VI.

The Influence of Light upon the Growth of unicellular Organs.

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The influence of light upon growth has been made of late years the subject of much careful investigation. The observations of SACHS[1]) upon the growth of internodes, and those of PRANTL[2]) upon that of the leaves of Dicotyledonous plants, shew that the daily periodicity which is evident in the growth of those organs is to be attributed to the alternation of day and night. It appears that light exercises a retarding influence upon the process of growth, a conclusion which agrees with the inferences to be drawn from the phenomena of etiolation.

In order to study more closely the action of light upon growth, it will be well to take the simplest possible form in which growth presents itself, and this is offered by unicellular plants or vegetable organs. In this way many of the influences which modify the growth of more complex structures, such for instance, as the various tensions existing between cells when combined together to form a tissue, more especially when differentiation of tissues is taking place, are avoided, and an approximate estimate of the action of any one particular external force may be formed. That light exercises a powerful influence upon such organs is evident from the fact, that many of them (e. g. cells of Vaucheria and Nitella. hyphae of Fungi etc.) are positively heliotropic, and others, (e. z. root-hairs of Marchantia) are negatively heliotropic. Recently BREFELD[3]) has called attention to the fact that the unicellular hyphae of a Mould (Pilobolus microsporus) exhibits many of the appearances peculiar to etiolation, when grown in the dark. He found that the hyphae on which the sporangia would be developed under ordinary circumstances, and which attain a height of about half an inch in the light, grew, in continued darkness, to a length of from eight to ten inches, and bore no sporangia.

1) Arb. des bot. Inst. in Würzburg. Heft II. 1872.

2) Arb. des bot. Inst. in Würzburg. Heft III. 1873.

3) Bedeutung des Lichts für die Entwickelung der Pilze. Sitzber. d. Gesellsch. naturforsch. Freunde zu Berlin. 17. April 1877.

Yellow light acted upon them in the same way as darkness, the rays which were active in checking over-growth and in causing histological differentiation belonging to the more highly refrangible portion of the spectrum.

At the time when BREFELD's paper was published, I was engaged in the following observations upon the growth of Phycomyces nitens, one of the larger Moulds. This plant is very sensitive to the action of light, for it exhibits a well marked positive heliotropism, but it is not so sensitive as the Pilobolus with which BREFELD experimented, for exposure to darkness or to yellow light during the whole period of its growth did not produce any appearance of etiolation. All that can be said in this respect, is that the hyphae were rather longer, when they had grown in the dark than when they had grown in the light, and that they grew longer in yellow light than in blue, but the differences were comparatively slight. The object of the experiments was to obtain evidence of the action of light in retarding growth in a very simple organism, and from the knowledge thus acquired to seek an explanation of the phenomena.

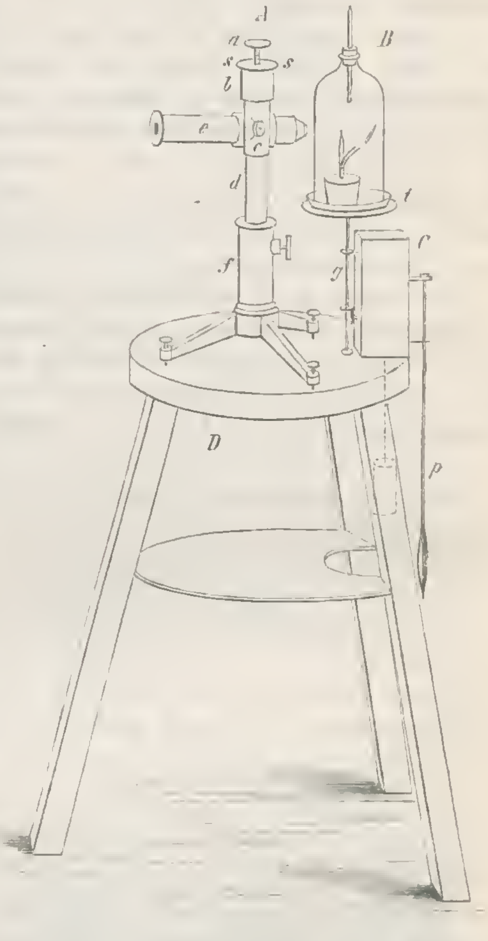
The method pursued in obtaining the material for observation was that suggested by BREFELD [1]). Spores of Phycomyces were diffused through the water contained in a watch-glass by placing in it a mature sporangium which immediately burst. A few drops of this water were then transferred by means of a needle to a piece of bread soaked with solution of grape-sugar. Under these circumstances the spores rapidly germinated and gave rise to a vigorous growth of the fungus. Upon this first crop a thick glass plate, with two or three holes in it, was laid, so as to arrest the further growth of the existing sporangiferous hyphae. In a few hours new hyphae had grown through the holes in the glass plate. In this way it was possible to obtain the hyphae sufficiently isolated to admit of observation, and their small number caused their growth to be more than usually vigorous.

