Botany. — *"The primary photo-growthreaction and the cause of the positive phototropism in Phycomyces nitens."* By Dr. A. H. Blaauw. (Communicated by Prof. F. A. F. C. Went.)

(Communicated in the meeting of December 27, 1913).

There are numerous investigations of the curvature movements, which plants execute, when energy is supplied unilaterally in the form of light or warmth, or when the organs of plants are displaced from the position, which they naturally occupy with respect to gravity.

The investigation of these "tropistic" movements, has proceeded especially in recent years with greater precision, after it was found in 1908, that for the understanding of these curvature-phenomena it is necessary to observe the effect *of definite quantities of energy*. But whilst in this way more and more data have been collected, concerning the curving of organs as a result of a unilateral action of energy, there lagged behind all the more the study of the effect of energy, when applied to the organs not asymmetrically but radially. The occurrence of curvatures as a result of asymmetrical forces, is a phenomenon so striking, that it is easy to understand that much more attention has been paid to the study of curvatures than to phenomena, which occur when the quantities of energy are supplied radially symmetrically to the organs of the plant. Yet it is as a matter of fact more natural to investigate first the influence exercised on an organ by energy, such as light or warmth, when its action is distributed uniformly on all sides of that organ, and only afterwards to consider as a special case what happens, when the energy reaches the plant not equilaterally, but from one definite side.

Now since it is a very important and well-known phenomenon, that the plant reacts to this asymmetric energy in a striking manner controlled by fixed laws, it was hardly conceivable that the plant would not also react distinctly in the more general case in which the energy acts radially symmetrically. With this equilateral action a marked curvature was no longer to be expected, but it was possible that any reaction taking place might not be limited to certain chemical changes in the cells, difficult to demonstrate, but might express itself more clearly in a change in the rate of growth, which change might be susceptible of measurement.

After earlier investigations with light applied unilaterally, it seemed to me desirable in consequence of the above considerations to pass no further judgment as to the value and essence of curvature reactions, until a further inquiry had been made into the way in which a growing organ reacts when light, warmth or centrifugal force acts in definite quantity on that organ uniformly from all sides. The first results of such an inquiry with respect to light will now be described.

For various reasons I have chosen in the first place the sporangiophores of *Phycomyces* as objects for investigation. The most important of these reasons was, that it was obviously desirable first to trace the influence of light on a single cell and only then to investigate it in multicellular organs such as the stem and the root of higher plants.

I have postponed for later more detailed description an account of the arrangement for securing a constant temperature, of the method of cultivation and of other details. I will here only mention, that the fungus was grown at the same constant temperature at which the experiment was afterwards carried out. During the experiments the temperature remained constant within $^1/_{50}$° C. I found that a rapid rise of temperature of, for example, only $^1/_{10}$° C., may exercise a considerable influence on the rate of growth of the sporangiophores, if it be only for a few minutes.

It can be noticed, that with the small, but sudden rise of $^1/_{10}$° C. the rate of growth may for a short time decrease by as much as 25°/₀, and then only rise again to the normal. In this case it is perhaps not the temperature itself, which directly affects growth, but a brief change in the degree of humidity of the atmosphere round the plant. I hope to deal with this more in detail. The chief point here is to show, how important it is to attain a high degree of constancy in experiments of this nature.

In the experiments sporangiophores are used, which are three to four cm. high. It is known from ERRERA's investigation (*Bot. Zeitung* 42[ei] *Jahrg.* 1884) that they are then in a condition, in which they possess a maximal and practically constant growth.

The sporangiophore employed, is placed in the centre of a box, which remains therefore at a very constant temperature and in which the atmosphere has a rather high degree of humidity, which throughout the experiment remains quite constant. The growth is observed through a double plate of thick glass, by means of a telescope placed outside the box and magnifying 40 times. The light for the observation was obtained from a weak, red lamp, which was switched on only during the observation, for as short a time as possible; its feeble light, also passing through a double glass plate, forms a silhouette of the plant on a red background. The illumination of the plant, placed in a central position, is carried out by allowing light to fall from above through a double plate of glass. Whilst the plant is prevented from being illuminated directly from above, the light first falls on 8 little mirrors, which are arranged in a circle at equal distances round the central sporangiophore at an angle of 45° with respect to the incident rays. In this way the sporangiophore receives radially symmetrically the same illumination on 8 sides. For various reasons — to be later dealt with in greater detail — this arrangement was the more satisfactory.

