V.

The Influence of Light upon the Growth of Leaves.

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The observations of SACHS[1]) upon the growth of internodes have shewn that it presents a certain daily periodicity, which he ascribes to the alternation of day and night. An examination of the curves which he gives shews that the maximum of growth usually occurs between six and nine in the morning, the minimum between three and six in the afternoon. If a correction for temperature be made by means of SACHS' formula $\frac{x}{t-n}$ (where x is the amount of increase in length during any given time, t the temperature, and n a number which increases from nothing to a little less than the smallest t), the occurrence of the maxima of the various curves in the morning and of the minima in the afternoon is rendered

1) Arb. des bot. Inst. in Würzburg. Heft II. 1873.

2) Note on SACHS' formula. As the true significance of this formula is frequently misunderstood (see, for instance, STEBLER in Jahrb. für wiss. Bot. Bd. XI. Heft 1. 1877), it may be well to append a short explanation.

The object of it is merely to eliminate all variations of growth which are produced by variations in temperature, and by this means to obtain a curve which represents more accurately the effect produced by the action of light upon growth.

Assuming that the increase in rapidity of growth is proportional to the rise of temperature, the expression $\frac{x}{t}$ would represent the amount of increase in rapidity for each degree of temperature (where x is the amount of increase in length in a unit of time, and t the temperature). This, however, would be incorrect, for growth does not commence at 0° C., but at a temperature of several degrees. In order therefore to ascertain the true value of the increased rapidity of growth due to each degree of temperature, the temperature must be calculated form that at which the growth of the plant begins. Taking m to represent this minimum temperature, the expression $\frac{x}{t}$ becomes $\frac{x}{t-m}$. The minimum temperature at which growth can take place in any particular plant, has not always been determined experimentally. A minimum temperature must therefore be assumed, and that one is selected which most effectually removes from the curve of growth the inequalities due to variations of temperature.

An example may perhaps serve to make this explanation clearer.

An internode grows 4 mm in an hour, in the dark the temperature being 20° C.

more uniform. Sachs explains these phenomena by ascribing the decrease in the rapidity of growth which immediately succeeds the attainment of the maximum to the action of the increasing light, and by regarding the increase which follows the occurrence of the minimum as being due to the gradual diminution of this retarding action. It must be noticed, that the maximum does not fall within the period of darkness, and that the minimum does not occur at the time, when the light is most intense. For the maximum is attained some time after dawn, the minimum toward sunset. The explanation given of this is, that the action of light upon the growth of plants is a gradual one; its effect in producing retardation is slowly manifested, and as slowly disappears. Hence the minimum of growth occurs in the afternoon after that daylight has acted upon the growing cells for several hours, and as the retarding influence gradually diminishes so does the rapidity of growth increase, until it reaches its maximum shortly after dawn, when the action of light begins again to make itself felt.

A daily periodicity has been observed by Prantl [1]) to occur in the growth of the leaves of Dicotyledonous plants. A comparison of his curve 1 with curves 5 and 6 of Sachs shews that they are very similar, and at once suggests, that the growth of these leaves is influenced by the action of light in the same way as that of internodes. Prantl's experiments, in which he varied the time of exposure to light, the results of which are given in his curves 2, 3 and 4, prove conclusively, that this suggestion is correct.

The same periodicity has been found by Strehl [2]) to occur in the

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When exposed to the light, it also grows 4 mm in an hour, the temperature being 22°. — In order to find the true value of the retarding effect exercised by light upon its growth, it is evidently necessary to estimate the effects due to the rise of temperature.

Here, $x = 4$, $t = 20$, and $m =$ any number between 0 and 20; say $m = 10$;

then $\frac{x}{t-m} = \frac{4}{20-10} = 0{\cdot}4$, that is the uniform acceleration of growth due to each degree of temperature.

In the second case, $x = 4$, $t = 22$ and $m = 10$,

$$\text{then } \frac{x}{t-m} = \frac{4}{22-10} = \frac{4}{12} = 0.3.$$

Here the uniform acceleration for each degree of temperature is 0.1 less than in the preceding case and this represents the value of the retarding action of light.

This formula is empirical in so far that the increase of rapidity of growth has not been proved to be accurately proportional to the rise of temperature, and further, in that a value for m has to be assumed. Its value, as a means of eliminating variations due to changes of temperature, cannot be doubted, as a comparison of the observed and calculated curves on Sachs' Plate VII will shew.

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

2) Unters. üb. Längenwachsthum der Wurzeln. Diss. Leipzig 1874.

growth of roots — and he accounts for it by means of the foregoing explanation.

There exists then a mass of facts relating to the growth of vegetable organs, the whole of which can be explained by the theory that growth is gradually retarded by the action of light. Nevertheless, the daily periodicity exhibited by the growth of leaves, more particularly those of Monocotyledons, has received another explanation. In a paper recently published Stebler[1]) argues that the periodicity observable in the growth of leaves is due to the action of light only in so far as this action affects the process of assimilation, or as he puts it, the maximum rapidity of growth occurs during daylight whilst assimilation is most active, and the minimum occurs when assimilation is no longer taking place.

