Botany. — *Light- and dark-adaptation of a plant cell.* By Dr. D. TOLLENAAR and Prof. A. H. BLAAUW.

(Communicated at the meeting of April 30, 1921).

Now that it has appeared that the growth in length of vegetative organs as a rule shows a very characteristic response to the light-stimulus, we possess in this response of growth to light an excellent criterion for the elementary study of sensitiveness to light. In this research of which all experiments have been made by Mr. TOLLENAAR, we have carried on the study about the way in which the light sensitiveness of an individual cell, the sporangiophore of *Phycomyces nitens*, reveals itself in the response of growth. The progress of the reactions is already known in case that fixed quantities of light of $^1/_4$ M.C.S. to 2 mill. M.C.S. are applied in a short time to cells that are kept in the dark (see Licht u. Wachstum I). Likewise how the response of growth is, when the cell already adapted to the dark is exposed to permanent light, e.g. of 1,64 or 4000 M.C. (see Licht u. Wachstum III). In 64 M.C. for instance we see acceleration- and retardation of growth interchange and gradually brought into equilibrium. When after this adaptation to light the growth has become constant again, its progress appears in 64 M.C. some percentages quicker than in the case of the cell adapted to the dark.

I. *Conversely, does the growth become some percentages slighter, when the cell after adaptation to light has been completely re-adapted to the dark in* $1\frac{1}{2}$ *or 2 hours?*

All experiments in this research have been made at 16° C. with horizontal and 4-sided illumination. For the cultures + stems were used.

Experiments of control. These are required, because the growth of the cells may somewhat change its speed in the course of 2 hours, even though the illumination remains constant, in consequence of chance causes or e.g. because the growth is still increasing or already decreasing. With cells that have been adapted to 64 M.C. the rate of growth differed after two hours, respect.: -1, $+3\frac{1}{2}$, $+1$, -1, $-7\frac{1}{2}$, $+7\frac{1}{2}$, $-2\frac{1}{2}$, $-1\frac{1}{2}$, -7, -5, $+3$, 0, $+1$, $+1\frac{1}{2}$, $+4$ %. average $-0,27$ %, i.o.w. after adaptation to 64 M.C. (in 2 hours) the average growth remained the same in the next 2 hours in 64 M.C

Experiments. 4 cells adapted to 64 M.C. and then left in the dark show after adaptation to the dark (after $1\frac{1}{2}$ — 2 hours) a change in growth of — 6.0 °/₀ (± 0.53): 14 cells from another series of experiments — 7,5 °/₀ (± 1,2). With one of these 18 cells the growth had increased after a 2 hours' stay in the dark, with two the growth was the same, with 15 decreased.