The apparatus for the measurement of growth was suggested by Professor SACHS, and is shewn in Fig. 1. It consists of a stand D supporting a clockwork C, of which p is the pendulum. Connected with the clockwork by a cog-wheel is a shaft g, bearing a plate t, on which the object to be observed stands. The piece of bread, on which the Mould was growing, was placed in a small glass dish moistened with water, and covered with a bell-jar B, so that the moisture of the air surrounding the Mould might vary as little as possible. Through the cork which closed the neck of the bell-jar, a thermometer passed into the interior,

1) Meth. z. Untersuch. d. Pilze. Verhandl. d. phys. med. Gesellsch. in Würzburg. N. F. Bd. VIII. 1874.

by means of which variations of temperature in the neighbourhood of the plant could be ascertained. On the stand stood also the micro-telescope *A*. This instrument consists of a heavy iron foot *f*, into which the shaft *d*, which bears the tube, fits. The shaft *d* can be moved upwards or downward and can be fixed in any position by means of a screw. This is the coarse adjustment of the instrument. The tube is fixed in a holder, which forms part of the cap *b*. This cap fits on to the upper end of the shaft *d*, and can be raised or lowered by means of the screw *a*. This is the fine adjustment of the instrument. On the upper surface of the cap is a graduated disc, and it is possible to ascertain the number of degrees through which the screw has been turned, by means of a pointer attached to it. The tube itself is a micro-telescope devised especially for observations of this kind by Professor Quincke, and constructed by Steinheil of Munich. The eye-piece contains a micrometer, by means of which the measurements are made. When the instrument was focussed upon a growing hypha, and the uppermost line of the micrometer scale was brought, by means of the fine adjustment, to mark the position of the apex of the hypha, it was easy to read off the number of divisions of the scale through which the hypha had grown in any given time.

Fig. 1.



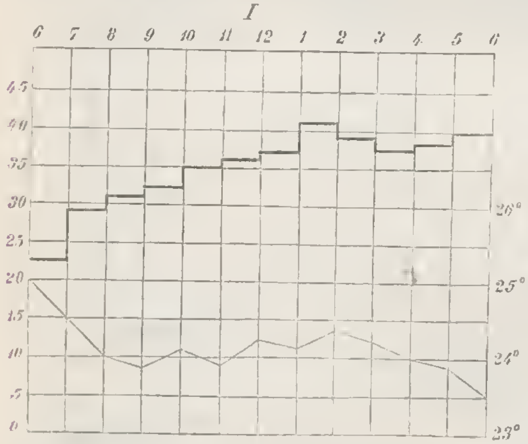
The object of the clockwork is to cause the object under observation to rotate so as to avoid heliotropic curvatures when it is exposed to light. In order that the conditions under which the observations were made might be as far as possible constant throughout, the rotation was continued when the plant was in darkness. In order to shut off the light, a thick paste-board cylinder was placed over the bell-jar. In the experiments with coloured light, double-walled flasks were used, the space between the walls being filled in the one case, with ammoniacal solution of copper oxide, in the other, with saturated solution of potassic bichromate.

The experiments went on during the months of May, June and July of the year 1877, and amounted to about forty. From them I have selected the following in illustration of the results obtained.

It was necessary, in the first place, to ascertain what was the natural course of growth of the plant, when exposed to conditions, which were kept as far as possible constant. Previous observations had shewn that the hyphae completed their growth in from 24 to 30 hours, that is the extent of the »grand period« of their growth. The following table gives an account of the variations of growth during a considerable portion of a grand period. The fungus was kept in the dark during the whole time of observation.

The course of the grand period is made more evident when a curve is constructed. The divisious of the abscissa are hours, and two of those of the ordinates are equal to one division of the micrometer [1]. The course of the temperature is represented also by a curve, each division of the ordinates representing half a degree centigrade.