In examining the correctness of Stebler's conclusions, it will be well to enquire what are the premises upon which his reasoning is founded, and what experimental evidence exists which would warrant their acceptance as general principles.

The conclusion arrived at by Stebler, which has been quoted above, suggests that the growth of leaves is immediately dependent upon the products of their own assimilation. This idea is by no means a new one. It appears to have suggested itself originally to De Saussure[2]). In one experiment he grew peas in a closed space over quicklime and found that, when the apparatus was exposed to sunlight, the plants died on about the fifth or sixth day, and that the air in the receiver contained only 16 % of oxygen and apparently no carbonic acid at the close of the experiment. When, on the other hand, a similar apparatus was kept in the shade, the plants grew and each gained, on an average, 371 milligrs in weight in the ten days during which the experiment lasted, and the air in the receiver contained, at the close of the experiment, 3 % carbonic acid. From this, and from other similar experiments, he concluded, that the presence of carbonic acid gas, or rather the decomposition of it, is necessary to the growth of the green parts of plants when exposed to sunlight, for they die, when this gas is removed.

Quite recently De Saussure's experiments have been repeated by Corenwinder[3]). From the first series of his experiments, performed in 1869, he arrived at the same conclusion as De Saussure, namely, that the leaves of plants, in order to live, must absorb carbonic acid from without. A subsequent series of experiments, however, performed three years later, in a somewhat different manner, yielded quite opposite results. In these latter experiments he used branches of trees of considerable size

1) Ueb. das Blattwachsthum. (Jahrb. für wiss. Bot. Bd. XI. Heft I. 1877.)

2) Recherches chim. sur la vegétation, deutsch von Voigt, p. 31 ff.

3) Comptes rendus. 1876.

and bearing many other branches which were well supplied with leaves. Such a branch was secured in a glass receiver filled with air which had previously passed through a solution of caustic potash. Under these circumstances the leaves borne by this branch were by no means arrested in their development. On the contrary, the more favourable temperature within the receiver so assisted their growth, that, at the end of the experiment, they were more fully developed than those which had grown in the open air. From these observations CORENWINDER concludes that leaves are able to assimilate not only the carbonic acid which they obtain directly from the air, but also the carbonic acid which reaches them from the tissues of the plant. In support of this view he quotes an experiment of DE SAUSSURE, in which a leafy branch, still in connection with the tree, was enclosed in a receiver full of air containing no carbonic acid. At the end of the experiment it was found that the percentage of oxygen in the air within the receiver was perceptibly higher than in ordinary air.

These facts, however, cannot be regarded as affording sufficient evidence to substantiate the statement that leaves do actually assimilate the carbonic acid which is evolved by their own tissues or which is obtained from other parts of the plant. The experiments of MOLL [1]) tend to prove that the contrary is the case. He finds that neither a leaf nor a part of a leaf, when in an atmosphere containing no CO_2, can form starch in visible quantity, although other parts of the plant, subaërial or subterranean, are surrounded by CO_2 in abundance. It is true that the starch, which makes its appearance in chlorophyll-grains, is only the excess of the products of assimilation [2]), and it may perhaps be assumed that, in MOLL's experiments, assimilation actually occurred, although it never produced such a quantity of carbohydrates, in excess of the demands of the growing parts of the plant, that a deposition of starch in the chlorophyll-grains of the leaves could take place. Such an assumption is clearly improbable, for the amount of CO_2 supplied to those parts of the plant which were not under observation, was so large that, had it penetrated through the tissues to the chlorophyll-grains of the leaf which was in an atmosphere derived of CO_2, it would most probably have given rise to the formation of starch within them. It is probably more correct to assume that the growth of the leaves in air deprived of its carbonic acid went on at the expense of nutritious substances conveyed from other parts of the plant to the growing cells, just in the same way as the growth of the stem is supported by material drawn either from the organs, which are the storehouses, or from those which are the factories of the plastic substances.

1) Ueber den Ursprung des Kohlenstoffs der Pflanzen. (Landw. Jahrb. 1877.)

2) GODLEWSKI in Arb. des bot. Inst. in Würzburg. Heft III, p. 343.

Recently this view of DE SAUSSURE's, which has just been discussed, has been revived by KRAUS [1]). His statement of it is 1) that young leaves, so soon as they are exposed to light, develope chlorophyll-grains, in which starch is at once formed by assimilation, and 2) that it is at the expense of this starch that the young leaf grows. The observations upon which this statement is based consist of comparative measurements of the length and breadth of normal and of etiolated leaves in different stages of their growth, as well as of measurements of their histological elements. — Commencing soon after the first appearance of the leaves when they are nearly equal in size, these measurements shew that the growth of the normal exceeds that of the etiolated leaves, so that in a few days the former are more than twice as large as the latter. The microscopical measurements shew, as might be expected, that the size of the histological elements of the normal leaves is greater than that of the elements of the etiolated leaves, and also that the total thickness of the former is greater than that of the latter. Tests for the presence of starch shew that the starch, which first makes its appearance in a young normal leaf, is a product of assimilation, and that it has not been conveyed from other parts of the plant, for 1) starch is not to be found in a very young leaf, 2) when it can be detected, it occurs in the chlorophyll-grains of the mesophyll, more especially toward the margins of the leaf, and first of all in the spongy parenchyma of the lower surface, and 3) the cells forming the sheaths of the fibrovascular bundles contain very small quantities of starch which increase as the leaves develope and expand to the light.