The cells from the dark, adapted after a few hours to light of

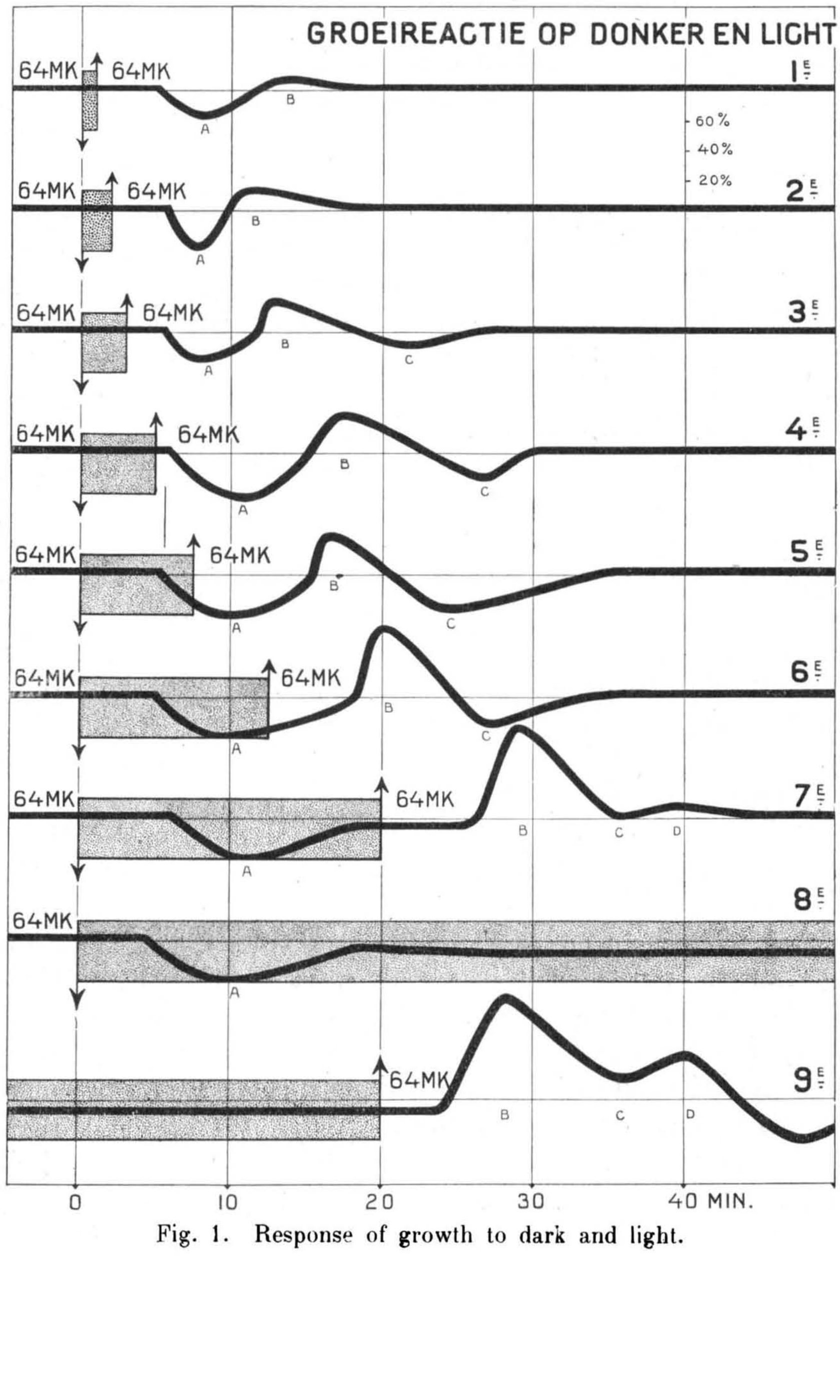

Fig. 1. Response of growth to dark and light.

64 M.C., grow some percentages quicker than in the dark; when left again in the dark, they constantly grow 4 — 10 °/₀ more slowly after dark-adaptation.

II. *Does the dark call forth a response of growth in a cell adapted to light, i.o.w. does the dark work as a stimulus, or is this decrease of growth of* 4—10°/₀ *in the dark quite gradual?*

Experiments. When the cell adapted to 64 M.C. is made permanently dark a decrease of growth sets in after $3^1/_2$—$5^1/_2$ min., so that after 8—$11^1/_2$ min. the rate has decreased to ± 73°/₀; next there follows an increase, by which after $15^1/_2$—$18^1/_2$ min. the rate is about recovered ($98^1/_2$ °/₀) in the light to decrease again a little and become gradually constant at ± 93°/₀ of the rate of growth in 64 M.C. (See fig. 1, curve 8).

So a disturbance of equilibrium takes place in consequence of the stoppage of the energy-supply, so that a typical response to stimulus ensues, which is contrary to the response of growth to light. If after the darkening the growth had *gradually* decreased to its dark-value, we could hardly have spoken of a response to stimulus. Now that there always occurs a reaction-time of $3^1/_2$—$5^1/_2$ min., just as with the response of growth to light and in consequence of the dark-fall an evident *disturbance of equilibrium* takes place, showing itself in *fluctuation of growth,* we may talk here of a typical *response to stimulus.*

For a cell adapted to constant light the dark (sudden stoppage of light-supply) works as a stimulus. For some minutes the rate of growth in the light is maintained in the dark, then a sudden reaction follows, contrary to that which light causes.

Responses to dark and to decrease of light have already been ascertained by SIERP for *Avena.* The response of growth to light of *Avena* is mainly a retardation of growth; the reactions observed by SIERP on dark- and light-decrease were accelerations of growth. It seems suitable to me to use the name of *dark-growth-response* for this phenomenon, as SIERP proposes with some reserve, provided an ample meaning is attached to the conception light- and dark-growth-response, viz. a response of growth to increase, resp. decrease of light.

Man states the result of the light-energy on the retina by himself much quicker through his impressions of brightness, than we can read the result of the light-stimulus on the metabolism in that cell in consequence of its change of growth. Moreover those processes take place here at 16° C., with man at 37° C. Yet we are of opinion that we have every reason to see similarity between the way of reacting of the plant cell *to dark* and the appearance of a positive after-image, followed by the appearance of *negative after-images* in definite circumstances in the eye. There too after the fall of the dark a fluctuation of the impression of brightness, by which the impression of brightness or rather of darkness, with the negative after-image, may fall in the beginning *below* the normal darkness (or so-called intrinsic light of the retina) of the eye adapted to the dark. In this way the after-images are to be taken as a disturbance of equilibrium of the sight-apparatus adapted to light through the coming of the dark (= the stoppage of the energy-supply). Especially these negative after-images, which appear in our eye 2—4 minutes after strong prolonged illumination should be noted.

