  of the roots reacted in this manner.

<sup>2)</sup> L. Jost und R. Stoppel. Studien über Geotropismus II, Zeitschr. für Bot. Bd. IV. 1912.

direct reversal of the reaction would only be possible through a reversal of the polarity of the cells, a hypothesis far from simple and hitherto not susceptible of experimental verification. For this reason I may direct attention to another possibility.

In the cells which are given preliminary illumination, phototropic reactions are in progress which cannot lead to curvatures, because they keep each other in equilibrium. In consequence of the geotropic stimulation this equilibrium is now upset. It might be imagined, for example, that the geotropic stimulation displaces or destroys a substance necessary for the phototropic reaction. The resulting curvature would in reality therefore be phototropic. It is not impossible that also in the experiments of Jost and Miss Stoppel an omnilateral stimulation (perhaps hydrotropic) thus expresses itself as a curvature.

## § 4. Changes of the geotropic and phototropic reactions under the influence of gravity.

According to Marie-Marthe Risz 1) an omnilateral gravitational stimulus has no effect on the sensitiveness with respect to a subsequent unilateral one. From the data in the second part of her paper, however, one may deduce that this is not correct. For Miss Risz there proves, that the component of gravity in the direction of the organ 2) weakens the reaction. After an omnilateral gravitational stimulus acting at an angle of 90° and having therefore a longitudinal component equal to 0, the reaction must be stronger than when the plant is placed vertically for the stimulation (longitudinal component + mg.). This was indeed the case in my own experiments.

Some boxes rotated for a certain time round the horizontal axis of the clinostat and were subsequently subjected to a unilateral gravitational stimulus simultaneously with a control box. I examined the curvatures forty minutes after the end of stimulation.

Differences such as those found here, are also observable when the boxes are placed for some time in the reverse position (longitudinal component — mg.).

Duration of unilateral geotropic stimulus 30 minutes. Previously placed on the clinostat during.

11

<sup>1)</sup> Marie-Marthe Risz. Über den Einflusz allseitig und in der Langsrichtung wirkender Schwerkraft auf Wurzeln. Jhrb. f. wiss. Bot. LIII. 1913.

<sup>2)</sup> I already pointed out in 1912 the importance of this component. Die roticrende Nutation und der Geotropismus der Windepflanzen. Rec. d. Trav. Bot. Néerl. 1X. p. 298-301.

2 hours	1 hour	½ hour	Control
_	2.5	2.2	2.1
1.7	1.7	1.8	1.5
2.7	_		2.3

Much more distinct differences occur when transverse and longitudinal gravitational stimuli are applied simultaneously. A slight modification of Miss Risz' procedure enables us to demonstrate also the influence of the longitudinal component, when the latter has a negative value. With this object two boxes are placed parallel to the vertical axis of the centrifuge so that the seedlings in one box have their apices turned towards the axis, in the other away from it. If now such a revolution-velocity is given to the axis as to apply to the seedlings a force mg. then the longitudinal component for the first box is + mg. and for the second - mg. Furthermore gravity acts on the seedlings at the same time. After centrifuging the boxes were again placed in their original position. A box which for the same length of time had been horizontal, served as control, since in this case the longitudinal component is 0.

With a stimulation of 30 minutes the curvatures were 40 minutes after its cessation:

— mg	С	+ mg
2.9	1.6	0.2
3.4	1.5	0.3
3.9	`2.2	0.9
		1

If a unilateral light-stimulus is applied after an omnilateral gravitational stimulus, then similar differences can be observed.

For this the boxes are again placed on the centrifuge, whose axis this time is horizontal. After 30 minutes centrifuging the seedlings are illuminated during 6 seconds with an intensity of 10 M.C. The control box, which remained in its ordinary position, was naturally subjected to the same conditions as the seedlings on the centrifuge, which had their apices pointing towards the axis. In both cases the longitudinal component was + mg.

1291

After 2 hours the curvatures amounted to:

— mg	С	+ mg
2.5	1.5	1.5

The influence of the longitudinal component is therefore once more evident.

The term longitudinal component of gravity is of course only a phrase. No way of explaining it physiologically has so far been found.

The phototropic curvatures of the coleoptiles of Avena when illuminated at different angles, showed a very marked deviation from the expected sine relation. As Arisz (l. c. 1914) has justly argued, the paraboloid shape of the apex must be a very important factor in this connection.

In geotropic reactions another factor must also be taken into account, namely, the polarisation of separate cells.

It is generally assumed that a difference exists in the sensitiveness to pressure of the protoplasm lining the inner and the outer walls of the cells. The idea that there may be a similar difference of sensitiveness between the apical and basal part of each cell, may therefore not be summarily rejected. In this way the longitudinal component can also be explained. In the rotating apices of climbing plants where I could establish its influence on growth as well as on the nature of geotropic curvature, this is probably the right conception. The paraboloid vegetation point of a stem which bents at its end like a hook, may here take up any sort of position and hardly deserves consideration in connection with gravitational stimuli.

Utrecht, March 1915.

Botanical Laboratory.

Astronomy. — "On the mean radius of the earth, the intensity of gravity, and the moon's parallar. By Prof. W. De Sitter.

1. Newcomb has more than once ) pointed out that the mean radius of the earth is more appropriate for use as a standard of reference, than the equatorial radius, which is always used in astronomical practice. The mean radius in fact, which — if we neglect quantities of the second order in the compression — is also the mean radius of curvature, is more nearly the quantity actually

<sup>&</sup>lt;sup>-1</sup>) Researches on the motion of the moon, second paper, page 41 Tables of the sun, page 12, footnote.