These facts are doubtless well-established, but they simply confirm the a priori ideas which would naturally be formed with reference to the development of leaves from the bud, and they are insufficient to justify the second clause of KRAUS' statement. It may be readily admitted that the starch which makes its appearance in leaves shortly after their emergence from the bud is a product of assimilation and that it has not been conveyed from other parts of the plant, for it is perfectly natural that as soon as the young leaves are under conditions in which assimilation is possible, they should at once begin to perform this function, and that starch should therefore make its appearance in the chlorophyll-grains; but there is no ground for the assumption that the further growth of these young leaves is simply and only dependent upon the starch which they themselves produce.

There are already facts on record which shew that leaves are capable of growth whilst they are not assimilating. KRAUS himself quotes a

1) Ueber die Ursache der Formveränderung etiolirter Pflanzen. (Jahrb. f. wiss. Bot. Bd. VII. 1869.)

paper by Sachs on the subject of etiolation[1]) in which it is shewn that the excessive elongation of the stem and the smallness of the leaves of etiolated plants are very general, but by no means universal phenomena. For example, the leaves of many Monocotyledons (Tulipa Gesneriana, Iris pumila, Allium Cepa) attain in the dark a greater length than when grown in the light, although they are not so broad; and the leaves of certain Dicotyledons (e. g. Beta) become nearly as large when growing in the dark as when growing in the light. It cannot be denied, therefore, that here are instances of the growth of leaves when it was impossible for them to assimilate.

The theory of the »self-nutrition« of leaves has already met with considerable opposition. Batalin[2]), from his experiments upon etiolated plants, concludes that the young leaves develope at the expense of the nutriment stored up in the seed, and that it is only when this is exhausted that their further growth becomes dependent upon the products of their own assimilation. Godlewski[3]) infers from his investigations of the relation existing between the formation of starch in the chlorophyll-grains and the proportion of Co_2 present in the air, that the modifications of form observable in etiolated plants are not due to the suppression of the process of assimilation. More recently this subject has been studied by Rauwenhoff[4]). He finds that leaves are not capable of nourishing themselves immediately after their escape from the bud, and he points out that etiolated leaves are not strictly comparable with those which are just emerging from the bud, as Kraus suggests, for they are much larger, and their tissues are more highly differentiated.

I may now speak of my own experiments with reference to this subject. The various experiments of Kraus and others (with the exception of those of Godlewski) upon which the different views abovementioned are founded are directed to one side of the question only. Darkness is certainly a means of arresting assimilation, but it is not the only means, and further, a plant kept in the dark is not only prevented from assimilating, but a disturbing element is introduced into many other processes such as transpiration etc., the effect of which cannot be eliminated in the estimation of the results produced[5]). It is therefore unjustifiable to assert that the many differences which exist between the leaves of a plant which has been kept in the dark and those of a similar plant

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1) Ueber den Einfluss des Tageslichts auf Neubildung und Entstehung verschiedener Pflanzenorgane. Bot. Zeit. 1863.

2) Bot. Zeitg. Oct. 1871.

3) Flora. 1873. p. 383.

4) Over de Oorzaken der abnormale Vormen van in het donker groeiende Planten. Amsterdam 1877.

5) See following paper on Influence of Light on the growth of unicellular organs.

grown under normal conditions are to be attributed entirely to the suppression of the assimilation of the former.

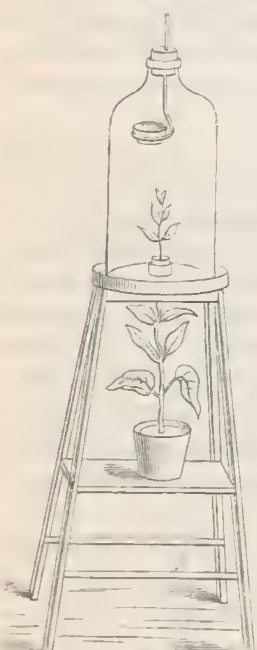
To the performance of the function of assimilation three principal conditions are essential, viz 1) the presence of light, or more accurately, of the less highly refrangible rays of the spectrum; 2) the presence of carbonic acid in the air, and 3) the presence of chlorophyll in the leaves. It is possible, therefore, to investigate the effect produced upon leaves by the cessation of their functional activity, by no less than four methods; 1) the plants may be kept in the dark, as in experiments of KRAUS, and their assimilation thus prevented. This end would be equally attained, if 2) the plants were exposed to a pure blue light, or if 3) all carbonic acid were removed from the air by which the plant is surrounded, as in GODLEWSKI's experiments; or if 4) the formation of chlorophyll were prevented.

The value of the first of these four methods has already been discussed, and, as the results were found to be unsatisfactory, it was not used. The following results were obtained by the last three methods.