I



	Hourly growth.	Temperature.
6—7 a. m.	2.30	25 0 C.
8 „	2.90	24.5
9 „	3.10	23.9
10 „	3.20	24.1
11 „	3.50	23.9
12 —	3.60	24.2
1 p. m.	3.70	24.1
2 „	4.10	24.3
3 „	3.90	24.2
4 „	3.70	24.0
5 „	3.80	23.9
6 „	4.00	23.5

The observations evidently commenced after the hypha had attained a considerable rapidity of growth. The curve gradually ascends until the maximum rapidity is attained eight hours after the commencement of the observations, and growth continues for a time with nearly that rapidity. The variations which occur are to be principally attributed to the course of the grand period, and secondarily to slight changes in the conditions to which the plant is exposed. Such irregularities of growth were observed by Sachs in the case of internodes (stossweise Aenderungen). An

1) A division of the micrometer = $\frac{1}{10}$ mm.

analysis of the variations may be made in the following manner. If the difference between the observed maximum and minimum be divided by the number of hours intervening between the times of their occurrence, an average acceleration is obtained, which may be regarded as the acceleration due to the course of the grand period. The difference between the average acceleration per hour and the observed acceleration will be the acceleration due to variations in the external conditions. The average acceleration in this case is $\frac{4.10 - 2.30}{7} = 0.26$ nearly. After the maximum has been attained, growth may be regarded as not undergoing, for a time, any alteration beyond that produced by varying external conditions.

	2.30	
	2.90 .... 2.90 — 2.30 — 0.26	= 0.34 +
	3.10 .... 3.10 — 2.90 — 0.26	= 0.06 —
	3.20 .... 3.20 — 3.10 — 0.26	= 0.16 —
	3.50 .... 3.50 — 3.20 — 0.26	= 0.04 +
	3.60 .... 3.60 — 3.50 — 0.26	= 0.16 —
	3.70 .... 3.70 — 3.60 — 0.26	= 0.16 —
Maximum	4.10 .... 4.10 — 3.70 — 0.26	= 0.14 +
	3.90 .... 3.90 — 4.10	= 0.20 —
	3.70 .... 3.70 — 4.10	= 0.40 —
	3.80 .... 3.80 — 4.10	= 0.30 —
	4.00 .... 4.00 — 4.10	= 0.10 —.

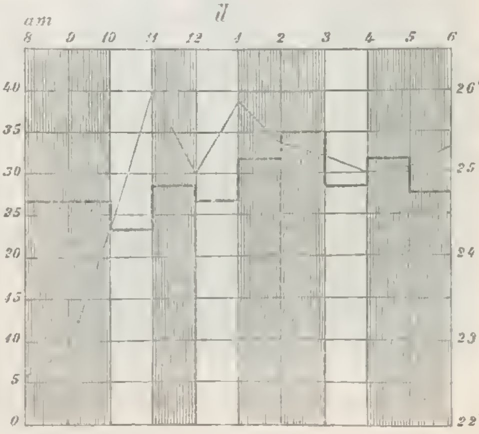
The signs after the figures in the last column shew whether the observed acceleration has been greater or less than the average acceleration. When the plus sign is used, it has been greater, when the minus sign, it has been less.

It appears therefore, that the curve of the grand period undergoes considerable variations under tolerably constant conditions. The effects of varying conditions may now be studied.

The following table with its accompanying curve shews how the course of the grand period is affected, when the plant is exposed to alternations of light and darkness.

	Hourly growth.	Temperature.
8—9 a. m.	2.70	22.9 °C.
10 „	2.70	24.3
11 „	2.30	26.0 *
12 —	2.90	25.0
1 p. m.	2.70	25.8 *
2 „	3.20	25.3
3 „	3.50	25.2
4 „	2.90	25.0 *
5 „	3.20	25.1
6 „	2.80	25.3

* exposed to light.

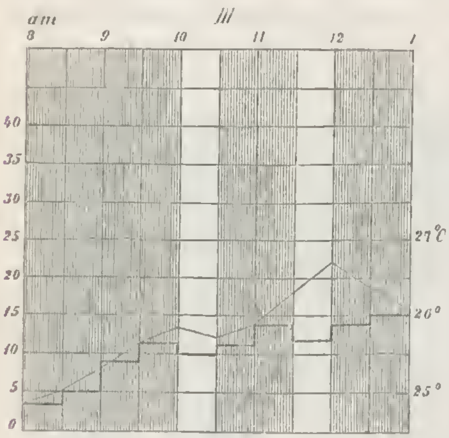


If this table be treated in the same way as the former one, the effect of exposure to light is brought out more markedly. Here the average is 0.13 nearly, the maximum is reached at 3 p. m. and the descent begins at 5 p. m.