The growth of the sporangiophore is always determined before illumination by several observations at intervals of 5 to 10 min. Whilst the variation in growth of different sporangiophores is considerable, the growth of any individual one in successive minutes is very uniform, especially when it is remembered with regard to the figures found, that with observations at short intervals the error of observation may be fairly large, because with weak, red light the measurement must always be made fairly rapidly. The figures of growth in the dark agree very well with those of ERRERA. In the first series of experiments with 8-sided illumination at 22° C. figures were mostly found, which fell below the maximal growth according to ERRERA, in the later experiments with unilateral illumination at 18°.3 C., after the method of culture had been somewhat modified, a value was generally found which agreed with the values found by ERRERA during maximal growth. The eventual relative variations in the rate of growth caused by the influence of light were however more important than the absolute rate.

In the first experiments the plant was illuminated via the mirrors on *each* of the 8 sides with 14 metre candle power during 15 sec., that is, eight times the quantity, which, given by one mirror only, would have effected a decided curvature. When a growing cell receives this amount of illumination, a very striking reaction of the growth takes place. This reaction is all the more marked, the closer the observations after illumination follow each other; for this reason observations were made as far as possible every two minutes after illumination. We then notice:

1. that immediately after illumination growth still remains the same for about 3 min.

2. that after about 3 min. growth at once markedly increases, to reach a maximum $4^1/_2$ to 8 min. after illumination; with this quantity of light the maximum is usually not less than 2 or 3 times the normal rate of growth.

3. that afterwards the rate of growth again diminishes to its normal value which is reached about 7—16 min. after illumination.

4. that often however the rate sinks to 10 to 30% below its

normal value for some minutes, and then later becomes quite normal again.

This is a short résumé of the reaction, which these growing cells execute after illumination by the above-mentioned definite quantity of light and there was among the dozens of cells, which I investigated in this manner not a single one which did not clearly show this remarkably strong reaction. Moreover the phenomenon equally occurred both in slow-growing and in rapidly growing cells.

Of this series of experiments, only a few examples will for the sake of brevity, be given in tables I, II, and III, of which the third is also represented graphically in fig. 1. If observations are not made every two minutes but at long intervals, the reaction then does not appear to be so striking, whilst with observations made at still shorter intervals than two minutes, for a very short time perhaps a still higher figure for the maximum growth might be found, than has here been noted in observations taken every two minutes.

If the cell is illuminated with the same intensity of light for a 4 times shorter period, there likewise always occurs a distinct acceleration of growth, but the latter reaches a somewhat lower value, about $1^1/_2$ to 2 times the normal; if the illumination is 4 times as strong and 4 times as long, that is to say 16 times as great, then growth increases not nearly so much as with the lesser illumination and reaches a value of $1^1/_3$ to $1^1/_2$ times the normal.

Whilst these experiments are being continued in greater detail and more accurately in order to determine on the one hand, with how small a quantity of light a measurable reaction still occurs and to trace, on the other hand, what happens further after giving a much greater quantity of light, my immediate purpose is to report the fact, that the growth of the cells responds with a sharply accentuated reaction to illumination with a certain quantity of light, a reaction which shows the typical character of what hitherto has been called in botanical literature a stimulus-reaction. This reaction of growth to light I should like to name *photo-growth-reaction*, but considering, that many as yet unanalysed phenomena in which light has an influence on growth or form, may also be included under this general name, I will in order to prevent confusion, distinguish this reaction as *primary photo-growth-reaction*. In the case of an accelaration of growth we can then speak of a positive, in the case of retardation of a negative photo-growth-reaction.