I. Growth of leaves in blue light.

In availing myself of this method, I made use of the arrangement represented in Fig. 1. — It consists of a light wooden stand upon which a large earthenware saucer is placed, having in the centre a tubulated opening. The plant stands on a stage beneath the saucer, and the growing end of the stem, or of a branch, is passed through the opening in the saucer, and is fixed by means of a split cork. Upon the saucer a large double-walled bell jar is placed, the space between its walls containing a strong ammoniacal solution of copper oxide. This layer of fluid, when tested with the spectroscope, is found to allow only the blue, indigo and violet rays to pass.

Fig. 1.



The following plants were used in these experiments: Ampelopsis quinquefolia, Gronovia scandens, Phaseolus multiflorus, Cucurbita pepo, Zea Mais, Tropaeolum nanum, and in all cases the same results were obtained. It will suffice, therefore, to cite a single example.

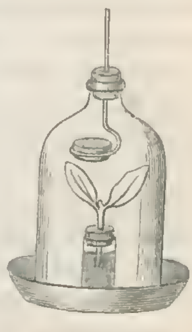
The extremity of a branch of Ampelopsis quinquefolia was introduced into the bell jar on June 23, and it was removed on June 29. When the experiment commenced, the portion of the branch within the bell-jar bore no leaves, but at the conclusion, it possessed six normal leaves and six tendrils. The length of the largest segment of the largest leaf was five centimètres. A careful examination of these leaves shewed that no starch could be detected in their cells by means of the well-known method with alcohol, potash, and solution of iodine, excepting only in the guard-cells of the stomata, whereas starch existed abundantly in the mesophyll of a leaf which had not been covered by the bell-jar.

These experiments prove that leaves can be developed and can grow under circumstances which prevent assimilation, if it be admitted that the blue, indigo, and violet rays are incapable of causing assimilation. The experiments of SACHS[1]) however, shew that although this function is almost entirely suppressed when the plant is exposed to blue light, yet it continues to some extent. This is confirmed by the observations of KRAUS on Spirogyra[2], Funaria, and Elodea. It will be at once suggested by those who hold the theory of »self-nutrition« of leaves, that in my experiments assimilation must have occurred just sufficiently to provide for the nutrition of the growing tissues, so that there was no formation of an excess of carbohydrates which might be deposited in the chlorophyll-grains in the form of starch. This explanation is evidently strained, for it is highly improbable that the amount of carbohydrates thus produced would suffice to support the growth which took place in these leaves. It is more natural to conclude that the amount of assimilation which took place was so trifling as scarcely to merit consideration, and that the material necessary for the growth of the leaves was obtained from other parts of the plant, as is the case in these leaves which attain a considerable size when growing in complete darkness.

II. Growth of plants in air containing no CO_2.

In these experiments I used seedlings as well as mature plants. In the first series the method was as follows. Seeds of Cucurbita pepo were sown in a mixture of sand and mould, and, after germination, the young plants were allowed to grow until the hypocotyledonary portion of the stem had attained a length of two or three inches, and the cotyledons had become green. The most vigorous one was then selected and cut off at the level of the earth. Its stem was then placed in a small glass containing a dilute solution of potassium nitrate, the glass was set on a saucer containing concentrated solution of caustic potash, and the whole

Fig. 2.



1) Handbuch der Experimental-Physiologie, p. 27.

2) Jahrb. f. wiss. Bot. VII. 1869—70.

covered with a tubulated bell-jar closed by a cork (Fig. 2). From the cork a watch-glass was suspended by means of a wire, and it was possible to introduce, through a perforation in the cork which could be opened or closed at pleasure, a small quantity of baryta-water into the watch-glass, to serve as a test of the absence or presence of carbonic acid in the air.

From a great number of experiments performed in this way I select the following as an example.

June 22. A young plant of Cucurbita pepo (1) was placed over potash as above described, and a similar plant (2) was placed under a bell-jar over water. Both were removed and measured on June 29. (cotyledons)

	June 22		June 29	
	length	breadth	length	breadth
No. 1	3.15 cm	1.9 cm	4.4 cm	2.5 cm
No. 2	3.0 cm	1.8 cm	4.8 cm	2.5 cm

No. 1: contained starch in guard-cells of stomata, and in sheath cells of fibro-vascular bundles only.

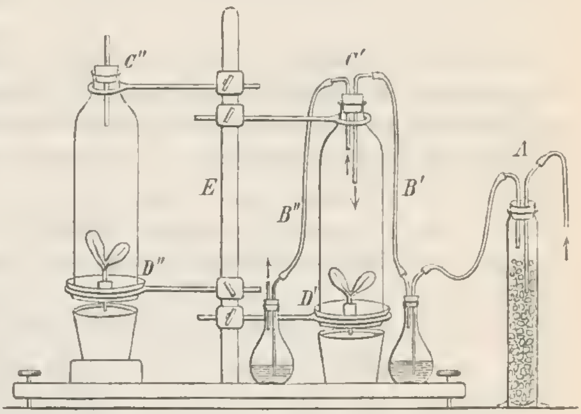
No. 2: the cells of the spongy parenchyma contained numerous starch grains.