	2.70		
	2.70	2.70 — 2.70 — 0.13 = 0.13 —	
	2.30	2.30 — 2.70 — 0.13 = 0.53 —	(light)
	2.90	2.90 — 2.30 — 0.13 = 0.47 +	
	2.70	2.70 — 2.90 — 0.13 = 0.33 —	(light)
	3.20	3.20 — 2.70 — 0.13 = 0.37 +	
maximum	3.50	3.50 — 3.20 — 0.13 = 0.17 +	
	2.90	2.90 — 3.50 = 0.60 —	(light)
	3.20	3.20 — 3.50 = 3.30 —	
descent	2.80	3.50 — 2.80 = 0.57 +.	

From these observations it appears that light exerts considerable influence the diminishing the acceleration of growth. It is noticeable that, as a rule, the acceleration falls below the average only during the hour of exposure to light, and that it rises in the subsequent hour above the average, but the acceleration in the hour after exposure to light is not so great as it was in the hour before exposure. This is an indication that the effect of the action of light persists for a time after the actual exposure has cessed. This persistent effect (Nachwirkung) was noticed by SACHS and PRANTL to occur in the case of internodes and leaves. In consequence of the very simple structure of the hyphae the effects produced by the action of light are rapidly manifested, but the persistence of the action is not great.

If the measurements be made at shorter intervals, the persistent effects become more evident. The following table and curve consist of half-hourly measurements.



	Half-hourly growth.	Temperature.
7½—8 a. m.	0.30	24.8° C.
8½ „	0.30	25.0
9 „	0.50	25.3
9½ „	0.90	25.6
10 „	1.10	25.8
10½ „	1.00	25.7 *
11 „	1.10	25.9
11½ „	1.40	26.3
12 —	1.20	26.7 *
12½ p. m	1.40	26.4
1 „	1.50	26.1

* light.

The average in this case is 0.12 per half hour.

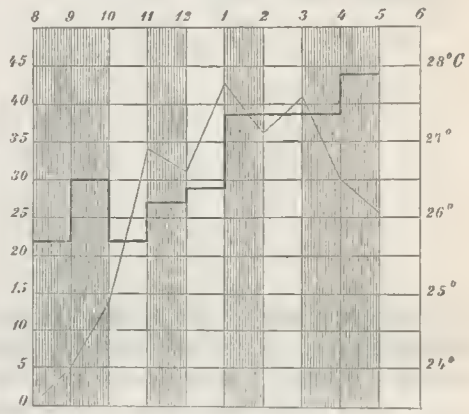
0.30
0.30 .... 0.30 — 0.30 — 0.12 = 0.12 —
0.50 .... 0.50 — 0.30 — 0.12 = 0.08 +
0.90 .... 0.90 — 0.50 — 0.12 = 0.28 +
1.10 .... 1.10 — 0.90 — 0.12 = 0.08 +
1.00 .... 1.00 — 1.10 — 0 12 = 0.22 — (light)
1.10 .... 1.10 — 1.00 — 0.12 = 0.02 —
1.40 .... 1.40 — 1.10 — 0.12 = 0.18 +
1.20 .... 1.20 — 1.40 — 0.12 = 0.32 — (light)
1.40 .... 1.40 — 1.20 — 0.12 = 0.08 —
1.50 .... 1.50 — 1.40 — 0.12 = 0.02 —.

The next experiments were made with the view to determine, which rays of the spectrum were especially active in causing this retardation. The following are the measurements made upon a hypha which was exposed at intervals to blue light.

	Hourly growth.	Temperature.
8—9 a. m.	2.20	24.0 ° C.
10 „	3.00	24.9
11 „	2.20	26.9 *
12 —	2.70	26.6
1 p. m.	2.90	27.8 *
2 „	3.90	27.1
3 „	3.90	27.6 *
4 „	3.90	26.5
5 „	4.40	26.1.

* blue light.

IV

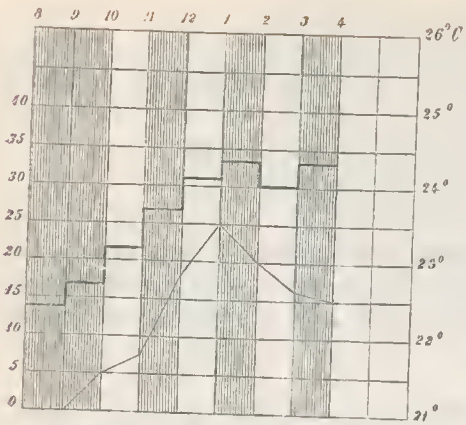


The average acceleration is here 0.27 per hour.