III. *What is the process of this dark-growth-response, when the cell has not been adapted to* 64 *M. C. but to slighter intensity?*

Experiments. Experiments were made in 8—1—$^1/_8$—$^1/_{64}$ and $^1/_{512}$ M.C. In 8 M.C. the average minimum of growth was 67 %. It further appears, that the growth also after slighter intensities of 1 and $^1/_8$ M.C. decreases to about the same value, viz. to ± 75 %. To be sure the reaction — just as with the common light-growth-response after weaker stimuli — appears *later*. The maximal decrease is from 8$^1/_2$—11 min. after 64 M.C. and 8 M.C., shifted to 11—14 min. after $^1/_8$ M.C. After still slighter intensity of $^1/_{64}$ M.C., the growth decreases only to ± 85 %, after $^1/_{512}$ M.C. to ± 89 %. Therefore only after these slight intensities the dark-growth-response becomes clearly smaller, while the minimum remains just as after $^1/_8$ M.C. at 11—14 min. after the beginning of the darkening.

It is evident in these and other experiments as before, that the moments at which maxima and minima occur in the experiments with the various individuals are exceptionally constant. Especially with threshold-determinations when we can hardly say with certainty whether from a greater or smaller number an increase resp. decrease of growth may be inferred, the constancy of the points of time, at which the phenomena occur is a great aid in stating the appearance or non-appearance of an actual response. We want to point out in this connection, that GRÜNBERG (1913) in his study on negative after-images was also struck with the uncommon constancy of the moments at which the after-images appear.

IV. *When the cell after adaptation to* 64 *M.C. is not permanently* *put in the dark, but the light is interrupted for a short time, what will be the process of the dark-growth-response?*

Experiments. The light of 64 M.C. was in the various experiments interrupted by dark for 1, 2, 3, 5, 7½, 12½ and 20 minutes. A summary result is found in the following table, in which the principal moments have been given, while fig. 1 curve 1—7 shows the average process.

TABLE I. Response of growth of cells adapted to 64 M.C., in consequence of different times of darkness.

Darkening for	Beginning of response in min. after beginning of darkening	Minimum growth		Max. growth		2nd min.	
		after	in perc. of the growth in 64 M.C.	after	in perc.	after	in perc.
1 *min.*	4 —6½	7 — 9	85½ perc.	11½—14	103½ perc.	—	—
2 *min.*	5 —6½	7 — 8½	77½ „	10 —12	112 „	—	—
3 *min.*	4½—6½	7 — 9	83½ „	11½—13	118 „	19½—23	93 perc.
5 *min.*	5 —7	10 —12	74½ „	15½ 18½	124 „	25 —28	85 „
7½ *min.*	4½—6½	8 — 10½	70 „	15 —17	126 „	22½—24½	79 „
12½ *min.*	4 —6½	8 —10	72 „	19 —21	145 „	26½—28	84 „
20 *min.*	5 —7½	10½—12½	74½ „	28 —29½	163 „	34½—37½	99 „
Perman.	3½—5½	8½—11	75 „	(15½ - 18½)	(98½ „)	± 94 perc. perman.	

In connection with fig. 1 the following may be observed. *Short times of darkness also call forth a typical dark-growth-response.*

With the short darkening of 1, 2, 3 minutes we were already struck with the fact, that after the minimum a constantly increasing maximum follows. (See esp. the table). When the cell remained in the dark, there was to be stated after the minimum also an increase of growth till just above the definite rate of growth in the dark, as had already been *previously* ascertained. But now that we darkened *for a short time* a maximum occurred, that becomes the greater according to the longer duration of the darkening, i.e. according as we put off the return of light.

It appeared *that a temporary darkening causes two successive reactions* resp. a dark-growth-response and a light-growth response.

In the successive experiments the *dark-growth-response* is mainly to be found on the same spot (see fig. 1 and table I) after 8—12 minutes. Only where the darkening after 1, 2, 3 minutes, i.e. very speedily is superseded by light, the dark-growth-response cannot fully develop: the retardation of growth is earlier changed into increase of growth, so that the minimum is slighter ($77\frac{1}{2}$—$85\frac{1}{2}$ % instead of 70—75 %) and *consequently seems to be a little earlier* (after 7—9 min. instead of 8—12 min.). The beginning and the maximum of the light-growth-response on the contrary show themselves later with longer darkening, demonstrating in that way that it is the response to the return of light. The maximum was found with 1, 2, 3, 5, $7\frac{1}{2}$, $12\frac{1}{2}$, 20 minutes of darkening, resp. at $10\frac{1}{2}$—13, 8—10, $8\frac{1}{2}$—10, $10\frac{1}{2}$—$13\frac{1}{2}$, $7\frac{1}{2}$—$9\frac{1}{2}$, $6\frac{1}{2}$—$8\frac{1}{2}$, 8—$9\frac{1}{2}$ minutes after the return of light, while this maximum with complete adaptation to the dark (see Licht u. Wachstum III p. 102) has also been found at 7—$8\frac{1}{2}$ minutes after the beginning of 64 M.C. This latter reaction has been added for comparison as 9th curve to fig. 1. This shows that the first maximum, even the successive sinking and a second maximum observed at one time (1918) in permanent 64 M.C., now 1920 showed itself again after a darkening of only 20 minutes. The successive curves demonstrate, how by taking the dark periods longer and longer, we are able *to analyse the response to a short darkening in a dark-growth-response (A) result of dark-fall, and a light-growth-response (B—C—D), result of subsequent exposure to light.*