With regard to the existence of a sharply-defined reaction of this kind, practically nothing can be deduced from the literature-references, at least the general opinion about the influence of light on growth

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TABLE I.
At 2.38¾ p. m. illuminated on 8 sides with 14 metre-candle power for 15 sec.

Time of observation	Position of the Sporangium. one scale division = 49μ	Increase in length per minute in scale-divisions
2.32½	48½	
2.40½	55¼	0.88
2.42½	57	0.88
2.44½	61	2.00
2.46½	65½	2.25
2.48½	67½	1.00
2.50½	69	0.75

TABLE II.
At 4.32 p. m. illuminated with ± 14 metre-candle power for 15 sec. on 8 sides.

Time of observation	Position of the Sporangium. one scale division = 49μ	Increase in length per minute in scale-division
4.15	25	
4.22½	31½	0.87
4.31	39	0.88
4.33	41	1.00
4.35½	43	0.80
4 37	45¾	1.83
4.38½	48	1.50
4.40	50	1.33
4.41½	51½	1.00
4.43	52½	0.67
4.46	54¼	0.58
4.51	57½	0.55
4.55	60¾	0.81

TABLE III. A specimen of weak growth illuminated at 2.52 p. m. with 14 metre-candle-power for 15 sec. on 8 sides.		
Time of observation.	Position of the Sporangium one scale division = 49μ	Increase in length per minute in scale division.
2.39½	39	
		0.36
2.50½	43	
2.52	Illumination	0.33
2.53½	44	
		0.40
2.56	45	
		0.50
2.58	46	
		0.75
3 p. m.	47½	
		0.75
3. 2	49	
		0.50
3. 4	50	
		0.50
3. 7	51½	
		0.35
3.12	53¼	
		0.38
3.22	57	

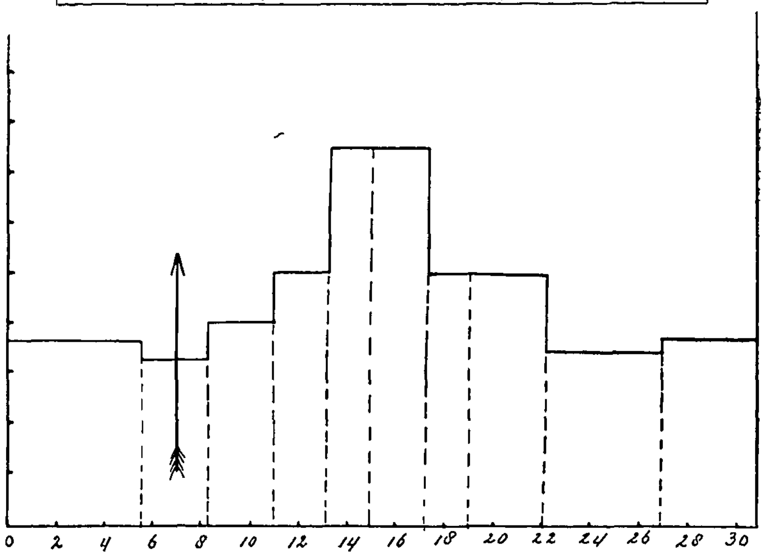

Fig 1. Graphical representation of a case of positive photo-growth-reaction (Table III). The arrow gives the moment at which there was illumination for 15 sec. with 14 metre-candle-power, on 8 sides. The abscissa gives the time in minutes, the ordinate the ratio of the rates of growth.

is completely at variance with these facts. In the first place so-far as concerns the positive or negative influence of light. The general conception, supported by numerous facts, is that light in general exercises a retarding influence on growth. In PFEFFER's *Pflanzenphysiologie* (2e *Aufl.* 1904, *Bd.* II. *blz.* 108) as a result of facts then known this conception is thus formulated: "Innerhalb der zulässigen Lichtgrenzen wird, so weit bekannt, in der phototonischen Pflanze durch Verminderung der Beleuchtung eine gewisse Beschleuniging, durch Zunahme der Helligkeit eine gewisse Verlangsamung der Zuwachsbewegung bewirkt".