This experiment affords distinct evidence of the growth of the cotyledons in the absence of assimilation. The only possible source of error is that the air may not have been absolutely free from carbonic acid. By means of the baryta-water test I found that during the night a sufficient quantity of CO_2 generally remained unabsorbed by the potash to cause a slight cloudiness in the baryta-water by the following morning, but the total precipitate of barium carbonate produced after an exposure of two or three days within the bell-jar was less than that produced by an exposure of a few minutes to ordinary air. It is evident that the amount of carbonic acid left unabsorbed was quite inadequate to provide the amount of carbon necessary for the amount of organic substance which would correspond to the growth which took place.

In order to avoid this source of error I made another series of experiments with the apparatus shewn in Fig. 3. It consists of a stout wooden stand, with a thick metal rod, *E*, upon which four supporting rings can slide. Upon the lower pair of these rings two small perforated saucers, similar to the one previously described, are supported (d' d''). Through the aperture of each of these saucers the cotyledons of a seedling are passed, and the stem is fastened by means of a split cork and some soft wax, the roots of the plant remaining in the pot below the saucer.

Into the one saucer, d', a strong solution of potash is poured, and into the other, water. Each of the plants thus arranged is covered with a bell-jar (c', c'',) which is firmly fixed in its position by one of the upper pair of rings which slide on the rod. Through the cork of the bell-jar c'' passes a tube which allows free communication between the external air and the interior of the bell-jar. Two tubes pass through the cork of the other bell-jar, c', each of which is connected by means of an india-rubber-tube, with a wash-bottle containing lime-water (b', b''). The wash-bottle b'' communicates with the air by the shorter of the two tubes which enter it, but the wash-bottle b'' is in connection with a large tube A filled with pumice-stone soaked with concentrated solution of potash, and the tube A is connected with an aspirator which is not shewn in the drawing. The aspirator is so arranged that, when it is in action, air is not drawn through the apparatus into the aspirator, but it is forced from the aspirator into the apparatus. By this means any possible entrance of air at the weak point of the apparatus, that is, at the place where the stem of the plant is fixed in the opening of the saucer, is effectually prevented, for, when air is being passed through it, the pressure within the apparatus is slightly greater than that of the atmosphere.

Fig. 3.



In the course of the experiments the aspirator was not kept constantly in action, but it was used regularly every morning before the plant was exposed to light, in order to remove all the carbonic acid which had been evolved during the night and which had remained unabsorbed, and it also allowed to run two or three times during the day.

The air forced into the apparatus from the aspirator had to pass over the pumice-stone soaked with solution of potash contained in the tube A, and, in order to test its freedom from carbonic acid, it had to bubble up through the lime-water contained in the wash-bottle b'. In all the experiments thus performed I never perceived the least precipitate in this wash-bottle, so that the air which reached the bell-jar c' could not have contained any carbonic acid. The air which was forced out of the bell-jar c' was conveyed to the surface of the lime-water in the wash-bottle

b''. Occasionally in the morning, when the aspirator was in action, a slight cloudiness became perceptible in the lime-water contained in b'', but it was so slight that the solution of potash under the bell-jar c' may be considered to have effectually removed the carbonic acid evolved by the plant.

The apparatus was placed close to a window, but it was never exposed to direct sunlight. A mirror was fixed behind it so as to strengthen the light, and to prevent any heliotropic curvature of the plants under observation.

In these experiments I used seedlings of Ricinus communis, Phaseolus multiflorus, Cucurbita pepo, and of Zea mais.

The following may serve as an illustration of the results obtained.

May 22. Two young plants of Phaseolus multiflorus.

No. 1: placed over potash (bell-jar c').
No. 2: placed over water (bell-jar c'').

	May 22		May 30	
	Length	Breadth	Length	Breadth
No. 1	6.8 cm	—	8.5 cm	3.0 cm
No. 2	4.8 cm	—	6.5 cm	2.5 cm

The length includes the petiole — the breadth could not be measured in the first instance, for the pinnæ were still folded together.

Each plant had also developed a young leaf in addition.

No. 1: contained starch in guard-cells of stomata only.
No. 2: contained starch abundantly in the mesophyll.

The third series of experiments was made with fully developed plants, a single growing branch being introduced into an atmosphere containing no carbonic acid, whilst the remainder of the plant was in the air. The arrangement was similar to that described in reference to the experiments with blue light (Fig. 1), but in this case the saucer was filled with strong solution of potash, and a simple bell-jar was used instead of one with double walls. The freedom of the air from carbonic acid was tested, as before, by means of baryta-water with the same results.

The plants used were Cardiospermum halicacabum, Dolichodeira tubiflora, Helianthus annuus.

With the first-named plant I obtained the following results, and those obtained with the others were quite similar.

The terminal bud of the stem was introduced into the bell-jar over potash on June 23., and was removed on June 29. Within the six days it had developed three perfectly normal leaves and three tendrils.

An examination for starch shewed that it existed only in the guard-cells of the stomata and in the sheath-cells of the fibro-vascular bundles. A leaf taken from another part of the plant contained starch abundantly in its mesophyll.