Meanwhile SIERP (1921) has considered with *Avena* the response of growth in short periods of dark. In this summary we can but refer to this. Though the transition from dark to light (64 M.C.) in the successive experiments is in a physical sense every time equally great, this transition causes an ever greater maximum in the growth (resp. $103\frac{1}{2}$—112—118—124—126—145 and 163 %), according as the cell has been darkened longer. By this it is already shown, that the cell adapted to 64 M.C. has greatly lost its sensitiveness and that the sensitiveness after the darkening increases very rapidly already from the first minutes. *This dark-adaptation* (= disappearance of light adaptation) is further shown by the following experiments.

V. *The adaptation to the dark of a cell used to light* may be demonstrated in two ways: *A.* by applying an equal quantity of light at different times after the darkening and considering how the response to this light-stimulus increases according as the cell has been longer in the dark; *B.* by determining how great the threshold of stimulation is at different points of time after the darkening.

Experiment A^1: A quantity of 256 M.C.S. (in 4 sec.) applied was to cells, adapted to 64 M.C. at different times after the beginning of the darkening. See Table II and Fig. 2 curves 1, 2, 3, 4, 5. The first ± 15 min. after the darkening 256 M.C.S. has no effect on

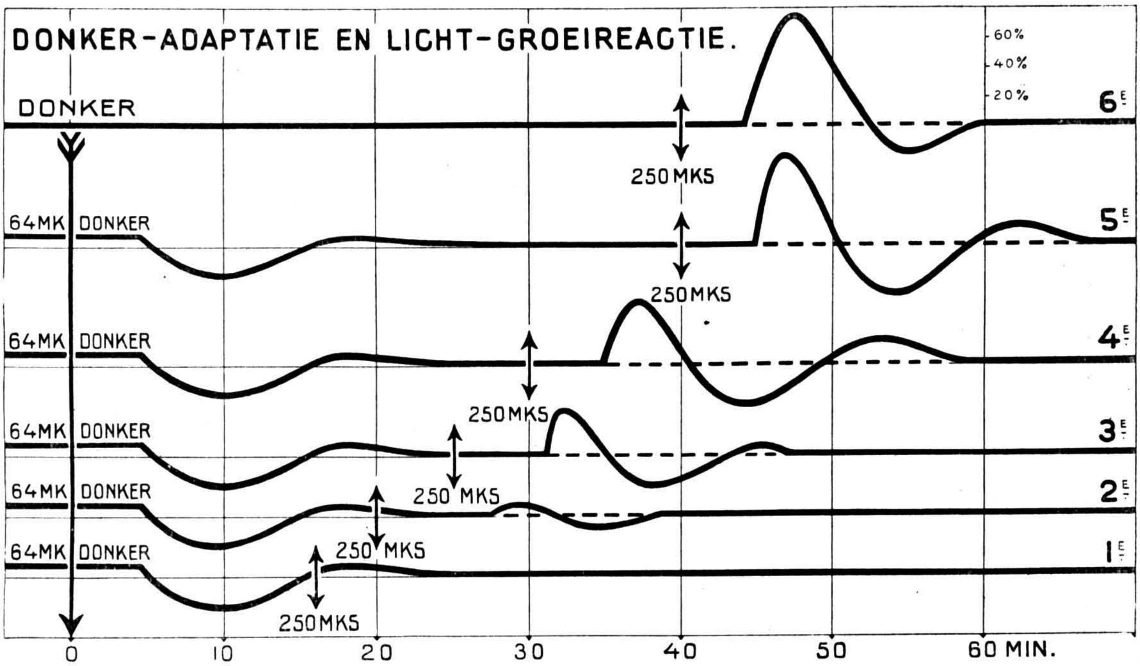

Fig. 2. Dark-adaptation and light-growth response.

the growth (curve 1), whereas this quantity does cause a maximal response by dark-adaptation (curve 6).

