

F. W. W e n t:

The Physiology of Photosynthesis in Higher Plants

(Earhart Plant Research Labor., California Institute of Technology)

In honour of the 85th anniversary of Profesor Bohumil N ě m e c

In recent years most work on photosynthesis has been carried out on algae. This has some excellent grounds: it is easy to get uniform experimental material; the Warburg technique is easy to reproduce, and in general algae offer the advantages microbiological material presents for biochemical and biophysical work. Since we know that basically photosynthesis in algae and in higher plants is the same, many of the problems of photoreduction of CO_2 can be and have been investigated using *Chlorella* or other algae as experimental material. The results have then been applied with good success to explain photosynthetic processes in higher plants.

It should be recognized, however, that photosynthesis in higher plants has its own problems, and offers certain advantages in research. Some of the problems for which a tomato or a wheat or a beet plant can be used to good advantage are:

A) There is a differentiation of tissues in the higher plant which does not occur in *Chlorella*. The latter has to photosynthesize, store photosynthetic products, grow, and synthesize all other cell components within the same cell. In the higher plant photosynthetically active leaf cells do not grow any more; their photosynthetic products can be removed to other parts of the plant, and synthesis of the many products occurs in different cells: lycopin is formed in the ripening fruits only, quercetin occurs especially in the glandular hairs, auxin is primarily synthesized in the stem tip and young leaves, etc. This enables one to study photosynthesis in its dependence upon growth, accumulation of photosynthetic products, or synthesis of other substances.

B) The multicellular structure of the higher plants provides certain geometrical patterns in relation to the incident light, which cannot be obtained with cell suspensions of unicellular algae.

C) Almost all of our agriculture and food production depends upon higher plants, and for this reason alone it is imperative that we fully understand photosynthesis in these plants, particularly those processes which cannot be studied in algae.

The utilization of light by higher plants is not solely dependent upon the process of photoreduction of CO_2 , but reactions and processes both preceding and succeeding photosynthesis *sensu stricto* influence it. In the following paper the significance of these reactions and processes for light utilization will be discussed, partly based on theoretical considerations, partly on experiments, which are discussed elsewhere in more detail (W e n t, 1957). The importance of such a discussion lies in the fact, that for a long time to come life on earth will depend in photosynthetic food production, and on other plant and animal products such as wood, cellulose, fats and proteins for plastics production. As the world population increases, larger amounts of food and other plant products are needed, which can be produced by 1) in-

creasing the land area under cultivation, 2) increasing the water supply for agriculture, 3) improving dry matter production under arid conditions, 4) improving agricultural practices, or 5) increasing the efficiency of photosynthesis in general. Among these possibilities, 1) and 2) are technological problems, 4) is a problem for the agricultural engineer, but 3) and 5) cannot be attacked until much more basic knowledge has been acquired.

In the study of photosynthesis there are two entirely different approaches: 1) measurement of photosynthesis during short periods of illumination, indicating the actual rate of photoreduction of CO_2 using gas-exchange methods of determination and 2) determination of dry matter production (or yield)

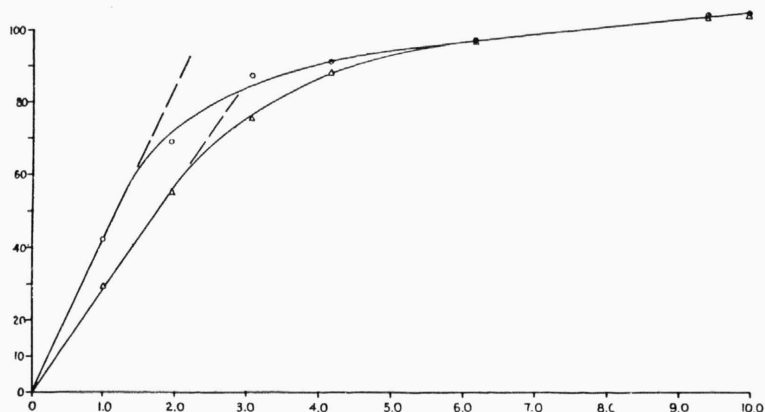


Fig. 1. Rate of photosynthesis of *Hormidium* cells (ordinate in mm^3 per hour) as a function of light intensity (abscissa, in arbitrary units). After van den Honert (1930).

over growing periods of a day or more. As has been argued elsewhere (Went 1957) the second method gives a composite picture of the effects of light on photosynthesis, as limited by the capacity of the plant to store or to utilize its photosynthates. This is the most important aspect of photosynthesis to know for ecologists, agriculturalists and economists; method 1) gives only the potentially maximal rate of photosynthesis, method 2) gives the actual overall rate.