2.20
3.00 .... 3.00 — 2.20 — 0.27 = 0.53 +
2.20 .... 2.20 — 3.00 — 0.27 = 1.07 — (blue light)
2.70 .... 2.70 — 2.20 — 0.27 = 0.23 +
2.90 .... 2.90 — 2.70 — 0.27 = 0.07 — (blue light)
3.90 .... 3.90 — 2.90 — 0.27 = 0.73 +
3.90 .... 3.90 — 3.90 — 0.27 = 0.27 — (blue light)
3.90 .... 3.90 — 3.90 — 0.27 = 0.27 —
4.40 .... 4.40 — 3.90 — 0.27 = 0.23 +.

The following observations were made upon a hypha exposed to yellow light.

V



	Hourly growth.	Temperature.
8—9 a. m.	1.40	21.0 ° C.
10 „	1.70	21.5 *
11 „	2.20	21.7
12 —	2.70	22.8 *
1 p. m.	3.10	23.5
2 „	3.30	23.0
3 „	3.00	22.6 **
4 „	3.30	22.5

* yellow light.
** daylight.

Here the average acceleration is nearly 0.27.

1.40
1.70 .... 1.70 — 1.40 — 0.27 = 0.03 +
2.20 .... 2.20 — 1.70 — 0.27 = 0.23 + (yellow light)
2.70 .... 2.70 — 2.20 — 0.27 = 0.23 +
3.10 .... 3.10 — 2.70 — 0.27 = 0.13 + (yellow light)
3.30 .... 3.30 — 3.10 — 0.27 = 0.07 —
3.00 .... 3.00 — 3.30 — 0.27 = 0.57 — (daylight)
3.30 .... 3.30 — 3.00 — 0.27 = 0.03 +.

A comparison of these results shews at once that the more highly refrangible rays of the spectrum are those which are especially active in retarding growth, whereas the rays of low refrangibility have no more effect upon it than darkness. This agrees with what is already known with reference to the influence exercised by the two halves of the spectrum upon the growth of organs of complicated structure.

These observations prove that the growth of so simple a structure as the hypha of a Fungus is affected by the action of light in the same way as that of a complex organ, with the single difference, that the former is able to react more rapidly than the latter.

It now remains to seek some explanation of the phenomena. It is not probable that the retarding action of light is an indirect one, that it affects the activity of the growing cells only in so far as it modifies the chemical processes of their nutrition. Whatever direct evidence can be obtained tends to prove that the chemical processes are more actively carried on in the presence than in the absence of light. The decomposition of carbonic acid and the formation of starch in the chlorophyll-grains, with evolution of oxygen, takes place only under the influence of light. PFEFFER[1]) has shewn, that the conversion of asparagin into proteid

1) Jahrb. f. wiss. Bot. Bd. VIII.

only occurs when the plant is exposed to light. The observations of WEBER[1]) upon the absorption of phosphoric acid and lime, of SCHULZE[2]) upon the formation of sulphuric acid, and of RAUWENHOFF[3]) upon the occurrence of crystals of calcium oxalate and of tannic acid in etiolated and in green plants, all point to the activity of light in the chemical processes of the plant. The fact that in very many cases the leaves of Dicotyledonous plants grown in the dark remain small, has been explained by KRAUS[4]) on the theory that leaves can only grow when they can assimilate[5]). This explanation has been shewn to be incorrect by BATALIN[6]), who found, that if etiolated leaves be exposed to diffuse daylight for a period which is not sufficiently long to cause the formation of chlorophyll, they will grow. It is well-known that the cotyledons of many plants do not grow in darkness, although their cells are filled with starch or oil, and this is also the case with the leaves of green plants which have been removed into the dark. KRAUS[7]) attributes this arrest of growth to the cessation of the process of conversion of starch into cellulose. It is difficult to reconcile this explanation with the fact, that the leaves of many Monocotyledons and those of many Dicotyledons[8]), when grown in the dark, attain as great as a size, or even a greater, than that which they would have normally possessed. Moreover roots grow in complete darkness, and etiolated stems become excessively elongated. In all these cases the process of the conversion of starch into cellulose must be in full activity. It is therefore not clear why it should be assumed that so fundamental a process as that of the conversion of starch into cellulose is arrested in certain cases only, by the absence of light. It cannot be doubted, however, that, in darkness, certain chemical processes, which are essential, as regards the leaves, to the growth of the cells, and as regards both leaves and stems, to the differentiation of the tissues, are suppressed. These are only some of the effects produced by etiolation. There are many others, of which the non-formation of chlorophyll is the most striking.