TABLE II. Response to 256 M.C.S. of cells, adapted to 64 M.C., at different points of time after darkening.

250 M.C.S. applied after:	Beg. of resp. in min. after exposure to 250 M.C.S.	Maximum		Minimum		2nd max.	
		after min.	in perc. of the growth in dark	after	in perc.	after	in perc.
20 min.	6½—8½	8 —10 m.	107½	13½—15½	96	—	—
25 min.	5½—7	6 — 7½ „	132	12½—14½	83	19 —21½	105
30 min.	4 — 6	6½— 8 „	144	12½—15½	74	21½—24½	116
40 min.	4 —6	6 — 7½ „	160	12½—15	69½	20 —23½	112½
2 hours (full adaptation)	4 —5½	6½— 8½ „	176	14 —16	83½	—	—

Table II and fig. 2 clearly show the increasing adaptation in consequence of the increase of response after longer darkening. Fig. 2 of course first shows the dark-growth-response, which has been left out in Table II.

Will the reaction begin earlier than by 256 *M.C.S. by exposure to* 1400 *M.C.S.?* This cannot be said with certainty, for cells adapted to the dark respond to 256 M.C.S. *for the eye* in growth more than to 1400 M.C.S. Moreover the question is, whether in the period of the dark-growth-response a light-response may be excited.

Experiments A^2. In the first ± 5 min. after the darkening 1400 M.C.S. has no effect (*see curve* 1 *of fig.* 3), so that the response to the dark takes place as usual. But applied after $6^1/_2$ min., light-growth-response already occurs, setting in therefore during the dark-growth-response.

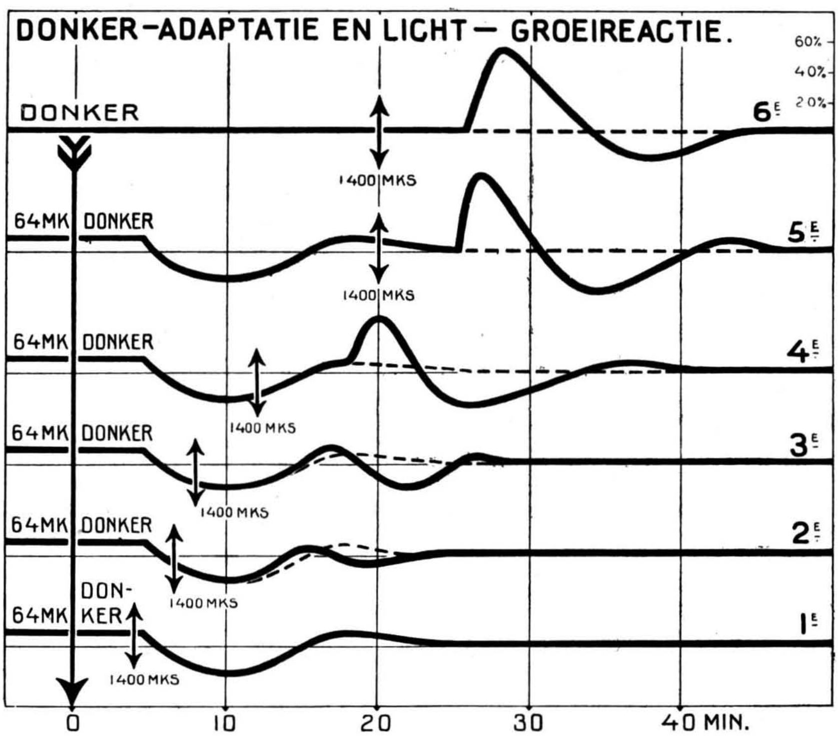

Fig. 3. Dark-adaptation and light-growth response.

See further fig. 3 and Tab. III. From this it appears in the same way as by application of 256 M.C.S., that the reaction grows stronger according as the cell has been further adapted to the dark. In fig. 2 and 3 the process of the growth is dotted, in case the latter light-stimulus had not been applied. Especially striking is the sudden sharp transition to the light-growth-response (see 3rd and 2nd curve).

After a darkening of 20 min. the response to 1400 M.C.S. has already much approached the response of cells adapted to the dark, which has been added for comparison in the 6th curve of fig. 3.

TABLE III. Response to 1400 M.C.S. of cells, adapted to 64 M.C. at different points of time after the darkening.