These three series of experiments together form a body of evidence which justifies the assertion that leaves can grow, whilst they are not performing the function of assimilation, so long as they are supplied with plastic material derived from other parts of the plant.

III. Growth of leaves without chlorophyll.

There are three methods by means of which the formation of chlorophyll in leaves can be prevented—viz, 1) by keeping the plant in darkness, 2) by lowering the temperature, 3) by withdrawing from it all supplies of iron.

The first of these three methods is that which is most frequently used when it is desired to obtain plants which contain no chlorophyll.

Plants grown in darkness, however, do not merely differ from normal plants in that they possess no chlorophyll, but as has already been pointed out, many other important modifications of structure and function are effected by prolonged absence of light, all of which, together with the absence of chlorophyll, are expressed by the word »etiolation«. The object of this series of experiments was to observe the growth of plants containing no chlorophyll, but differing as little as possible, in other respects, from normal plants. This method, therefore, could not be used.

The second method[1] may frequently be seen to be in active operation in nature. It is a common occurrence that the leaves of plants which require a tolerably high temperature, such as Zea mais, Cucurbita Pepo, Phaseolus multiflorus etc., are not green in the early spring, but have a pale yellow colour. These leaves appear to differ from the green leaves only in that they contain no chlorophyll, in size and in other respects they closely resemble them. This method is not a convenient one, and therefore I have not availed myself of it. I have said enough, however, to shew that it affords evidence of the growth of leaves which are incapable of assimilating.

The third method is that which I have adopted. I sowed seeds of Zea mais and of Secale cereale in damp sawdust, and after germination the young plants were removed and fixed, by means of perforated corks in glass vessels, in such a way, that their roots were immersed in the fluid which the vessels contained. The fluid had the following composition.

1) See Sachs: Ueber den Einfluss der Temperatur auf das Ergrünen der Blätter. Flora 1864.

Distilled water . . .	1000	grammes.
Potassium nitrate . .	1	»
Calcium sulphate . .	0.5	»
Magnesium sulphate .	0.5	»

and a trace of calcium phosphate.

After having grown for a few days under these conditions, the leaves of the young plants, though perfectly vigorous, began to assume a yellow colour. A small quantity of ferrous sulphate was then added to the liquid contained in some of the vessels, and the leaves of the plants growing in those vessels rapidly assumed their normal green colour. When the plants had grown for a week in the glass vessels, the leaves of those which had grown in solutions containing no iron were of a pale yellow colour, and some were even white, but in every other respect they were similar to those of the plants which had grown in the solutions to which iron had been added.

This experiment is merely a repetition of a process which frequently occurs in nature. It is not an uncommon occurrence in gardens, that trees or shrubs turn yellow, become chlorotic, as it is termed, and it is well-known, from the observations of GRIS, father and son, of Sachs and of others, that this condition is a consequence of an insufficient supply of iron. That this is so is proved by the fact that the chlorosis can be removed by watering the plant with dilute solutions of iron salts. Here, then, are many instances of the growth of leaves under circumstances which prevent assimilation.

In concluding the discussion of this part of the subject, a brief summary of the results obtained may be given. It has been shewn,

1) that leaves can grow in blue light,
2) that they grow in an atmosphere containing no CO_2,
3) that they grow although they contain no chlorophyll.

Now it is admitted on all hands that for the performance of the function of assimilation the following conditions are necessary:

1) the presence of the less refrangible rays of the spectrum,
2) the presence of CO_2 in the surrounding medium,
3) the presence of chlorophyll in the assimilating organs.

In the foregoing experiments one or other of these conditions was left unfulfilled, and therefore the leaves did not assimilate. But it is undeniable that they grew. The obvious conclusion is that the theory of the »self-nutrition« of leaves is contradicted by experimental evidence.

It now remains to discuss STEBLER's views as to the cause of the periodicity observable in the growth of leaves. He says[1]), that the linear leaves of Monocotyledons with which he experimented exhibited such a daily periodicity, that the rapidity of growth always rose with increasing, and fell with diminishing intensity of light. The maximum of growth corresponded with the greatest intensity of light, and the minimum occurred shortly before daybreak. He explains these facts by regarding the process of assimilation as their cause, or as he states it, growth rises with increasing assimilation, and falls when assimilation diminishes. With reference to the growth of the leaves of Dicotyledons he says that the daily period is modified in such a way that, after the occurrence of the maximum of growth in the forenoon, a retardation takes place, so that the curve of growth gradually sinks, until the minimum is reached shortly before daybreak on the following morning. After dawn growth rapidly increases and attains its maximum in the forenoon. If the light be very intense, the maximum occurs earlier, if less intense, it occurs later. His explanation is that in the case of the leaves of Dicotyledons, the daily period is produced by assimilation as in the case of the leaves of Monocotyledons. The retardation which occurs in the course of the day after the maximum of growth has been attained, he ascribes to the influence of light.