If this evidence be considered sufficient to prove the correctness of the statement, that the chemical processes which are essential to the nutrition of plants are favoured by the action of light, the explanation of the retarding action of light upon growth must be sought in another di-

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1) Landw. Versuchsst. XVIII.

2) Landw. Versuchsst. XIX.

3) Over de Oorzaken der abnormale Vormen etc. Acad. Amst. XI. 1877.

4) Jahrb. f. wiss. Bot. Bd. VII.

5) This view is discussed in another paper. Arb. Heft V.

6) Bot. Zeitg. 1871.

7) loc. cit. p. 214.

8) SACHS: Einfluss des Tageslichts etc. Bot. Zeit. 1863. Beilage.

rection. The question at once suggests itself, does light directly influence the growing cells, and if so, what is the nature of its action?

An attempt to indicate such an influence was made by BATALIN[1]). He suggested, that the usual smallness of etiolated leaves of Dicotyledons might be due to an arrest of the process of cell-division, a process which he regarded as being favoured by the presence of light. SACHS[2]) has however pointed out, that cell-division is only a consequence of growth. The leaves remain small, not because their cells do not divide, but because their cells do not grow. A good example of this is afforded by the smaller Algae. Their cells divide only during the night, most probably because it is then that growth is actively proceeding.

In order to obtain a clear idea of the problem the physical conditions of growth must be briefly considered. These conditions are principally three: 1) the growing cell must be supplied with a sufficient quantity of nutritious material; 2) the temperature of the surrounding medium must not vary beyond certain limits; and 3) the cell must be supplied with water so that it may be tense, or as it is technically termed, in a state of turgidity. Of these three conditions the first two are but little affected by light. In darkness as well as in light the mycelium of Phycomyces could always obtain an adequate supply of food, and the rise of temperature which generally took place when the plant was exposed to light, was never sufficiently great to endanger the life of the plant. Under these circumstances, the action of light must have affected the last of the three conditions: — it must, in some way or other, have modified the turgidity of the growing cell.

The importance of a turgid condition for the process of growth in a cell was first insisted upon by SACHS[3]). He defines it as follows. — »By turgidity we understand the hydrostatic pressure which the water absorbed by endosmosis exerts upon all parts of the cell-wall equally, and which reacts on the cell-contents in consequence of the elasticity of the cell-wall. Thus, in a turgid cell, the cell-wall is tense and the cell-contents are under pressure«. The result of this state of turgidity is to cause the cell-wall to stretch as much as possible. In order that it may be able thus to yield to the pressure, from within it must be saturated with water. The process of its extension consists in the gradual separation frome one another of the minute solid particles of which it is composed (»micellae« NÄGELI und SCHWENDENER Mikroskop — »tagmata«. PFEFFER Osmot. Untersuch.), the spaces between them being occupied by water. If the cell be young and capable of growth, new micellae are

1) Bot. Zeitg. 1871.

2) Lehrbuch 4. Auflage p. 733.

3) Lehrbuch 4. Auflage pp. 741—852.

deposited in the watery areas, and the form assumed by the cell-wall in its extended condition is rendered permanent.

The turgidity of a cell may therefore be modified in two ways. In the first place, the extensibility of the cell-wall may either increase or diminish, and the reaction which it exerts upon the cell-contents will vary accordingly. In the second place, the osmotic properties of the cell-contents may be so altered, that the amount of fluid contained within the cell may vary, and therefore the pressure exerted upon the cell-wall from within will vary also.

A diminution of the extensibility of a cell-wall occurs as the cell becomes older, and as the cell-wall itself undergoes differentiation [1]. The observations of KRAUS and KOCH tend to shew, that the action of light is favourable to the thickening and differentiation of cell-walls. Even if it be assumed that the retardation of the growth of a hypha of Phycomyces depends upon a diminished extensibility of its cell-wall, the fact that it is so rapidly produced makes it difficult to believe that a thickening of the cell-wall is the immediate cause. It seems more reasonable to imagine that light exerts its influence directly upon the micellae in such a way as diminish their mobility. PFEFFER [2] has already suggested the possibility of such a direct action of light upon cell-walls, but any positive evidence upon the subject is not to be obtained. This being the case, it will be well to proceed to the discussion of the second of the two possible ways in which the turgidity of a cell may be modified, in order to obtain a more satisfactory explanation.