In particular this was also deduced from the experiments of VINES (*Arb. Würzburg II,* 1878), who observed the growth of the sporangiophores of *Phycomyces* every hour or half hour in daylight and in the dark and found a slightly smaller growth in the light period than in the dark. In this investigation, as in that of others, too large and too indefinite quantities of light were used; moreover most investigators, including VINES, used intermittent stimulation, for which reason the influence of illumination made itself felt as an after effect also in the dark periods and conversely. Further in VINES' experiments the temperature is very variable, in some it changed for example from $22^1/_2$° C.—26° C.

Whilst nearly all earlier investigators found a smaller growth in the light than in the dark, HELENE JACOBI (*Sitzungsber. d. K. Ak. d. W. z. Wien, Abt. I, Bd.* 120, 1911) made the statement that, for example, plants of *Triticum* and *Phaseolus*, which had been illuminated 24 hours before for a fairly short time, had become slightly larger, than the non-illuminated controls. In this investigation, however, the growth was not measured until 24 hours later and then only with the naked eye, whilst the humidity and the temperature varied very greatly during many experiments. In comparison with this VINES' investigation of 1878 may almost be called modern, for he worked with a telescope, ensured a fairly constant humidity and did not wait for 24 hours before taking his readings.

Further more the representation in the literature of the nature of the growth reaction induced by light is at variance with the above facts. The current conception of this nature is summarised by PFEFFER as follows (blz. 109): "Selbst bei dem Uebergang von einer hellen Beleuchtung zu voller Finsterniss, oder umgekehrt, wird die Wachsthumsschnelligkeit gewöhnlich nur um 5—30 %, selten um 50 % oder mehr beschleunigt, resp. verlangsamt, und bei schwächerem Beleuchtungswechsel lässt sich eine Reaktion nicht immer nachweisen". PFEFFER further indicates, that a change in the rate of growth does not occur rapidly but gradually, and concludes: "Neben dieser allmählichen Verschiebung der Wachsthumsschnelligkeit scheint durch einen plötzlichen Beleuchtungswechsel der Regel nach keine auffällige transitorische Reaktion veranlasst zu werden".

These conceptions, which contrast with the photo-growth-reaction now demonstrated in *Phycomyces*, are caused by various facts: that very large quantities of light were used, which greatly exceeded the optimum; that the illumination was very prolonged, so that the plant partly adjusted itself again to the light; that the illumination was frequently intermittent, so that the phenomenon was not analysed, but became more complex; and because observations were made at too great intervals, so that the values for a possibly accentuated reaction were lost in a more average value.

TABLE IV.

From 1.1½ p.m. to 1.2½ p.m. unilateral.

Illumination with 14 metre candle power for 60 sec.

Time of observation.	Position of the sporangium.	Increase in length per minutes in scale divisions	Remarks.
1.37½ p.m.	40	1.07	
1.51½	55	1.00	
1.58½	62		
2. 1½—2½	Illumination	0.85	
2. 5½	68	2.00	
2. 7	71	2.00	
2. 9	75	1.20	
2.11½	78	1.25	
2.13½	80½	[0.88] *)	Begin. of pos. curvature.
2.15½	[82¼]	[0.88]	Increasing curvature.
2.17½	[84]	[0.75]	" "
2.19½	[85½]		

*) From this time onwards the amount of growth is uncertain on account of the occurrence of the curvature.

After the completion of these experiments with *Phycomyces* I hope to study the behaviour of the stem and the root in higher plants.

After the phenomenon described above had been established qualitatively, I was naturally curious as to how far this photo-growth-reaction was related to the well-known phototropism of *Phycomyces.* In order to investigate this, the plant was illuminated unilaterally with, for example, 14 metre candle power during 60 sec. and at the same time the growth and the occurrence of a curvature were watched through a telescope.

It was then found that — excluding the special case, which is described below — *a positive curvature never appears, unless the above-described acceleration of growth has previously taken place.* The positive photo-growth-reaction occurs in the usual manner after about 3 min. — this time of reaction can with the weakest illuminations rise to 7 min. — it reaches its maximum, then the rate of growth diminishes again, and from this moment does the positive phototropic curvature become visible, which, according to the conditions of illumination becomes more or less strong. A few examples are given in tables IV and V.