It is evident that KRAUS' theory of the »self-nutrition« of leaves has afforded the stand-point from which STEBLER regards his observations. It has already been shewn that this theory is in contradiction to experimental evidence, and therefore any inferences which may have been drawn from it cease to be tenable. Still the question at issue, namely, whether or not the influences which produce the daily periodicity in the growth of leaves are different from those which produce a similar periodicity in the growth of other vegetable organs, is of such importance, that a closer examination of STEBLER's inferences is desirable.

In the first place, a careful analysis of his figures shews, that the coincidence of the maximum and minimum of growth with the maximum and minimum of assimilation is by no means so frequent an occurrence as might be supposed. The following tables, which include all his experiments upon plants under normal conditions, bring this out very clearly.

In drawing up these tables, the observations made upon one plant during one day are regarded as forming one experiment. The period of the greatest intensity of light is, in some cases, between 10 a. m. and 2 p. m., in others, between 9 a. m. and 3 p. m. This difference is due to the fact that in some of STEBLER's observations the measurements were made every four hours, in others, every three hours. Si-

1) loc. cit. p. 122.

milarly the expression »shortly before dawn« is regarding as including the time between 10 p. m. and 2 a. m., in some eases, and in others the time between 9 p. m. and 3 a. m.

The following table gives some information as to the occurence of the maxima in these observations.

	Actual numbers			Percentages		
	Before 10 a. m.	10—2	After 2 p. m.	Before 10 a. m.	10—2	After 2 p. m.
Secale cereale STEBLER's tables 5, 10, 11	21	37	17	28	49	23
Allium cepa Table 7	—	3	7	—	30	70
	Before 9 a. m.	9—3	After 3 p. m.	Before 9 a. m.	9—3	After 3 p. m.
Triticum vulg. Table 6	1	7	—	12.5	87.5	—
Allium cepa Table 8 *a*, *b*	—	7	1	—	87.5	12.5
	Before 10 a. m.	10—2	After 2 p. m.	Before 10 a. m.	10—2	After 2 p. m.
Cucurbita pepo Table 9	16	2	—	89	11	—

From these tables it appears that the number of eases in whieh the maximum fell within the preseribed limits stood in the following proportion to the number of cases in whieh it fell outside those limits. Since the number of experiments is so nearly 100, no percentages are ealculated.

Totals.

	Before 9 - 10	9—3 10—2	After 2 - 3
Monocotyledons	22	54	25
Dicotyledons	16	2	—

The following tables give the results for the minima. From the same tables of STEBLER.

	Actual numbers			Percentages		
	Before 10	10—2	After 2 a. m.	Before 10 p. m.	10—2	After 2 a. m.
Secale	6	54	15	8	72	20
Allium	2	7	1	20	70	10
	Before 9 p. m.	9—3	After 3 a. m.	Before 9 p. m.	9—3	After 3 a. m.
Triticum	—	8	—	—	100	—
Allium	—	3	5	—	37.5	62.5
	Before 10 p. m.	10—2	After 2 a. m.	Before 10 p. m.	10—2	After 2 a. m.
Cucurbita	8	10	—	44	56	—

Totals.

	Before 9 p.m. - 10 -	9—3 10—2	After 2 a. m. - 3 -
Monocotyledons	8	72	21
Dicotyledons	8	10	—

These figures shew that, with regard to Monocotyledons, the occurrence of the maximum outside the assigned limits took place in about 47 per cent of the observations, and that of the minimum in about 29 per cent. With regard to Dicotyledons, the occurrence of the maximum outside the assigned limits took place in about 89 per cent of the observations, and that of the minimum in about 44 per cent.

Although in this analysis the utmost latitude has been allowed, yet the figures do not justify the significance which has been attached to them. The only indication that they give is, that the maximum of growth is attained, on the whole, somewhat earlier by Dicotyledonous than by Monocotyledonous plants. In order to account for this difference, Stebler suggests that it is due to the retarding action of light. He says that the daily periodicity observed in the growth of the leaves of the former group of plants is a function of assimilation modified by the retarding action of light, whereas the daily periodicity observed in the leaves of the latter group of plants is exclusively a function of assimilation.

It is difficult to accept this explanation, for it is not evident why the leaves of Dicotyledonous plants should be held to be more sensitive to the retarding action of light than those of Monocotyledons. The observations of Sachs [1]) upon the development of etiolated leaves led him to conclude that those leaves which, under normal conditions, attain a considerable length in more or less complete darkness, in consequence of being invested by older leaves, become excessively elongated when etiolated. This is the case with the leaves of most Monocotyledons, and it cannot be denied, therefore, that the retarding action of light has an influence upon their growth.

Having established this fact, it is natural to infer, that the periodicity observed in the growth of the leaves of these plants is, to a great extent, produced by the retarding action of light. A comparison of the results obtained by Sachs, Prantl and Stebler will afford a means of testing the value of this suggestion.