The wall of a growing cell is lined by a layer of protoplasm, which, so long as the cell is turgid, is in close contact with it. It is evident, therefore, that the endosmosis, by means of which the cell is maintained in a turgid condition, has to take place through this protoplasmic layer. It may be, that the effect of light in retarding the growth of a cell is produced by some change in the physical properties of the protoplasm in consequence of which turgidity is diminished. A short discussion of the use of the protoplasm in producing and maintaining the turgidity of a cell will afford some grounds on which to form an estimate of the probability of this suggestion.

NÄGELI [3] was the first to point out, that the protoplasmic layer lining the cell-wall offers a considerable resistance to the passage through it of certain substances, more especially colouring matters, which are dissolved in the cell-sap, although the cell-wall easily allowed them to pass. DE VRIES [4] repeated NÄGELI's observations upon the parenchymatous cells

1) NÄGELI: Pflanzen-phys. Untersuch. Heft. 1. p. 24.

2) Periodische Bewegungen p. 119.

3) Pflanzen-physiol. Untersuch. Heft 1.

4) Sur la perméabilité du protoplasma des betteraves rouges. Arch. Néerland. 1871.

of the beet-root. He found that, after remaining for fourteen days in water, they allowed neither their colouring matter nor their sugar to escape. His further experiments[1]) demonstrate still more clearly the importance of this protoplasmic layer in producing a turgid condition of the cell. By placing growing cells in solutions of different salts, especially in solutions of saltpetre, which were more concentrated than the cell-sap, he was able to diminish the turgidity of the cells, and when the solution contained as much as ten per cent of the salt, the protoplasm contracted away from the cell-wall and the turgidity of the cells was entirely removed. To this condition he gives the name of »Plasmolysis«. His experiments do not, however, merely demonstrate this important function of the protoplasm, but they also prove the absolute necessity of a turgid condition to the growth of a cell. He found, that immersion of the cells in strong solutions of salts for a sufficient time to produce complete plasmolysis, did not kill the cells, and that, if they were placed in water, the salt was gradually removed, the protoplasm slowly resumed its former position. The growth of branches, peduncles etc., was more or less diminished when they were placed in the more dilute solutions, and was entirely arrested when the solutions were sufficiently concentrated to cause complete plasmolysis of the cells. After thorough washing in water they resumed their growth.

From these observations it is evident that this protoplasmic layer is very extensible. The fact, that it is impermeable to the cell-sap contained in the vacuole, which it surrounds, and that the cell-sap, by virtue of its endosmotic properties, ever tends to increase in quantity, justifies the conclusion that, under normal conditions, the protoplasm of a growing cell is in a state of tension. So long as it yields to the pressure from within, growth is possible, but should its extensibility be so diminished that it completely neutralises this pressure, growth must cease. The cell-wall may be regarded as being completely passive in this process. It is stretched by the tense protoplasmic layer by which it is lined, but is, of itself, incapable of so resisting the escape of the cell-sap as to cause any turgidity of the cell.

It may be concluded, therefore, that the retardation of the growth of the hypha of Phycomyces, produced by the action of light, is to be attributed to a diminished mobility of the micellæ of the protoplasm rather than to a diminished mobility of the micellæ of the cell-wall. It may be further inferred, that this holds good also in the case of the growing cells of a multicellular organism.

This statement receives considerable support from the facts, which are already known as to the action of light upon protoplasm. The so

1) Unters. über Zellstreckung. 1877.

called heliotropism of the plasmodia of Myxomycetes and the change of position exhibited by the chlorophyll-grains of different organs when exposed alternately to light and to darkness prove, that light can act directly upon protoplasm. PFEFFER[1]) recently concluded upon purely physical grounds, that the diminution of extensibility which cells undergo when exposed to light, was due to the molecular activity of light in the primordial utricle (plasma-membrane).

If this be the correct explanation of the action of light in retarding growth, it must be applicable also to the phenomena of heliotropism and to those resulting from the action of light upon spontaneously motile organs.

In considering those special cases of the action of light upon growth, which are included under the term »heliotropism«, I shall only allude to those in which the heliotropism is positive, for the true nature and significance of negative heliotropism is at present quite uncertain. The curvature is due, as SACHS has shewn, to a greater rapidity of the growth of the side most distant from the source of light. This is stated of a multicellular structure, but there is no reason to believe that the case is otherwise with a single cell. The protoplasm of the concave side may have had its extensibility diminished by the action of light and consequently its growth is less rapid than is that of the convex side. PFEFFER[2]) ascribes the heliotropism of unicellular organs to an action of light upon the cell-wall. This suggestion is, however, not in harmony with his view already quoted, that light can directly affect the extensibility of the plasma-membrane. Further it compels the assumption that there are two kinds of positive heliotropism, viz, that of multicellular organs, due to a gradual diminution of the turgidity of the cells extending from the less strongly to the more strongly illuminated side, and that of unicellular organs. Under these circumstances it is evident, that the explanation given above offers fewer difficulties.