1400 M.C.S. applied after:	Beg. of resp. in min. after exposure to 1400 M.C.S.	maximum		minimum	
		after	in perc. of the growth in dark	after	in perc.
6½ min.	5½—7½	7½ 9½ min.	102	11½—13½ m.	98
8 „	6 —8	7 —10 „	110	13 —15 „	86
12 „	5 —7	6 —8 „	133	12 —14 „	78½
20 „	4½—6½	5½—7½ „	148	12½—15 „	73
2 hours (full adaptation)	5 —7	7¼—9¼ „	152	17 —19½ „	85

In the experiments of Tables II and III the process of the dark-adaptation — increase of sensitiveness — has *to some extent* been graphically represented by the percentages of the maxima of growth attained. Yet the quantitative proportion of the *sensitiveness* at different points of time of the adaptation-process has *not* been expressed in them, but the increase of the reaction-energy, being the result of that increased sensitiveness. But it is more important to express quantitatively the increase of the sensitiveness itself, and for that it is necessary to determine the quantities of light, causing an *equal effect* at different points of time of the adaptation-process, in order to make the sensitiveness inversely proportional. For this we prefer to choose the minimum effect, which is still perceptible to us, i.e. the limit or minimum-quantity, by which the light-growth-response occurs or with the classical term, the thresholds of stimulation.

Since it seems quite evident, that the effect of the light-energy in the cell with increasing stimuli gradually appears as response of growth and increases, we should be with this stimulus-process — and probably a great many others — careful with the tendency, lying in the word threshold. For convenience' sake we shall use the word here with that reserve.

Experiments B. In order to draw a comparison with the sensitiveness of the cell still completely adapted to 64 M.C., the threshold of stimulation was determined in cells being in 64 M.C.

When an additional 2000 M.C.S. was applied, no trace of a response was found; when 3000 M.C.S. was administered (500 M.C. × 6 S.), in one of the 6 experiments a faint response was observed; with 4000 M.C.S. (1000 M.C. × 4 S) all 5 cells show a distinct response. *For 64 M.C. therefore the threshold lies between 3000 and 4000 M.C.S., i.e. at ± 3500 M.C.S.*

Next there were applied in the dark 2000 M.C.S. (500 MC. × 4 S), 256 M.C.S. (64 M.C. × 4 S), 32 M.C.S (8 M.C. × 4 S), 4 M.C.S. (1 M.C. × 4 S) $^1/_2$ M.C.S. ($^1/_8$ M.C. × 4 S), $^1/_{16}$ M.C.S. ($^1/_{80}$ M.C. × 5 S) and determined at what points of time these quantities are threshold-values. Moreover the threshold-value was determined for complete dark-adaptation. We had noticed that this was a good deal lower than the smallest quantity ($^1/_4$ M.C.S.) which was used before (see Licht u. Wachstum I).

The limit or threshold-value for the photo-growth-response of these cells adapted to the dark is at about $^1/_{100}$ M.C.S. This is a quantity much smaller than was hithertho used for stating vegetative reactions. By smaller quantities a reaction was sometimes perceived, but in the dark the limit is very difficult to fix, because with strongly decreasing quantity of stimulation the effect of growth decreases but slowly, about according to the cube-root of the quantity of stimulation (see L. u. W. I, which point we will further develop). So it already appears *that the cell in the dark is ± 350.000 times more sensitive for the light-stimulus than when adapted to 64 M.C.*

Table IV gives a survey of the process of adaptation from 64 M.C. to the dark.

TABLE IV. Process of adaptation or increase of sensitiveness after discontinuance of exposure to 64 M.C.

		Limit	Proportion of sensitiveness
In 64 M.C.		± 3500 M.C.S.	1
after 5 Min.		2000 „	1.75
	13 Min.		
„ 18 Min.		256 „	13.6
	$10^1/_2$ Min.		
„ $28^1/_2$ Min.		32 „	109
	$12^1/_2$ Min.		
„ 41 Min.		4 „	875
	14 Min.		
„ 55 Min.		$^1/_2$ „	7000
	15 Min.		
„ 70 Min.		$^1/_{16}$ „	56.000
Adapted to the dark (after 90—120 min.)		± $^1/_{100}$ „	350.000

In the first place it appeared, that also **after the dark-growth response is finished and the growth after ± 30 min. has grown fairly constant, internally in the metabolism the dark-equilibrium has not been attained by far and will recover itself only after one and a half to two hours.**

During the adaptation process the points of time may be defined fairly exactly for a fixed light-portion as threshold. For instance 32 M.C.S. gave after 25, after 26, after 27 min. no reactions, after 28½ min. three responded, one did not. In connection also with fig. 2 and 3 on the further increase of the reaction we see that the response of growth "turns up" quickly, when once the adaptation has sufficiently advanced for that light-portion. When however the dark-adaptation has for the greater part been attained, those time limits are fainter, since the sensitiveness does not increase so rapidly as during the full adaptation-process.