TABLE V.

From 3.41 to 3.42 p.m. unilateral illumination with 14 metre candle power for 60 sec.

Time of observation	Position of the Sporangium.	Increase in length per minute in scale divisions	Remarks
3.25½ p.m.	30	1.00	
3.33	37½		
3.41 3.42	Illumination	0.95	
3.43	47	1.13	
3.45	49¼	1.50	
3.47	52¼	1.50	
3.49	55¼	[1.00]	Beginning of curvature
3.51	[57¼]	[0.88]	Obvious curvature
3.53	[59]	[1.00]	Increasing curvature
3.55	[61]		" "

When one considers that the rays, which practically run parallel, fall on the sporangiophores, as on a cylindrical lens, then the course of the rays in the body of the cell can be conceived as in fig. 2. It will be seen that the illumination of the front and of the back of the cell necessarily must differ rather widely. There passes indeed as much light through the front-*half* as through the back *half*, but by far the greater part of the posterior wall the peripheral protoplasm is more strongly illuminated than that of the anterior wall; in the middle of the posterior wall about twice as strongly as in the middle of the anterior wall. With illumination which is neither too strong nor too weak, the photo-growth reaction of both sides commences at the same moment after about 3 min., but this acceleration of growth continues at the end of the reaction somewhat longer at the back than at the front and consequently after the cell has shown a certain acceleration of growth, a curvature arises by the action from that side, which is most strongly illuminated.

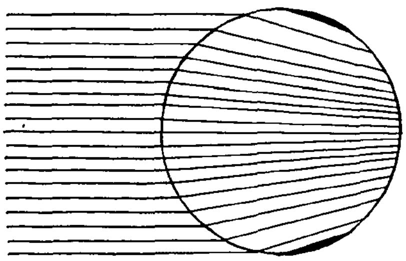

Fig 2.

The experiments concerning the absence of positive curvature and occurrence of a negative one with large quantities of light, will be continued in connection with results, to be obtained with the photo-growth-reaction after omnilateral strong illumination. But in my opinion the explanation of the positive phototropism in *Phycomyces* has already been given by the above, and moreover I found in the following facts new supports for this conclusion.

I subsequently investigated what happens, when the unilateral illumination is made weaker so that the lower limit of phototropism is approached. We may now expect, according to the course of the rays (see fig. 2) that a quantity of light would finally be reached, which is too small to effect an increased stretching of the cell-wall on the anterior side, but in consequence of refraction is just sufficient to cause acceleration of growth on the posterior side. And that is indeed what is found! Table VI gives an example of the different cases of this kind which I observed.

In this way acceleration of growth was no longer observed; at the moment at which it would otherwise occur — that is after a reaction-time of 5—7 min. with this very weak illumination — the growth of the most strongly illuminated part of the cell-wall only is accelerated and the only result is a curvature, which is weak and often disappears again after a few minutes.

TABLE VI.

At 3.40 p.m. unilateral illumination with about 2½ metre-candle for 4 sec.

Time of observation	Position of the Sporangium	Increase in length per minute in scale divisions	Remarks
3.18¾ p.m.	30	0.92	
3.30¾	41	0.96	
3.37	47		
3.40	Illumination	1.00	
3.41	51	1.00	
3.43	53	0.88	
3.45¼	55	1.00	
3.47¼	57	1.00	Beginning of curvature
3.49¼	59	1.00	Increasing curvature
3.51¼	61	0.90	Curvature stops
3.56¼	65½		Curvature goes back

The curvature is thus seen to occur with a very small quantity of light (2½ to 10 metre-candle-seconds) and these curvatures, which already appear after 5—7 min. and are mostly weak, have not been noticed by me before. Formerly I found a curvature only with the most sensitive specimens, for example, after 50 metre-candle-seconds. That was the curvature discussed above which occurs, when the acceleration of growth has already passed off and of which the reaction-time (observations being made with a telescope) amounts to 8—15 min. at least. We see therefore, that as a necessary result of the photo-growth-reaction and the refraction of light, weaker curvatures also occur with still less illumination and these of necessity have a rather shorter reaction-time.