With reference to the spontaneous movements, it is well-known, that they are generally arrested when the plants, which exhibit them are exposed to light. SACHS[3]) has already drawn attention to the similarity between this phenomenon and the retardation of growth effected by light, and has suggested that the mode of action is the same in both cases.

The mechanism of the spontaneous movements has not been directly investigated, but they are so similar to the movements which are induced by stimulation that our knowledge of the mechanism of the latter may be fairly applied to explain that of the former. The mechanism of

1) Bot. Zeitg. 1876. p. 77.

2) Osmot. Untersuch. 1877. p. 208.

3) Lehrbuch p. 852.

these induced movements consists essentially in a change in the turgidity of the parenchymatous cells of the motile organ. BRÜCKE[1]) proved that the downward movement of the leaf of Mimosa pudica, which follows a stimulus, is due to a diminution of the tension in the lower portion of the motile organ. The experiments of PFEFFER[2]) upon the stamens of Cynareae and upon the motile organs of Mimosa pudica demonstrated, that a considerable quantity of water is expelled from the tissues during the movement. PFEFFER suggested that, assuming the permeability of the tense cell-wall to remain unaltered, the expulsion of cell-sap from the cell may be dependent upon changes in the protoplasm. Under ordinary circumstances, as has been already mentioned, the protoplasm does not permit the escape of cell-sap, but it may be that some influence so acts upon the protoplasm at the time of movement, that it becomes permeable. In commenting upon this suggestion SACHS[3]) remarks, that such variations in the permeability of protoplasm are known to occur. For instance, when the protoplasm of a cell of Spirogyra contracts previously to conjugation, it must have become permeable, for a quantity of cell-sap escapes.

The force which causes the expulsion of the cell-sap, is regarded by PFEFFER[4]) as being merely the pressure of the elastic cell-wall upon the cell-contents, to which the now permeable protoplasm offers but little resistance. He believes that the cause of the variation of pressure is to be sought in some change effected in the osmotic properties of the cell-contents by the action of the stimulus. It is by no means easy to understand, how such a diminution of the osmotic properties of the cell-contents could be so rapidly produced. It seems more simple and satisfactory to regard the expulsion of the cell-sap as being due to a contraction of the protoplasm, that is, to an approximation of its micellae in consequence, probably, of an increase of the attraction existing between them, effected either by a stimulus acting from within (spontaneous movements) or by a stimulus acting from without. The escape of the fluid under these circumstances is to be regarded as a phenomenon not of osmosis, but of filtration under pressure.

The position which spontaneously motile organs assume when exposed to light is that in which they are fully expanded. Proceeding upon the assumption that the mechanism of the movements of these organs is essentially the same as that of the induced movements of irritable organs, this expanded position must be ascribed to the maintenance of the micellae in a condition of stable equilibrium. The influence of light upon the micellae is of such a nature that it prevents their approxi-

1) Arch. f. Anat. u. Physiol. 1848.

2) Physiol. Untersuch. 1873.

3) Lehrbuch p. 866.

4) Osmot. Untersuch. p. 192.

mation in obedience to the periodic action of internal stimuli, although this influence is not sufficiently strong to prevent contraction in obedience to stimuli acting from without.

The conditions of growing and of »contractile« cells are in some respects the same. Turgidity is essential to the proper fulfilment of the functions of both, and it has been shewn that light has the power of inhibiting, more or less completely, the activity of both. The most general case of the action of light upon growing cells has been shewn to be a diminution in the rapidity of their growth. The cell with diminished or arrested growth may be fairly compared with one of the cells of a rigid motile organ. In both, the micellae of the protoplasm are in a state of stable equilibrium so that they do not yield, in the former case to the force which tends to separate them, namely the pressure of the cell-contents, and in the latter to the force which tends to bring them nearer together.

The theory, that the action of light upon growing cells and upon those of motile organs is due to such a modification of the relations existing between the micellae of the protoplasm that the mobility of the micellae is diminished, thus gives a satisfactory explanation of many phenomena which, at first sight, seem not to have much in common. It may be that this is only a special case of the general principle, that the influence of all physical forces upon vegetable cells is especially exerted upon the protoplasm of those cells, and modifies the relations existing between the micellae.