The rate at which the sensitiveness increases and rises to the end- or dark-sensitiveness, may be imagined by observing in the table that from 5 — 70 min., thus *during by far the greatest part of the adaptation-process, respect. in* 13, 10½, 12½, 14 *and* 15 *min. the sensitiveness becomes every time* 8 *times greater*. Between 18 and 28½ min. the geometrical rise appears to be strongest, between 0 and 5 min. it is geometrically yet a little slighter than between 5 and 18 min. By representing in a system of coördinates the times as abscissae, as ordinates the logarithms of the values of sensitive-

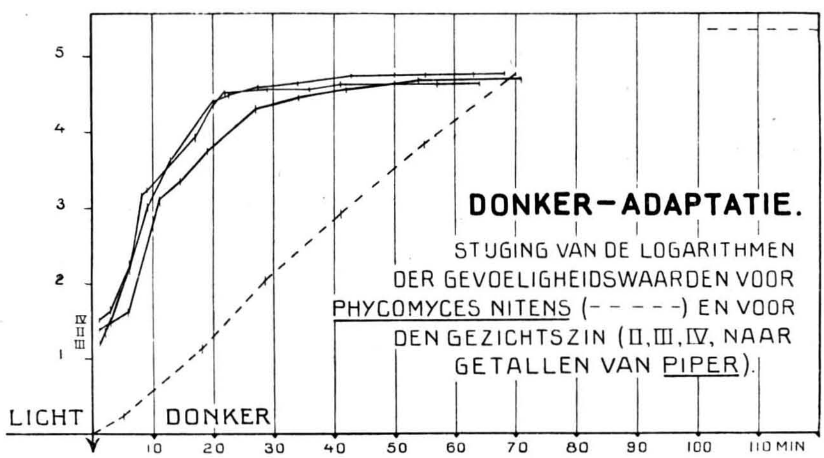

Fig. 4.

Dark-adaptation. Rise of the logarithms of the values of sensitiveness for *Phycomyces-nitens* (. . . . .) and for the sense of sight (II, III, IV according to figures of *Piper*).

ness (see fig. 4), a good image may be got of the geometrical increase of the sensitiveness during the adaptation. In this figure the logarithm of the value of sensitiveness has also been represented, which is finally reached after complete dark-adaptation after 1½ — 2 hours. When however as ordinates the sensitiveness itself is represented, the ascent of the curve shows the rate of the arithmetical increase of the sensitiveness as PIPER (1903) carries it out and discusses it for the adaptation of the sense of sight.

When therefore we would graphically represent the adaptation of these cells in the way of PIPER, it would give the impression (see Table IV), that there is but a very slight adaptation in the first 30 min., that after 70 min. only $^1/_7$ of the dark-adaptation is finished, and only after that the adaptation progresses fastest (curve steepest). If PIPER's adaptation-curves are converted, by representing the values of sensitiveness instead of the sensitivenesses themselves, and if they are compared with the same representation for the cell, the strongest rise of sensitiveness in man is found earlier than in PIPER's report and only then it becomes quite clear that the adaptation-process of our sight-impression is mathematically not so simple as with these cells. For three curves with an average course (II, III and IV of PIPER's observers) the logarithm of the values of sensitiveness has been represented in fig. 4. In the main 4 phases may be distinguished: a rather rapid one (first 3—6 min.), a very rapid one (3—6 to 8—12 min.) a rather rapid one (8—12 to 20—27 min.) and a very slow one (after 20—27 min.). When comparing we get the impression, that with the cell-adaptation we have to deal with a simpler process, though the same phases may be faintly distinguishable.

We have still to add that we determined the thresholds in these cells with fixed *quantities* of light, while for the human eye only *intensity*-thresholds have been determined. That makes the comparison more difficult. Determination of quantity-thresholds for the eye might picture the adaptation-process differently and more accurately. Moreover PIPER is wrong in not giving *the exact intensity* to which the eye was previously exposed, in beginning his first observations only after about 1 min. dark without an observation *in* light and in taking this first observation as *zero* in his curves.

Finally we may observe, that the width of adaptation with these cells is 1 : 350.000. With man it is according to PIPER only 1 : 2 to 8000; in consequence of the measuring of the intensity-threshold, and the mis-stated initial intensity a perfect comparison is not possible, though it seems a great deal slighter than with the *Phycomyces*-cells.

VI. After it had already appeared in the research on the adaptation to dark, that the sensitiveness to light being in 64 M.C. is 350.000 times less than in the dark, we could further consider the course of adaptation when the cell has been previously adapted to fainter or stronger light. For the present however we had to restrict ourselves to the question: *How much changes the tone or degree of sensitiveness, when the cells have been adapted to different intensities of light*?

Experiments. After a stay of at least 2 hours in different intensities it was determined, what quantity of light was just able to call forth a light-growth-response, while the cells remain in that intensity. In Table V the result of these experiments is briefly summarized.