Whilst then these small curvatures are visible with 2½ to 10 Metre-candle-seconds in proof of a liminal local acceleration of the stretching of the cell wall, there occurs with a slightly stronger illumination or with the same illumination in "more sensitive" specimens — a reaction, which also could have been anticipated. In such cases, as those of table VII the quantity of light is just sufficient to cause a slight acceleration of growth in the anterior wall. Since the posterior side is somewhat more strongly illuminated than the anterior one, which only just reacts, the posterior side therefore begins to react sooner: after 4 to 5 min. a very slight curvature occurs, after about 7 min. the anterior wall also reacts, the very slight curvature does not continue or may even disappear, but a distinct acceleration of growth of the entire cell can be observed and as this passes off, there again occurs also a very slight curvature, since the rather more strongly illuminated posterior wall not only begins to react earlier, but continues to react somewhat longer than the anterior wall, which falls just within the reach of a growth acceleration. The phototropic curvature is thus divided here into

TABLE VII.

At 4.1½ p.m. unilateral illumination with about 2½ metre candle power for 5 sec.

Time of observations	Position of the sporangium	Increase in length per minute in scale-divisions	Remarks
3.42	47½	0.97	
3.49¼	54½	0.96	
3.55	60		
4. 1½	Illumination	1.00	
4. 2½	67½	1.00	
4. 4½	69½	1.00	
4. 6½	71½	1.25	Beginning of curvature
4. 8½	74	1.63	Curvature slightly greater
4.10½	77¼	1.50	Curvature no greater
4.12½	80¼	1.10	Curvature back
4.15	83	0.80	
4.17½	85	0.75	Curvature again
4.19½	86½	0.83	Very feeble curvature
4.22½	89		Curvature no greater

two and both parts remain very slight. If somewhat more light is supplied, the reaction-times of the anterior and the posterior-wall become very much the same and the curvature — and that is the definitive phototropic curvature of *Phycomyces* — only appears after the maximum of the acceleration of growth, because the growth-reaction of the less illuminated anterior wall diminishes somewhat more rapidly than that of the posterior wall.

To be on the safe side I will not extend the scope of these facts further than to the positive phototropism of *Phycomyces,* but of this phenomenon I think, that proof has now been furnished, that *the appearance of these curvatures is the result of an asymmetrical modification of the growth of different sides of the cell, caused by the asymmetrical illumination of these sides; that for this case therefore* DE CANDOLLE'*s simple and ancient theory* — more particularly in contradiction to the later conception of SACHS — *is reestablished and with this a theory of a perception of the light-direction itself is superfluous.*

In the meantime I do not wish to generalize, but only to await the results of further investigations, which are being continued in various directions, on *Phycomyces* and on the root and stem of higher plants. Only, in my opinion, for no single one of these cases can any decisive proof in the literature be found against DE CANDOLLE's theory.

Finally I desire to express my great indebtedness for the facilities afforded me in the Laboratory of the TEYLER Foundation, for carrying out these experiments — and it is no mere formality, that I tender my thanks especially to the conservator, Jhr. Dr. G. ELIAS, for his assistance and interest in the arrangements for this investigation.

Haarlem, Dec. 1013.

Physics. — "*Magnetic researches.* X. *Apparatus for the general cryomagnetic investigation of substances of small susceptibility.*" By H. KAMERLINGH ONNES and ALBERT PERRIER. Communication N°. 139*a* from the Physical Laboratory at Leiden. (Continued). (Communicated by Prof. H. KAMERLINGH ONNES.)

§ 7. *Sources of error. Sensibility. Accuracy. Disturbing magnetic influences.* The action of the magnet upon the carrier without the experimental tube appeared to be negligible, even when the lower end of the carrier was reduced to the temperature of liquid hydrogen. The action upon the coil of the carrier was also imperceptible even when a much stronger current i_m was passed through this coil than