It has already been mentioned that the periodicity of growth of internodes is attributed by Sachs to the retarding action of light, and that the occurrence of the maximum during the day and of the minimum in the evening or during the night, is due to the fact that this action of light does not make itself instantaneously manifest, and that it persists after the exposure to light has ceased. This view is supported by the observations of Prantl upon the growth of the leaves of Dicotyledons. If the curves II, III, IV, V, VI given by Stebler be compared with those given by Sachs and Prantl, they will be found to differ principally therein, that the highest points of Stebler's curves occur somewhat later in the day, and the lowest points farther on in the night, than the corresponding points in those of Sachs and Prantl. This difference, however, offers no obstacle to the suggestion that they are susceptible of a common explanation. In fact Stebler's curves can be intelligibly explained upon the some principle as those of Sachs and Prantl. The above mentioned peculiarity of Stebler's curves is probably to be traced to a more gradual action of light upon the growing cells of the leaves of Monocotyledonous plants. This greater slowness of action is to be attributed, to some extent at any rate, to the small amount of light which can penetrate to the growing cells of these leaves. Stebler endeavours to shew that some light reaches these cells under ordinary circumstances, and that this light contains some of the highly refrangible rays, but he places more reliance upon his experiments with plants in which the growing leaves had been fully exposed to the light. The curve V, for example, represents the

1) Bot. Zeit. 1863 Beilage p. 11.

course of growth of a leaf of Allium Cepa which had been thus treated. Under these circumstances it must be concluded that the growing cells of the leaves of Allium Cepa are more slowly affected by the retarding action of light than are those of internodes and of the leaves of Dicotyledons, and this may be true also with regard to the leaves of other Monocotyledons.

It is possible, therefore, to explain all these phenomena of the action of light upon growth upon the same theory, and this is more satisfactory and more scientific than to attempt to find a distinct cause for each one.

In order to be able to support these theoretical considerations by experimental evidence, I made the following experiments with Secale cereale, a plant which STEBLER used in many of his observations. I sowed the seeds in small glass bottles filled with moist sand, and, after germination, I placed one of these bottles in a glass jar which was closed by a cork through which a thermometer passed into the interior. Into this jar a sufficient quantity of concentrated solution of potash was poured to form a layer about half an inch thick. The measurements of the growth of leaves of the seedlings were made by means of a micro-telescope[1]). The plants were kept in darkness for at least twelve hours before the commencement of the observations in order that no persisting effects of the action of light might interfere with the results obtained. The leaves were green. I found that, when the plants were kept in darkness, the growth per hour was very nearly uniform, the variations being such that they might be either attributed to changes of temperature, or regarded as those irregularities which are always to be detected in the process of growth (»Stossweise Aenderungen« SACHS). In illustration of a number of such experiments (25) the following may be cited.

Time.	Hourly growth.	Temperature.
8 a. m.	—	—
9 „	0.50	23.3° C.
10 „	0.40	23.3
11 „	0.40	23.2
12 —	0.40	23.0
1 p. m.	0.30	23.1
2 „	0.40	23.2
3 „	0.30	23.7
4 „	0.50	23.4
5 „	0.30	22.8
6 „	0.40	22.7

In these experiments the conditions were such that no assimilation could possibly take place, and yet growth continued. That the uniformity of growth here observed is due to the fact that the plants were not exposed to the action of light, is shewn by variations of this experiment in

1) For description of this instrument see the following paper.

which the glass jar containing the plant in an atmosphere free from CO_2, was exposed for a time to light. The following is one of these experiments.

	Time.	Hourly growth.	Temperature.
	7—8 a. m.	1.10	22.4° C.
	9 „	1.20	22.4
	10 „	1.50	23.5
exposed to sunlight	11 „	1.50	24.0
exposed to sunlight	12 —	1.40	24.8
	1 p. m.	1.30	26.4
	2 „	1.30	25.8
	3 „	1.70	25.0
	4 „	1.70	25.3
	5 „	1.80	24.6
	6 „	1.60	24.2
	7 „	1.50	24.0

These experiments prove that the retarding effect of the action of light upon their growth can be produced when the leaves are not assimilating. They afford also some data for the discussion of another of STEBLER's conclusions, namely, that a daily periodicity is perceptible in the growth of the leaves of etiolated Monocotyledonous plants, which he believes to be an inherited property. It this be so, it is evidently unnecessary to ascribe the daily periodicity of the growth of green leaves to variations in the activity of the process of assimilation, for they, doubtless, are in possession of this inherited peculiarity as well as etiolated leaves. Still more unnecessary is it to assume, as STEBLER does, that the property possessed by green plants of so reacting to light that there is a greater growth during the day, is inherited.

I do not propose to discuss any further at present the question whether or not a daily periodicity of the growth of vegetable orgaus exists which is quite independent of variations in external conditions, for it is beside the principal object of this paper. I would simply call attention to the fact that, in his observations upon the growth of internodes, SACHS failed to discover any such independent periodicity, that the experiments of PRANTL upon the growth of the leaves of Dicotyledons and the observations of STREHL upon the growth of roots, render its existence in these organs inprobable, and that I have been unable to detect it in the above mentioned experiments.

The following are the principal results arrived at:

1) That it is possible for leaves to grow when they are not assimilating.

2) That the effect of light in retarding growth is exhibited by leaves which are not assimilating.

3) That, therefore, the daily periodicity observable in the growth of leaves (of Monocotyledons) is not a function of assimilation, but is an expression of the effeet directly produced upon the growing cells by the alternation of day and night.

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