TABLE V. Proportion of sensitiveness after adaptation to different intensities.

Adapted to	Limit	Proportion of sensitiveness.
64 M.C.	3000—4000 M.C.S.	1
8 „	200 — 400 „	8,75—17,5
1 „	25— 50 „	70—140
$^1/_8$ „	3— 6 „	580—1160
$^1/_{64}$ „	0,4 — 0,8 „	4375—8750
$^1/_{512}$ „	0,1— 0,2 „	17.500—35.000
Dark	± 0,01 „	± 350.000

Now it appears, that for intensities of $^1/_{64}$ M.C. to 8 M.C. the sensitiveness decreases proportionally to the intensity to which the cell has been adapted. In 64 M.C. the sensitiveness seems to have lessened still more than would be expected according to this rule. To the very lowest intensities this rule could not hold good, because then the sensitiveness would become infinitely great in the dark. So we see after all that in $^1/_{512}$ M.C. the sensitiveness in comparison with $^1/_{64}$ has not increased 8 times, but only 4 times more. Yet it is already striking that it holds good to $^1/_{64}$ M.C.

One would be inclined to simply accept that one had to deal here with the law of WEBER. Yet we should be careful in making a comparison. We have here the very elementary case of one single cell, for which we have demonstrated as follows:

When the growth of Phycomyces-cells has been adapted to intensities of $^1/_{64}$ to 8 M.C., the quantity of light still calling forth a response of growth (the threshold of stimulation) rises proportionally to that intensity.

In verifying the law of WEBER two stimuli are compared with each other, which are unequal but applied in the same way, and the proportion is determined which is still observed as different. Here however the cell has been adapted to an intensity and we simply determine the *quantity* of stimulus which — applied in a short time — is threshold of stimulation with that adaptation. The cell therefore has been adapted to one stimulus, while the other stimulus is quickly applied as a portion. In fact this is another and more elementary experiment than the comparison of two intensities. As however the rule obtained so much resembles the law of WEBER for the comparison of two intensities, it is very probable that in point of principle we have to deal with the same phenomenon. Not in that sense that with the sensitiveness to light of this single cell there would be question of any psychical condition or power of discrimination, but conversely that these psycho-physical rules for the human perceptive faculty are at bottom based on simpler reactions in the individual cells to which those rules are already applicable.

It further deserves attention, also with a view to experiments and placing in so-called weak light, *that in a so slight intensity as $^1/_{512}$ meter-candle* these cells are already ± 15 times less sensitive than in the dark.

After these quantitative measurings of the adaptation or tone-change we have still to emphasize what follows. While the growth e.g. in 64 M.C. is only 6 or 7 % more than in the dark, so that for the rest such a cell at its growth cannot be distinguished at all from a cell in the dark, there is inwardly after adaptation to light quite a different condition, a different "*tone*". For that appears directly from the quantity of light that is wanted to induce such a cell adapted to light to a light-growth-response. The tone (condition of adaptation or degree of sensitiveness) is quite different and especially in this response of growth the phenomenon of adaptation appears in much purer form than in phototropical movements. The phenomena of tone already appearing in phototropical reactions and the subject of much study [see e.g. BLAAUW (1909), PRINGSHEIM (1909), especially ARISZ (1915), BREMEKAMP (1918), v. D. SANDE BAKHUYZEN (1920),] occurring in consequence of longer exposures must not be exclusively taken as a consequence of the progress of the responses of growth.

It is perfectly true that part of the phototropical "tone"-phenomena may be solved as a result of the process of growth at the front- and backside (see v. D. SANDE BAKHUYZEN). But it should not be forgotten, that there is also a real change of tone which has a deeper base and is much more important in principle. In prolonged exposure real changes of tone (= phenomena of adaptation, i.e. changes in the degree of sensitiveness to light) *principally act a very important part* in part of *those* processes, which *underlie* the growth and *precede* the result of the growth. *The result* of this altered sensitiveness appears to us in the response of growth as an external symptom. We had better not use the word sensitiveness *of growth* (as we previously did occasionally, see L. u. W. III), because it might be easily forgotten, that at bottom sensitiveness to light rests with part of those deeper processes of metabolism, from which the growth secondarily results. Yet for convenience' sake we may call the growth (as well as the whole plant) "sensitive to light" as it is generally done in physiology with a number of phenomena of sensitiveness; provided we remember, that in most cases but some primary fraction of the larger complex is really sensitive to that factor and perceives it, while all the rest of the phenomena are only resulting reactions.

We have had to restrict ourselves to a summary of our research. The full data and a further discussion of the results and the literature will be published later on, while the researches on responses of growth are being continued.

Wageningen, March 1921.

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