As far as data are available the two methods, 1) and 2), as applied to algae, A, and higher plants, B, are compared in the following set of arbitrarily chosen examples.

1) A: Here some data of van den Honert (1928) are presented, who used a unicellular layer of algae (*Hormidium*) which was exposed to an air mixture containing 400 p. p. m. CO_2 , a concentration which under his experimental conditions did not limit photosynthesis. Up to half maximal rate of CO_2 reduction, this rate is proportional to the light intensity; from there on the rate decreases gradually to reach the maximal rate at 3–6 times the light intensity at which half-saturation occurs (figure 1). This shows that the photochemical reaction is in the same reaction chain as the Blackman reaction limiting at high intensity. The same effects were found by many other investigators with other algae.

2) A: For this case data of van Oorschot (1955) are taken. He cultured *Chlorella* in bottles through which air enriched with 5% CO_2 was bubbled. He harvested the cells after one or more days, and determined the amount of dry weight of cells produced at 30° C per 10 hours per 30 cc. of culture medium. In figure 2 it can be seen that, depending upon the concentration of the nutrient solution, different processes limited dry matter pro-

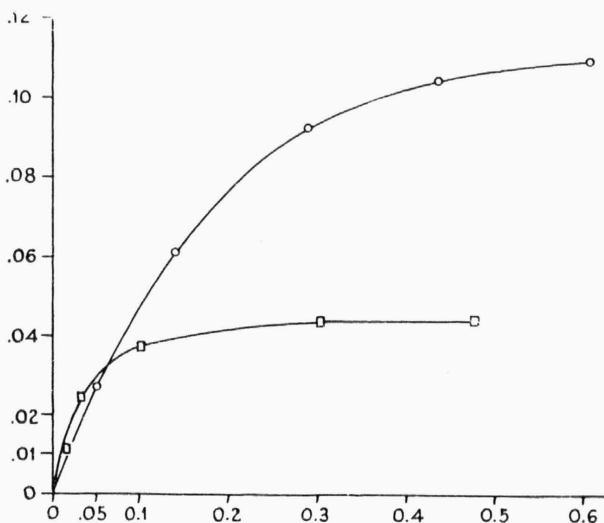


Fig. 2. Dry matter production (ordinate, in grams per 10 hours) of *Chlorella* (inoculum containing 2 mg. of chlorophyll, in 100 cc. nutrient solution) as a function of light intensity (abscissa, in cal./cm.²/min.).—Circles: cells in complete nutrient. Squares: cells in nitrogen-deficient nutrient medium. Data from van Oorschot (1955).

duction. At and below intensities of 0.1 cal./cm.²/min. (about 8% of the maximal sunlight intensity at sea level) the photochemical process was limiting. Above this intensity growth became the limiting factor in the nutrient-deficient solution with a rather sudden transition. In the complete nutrient solution the culture was hardly saturated at 0.6 cal./cm.²/min., and not growth, but probably the Blackman reaction was limiting (compare the upper curve with the upper one of figure 1).

In figure 3 the efficiency of light conversion for the algae shown in figure 2 is plotted. It is obvious that only at very low light intensities a good efficiency of light utilization occurs, but at intensities like full sunlight only 4–6% of the light energy is transformed into chemical energy, the rest is absorbed and transformed into heat.

1) B: Many measurements of photosynthesis in leaves and whole plants have been carried out with the gas-exchange method. In most of these determinations the rate of air movement past the leaves was probably too small, resulting in limitation of photosynthesis by the CO_2 supply (see Went 1957). In figure 4 some data of Willstätter and Stoll (1918) with leaves in a stream of 5% CO_2 are plotted, showing that for individual leaves about the same relationship between light intensity and rate of photosynthesis holds as for the algal cultures of van den Honert (figure 1), except that the

proportionality between light intensity and rate of CO_2 reduction goes somewhat further, if light exposure times do not exceed 1 hour. This figure shows that up to about 1000 ft.-c. (about $0.1 \text{ cal./cm.}^2/\text{min.}$) elm leaves are not saturated with light, but above this intensity very little more light can be used effectively for CO_2 reduction.

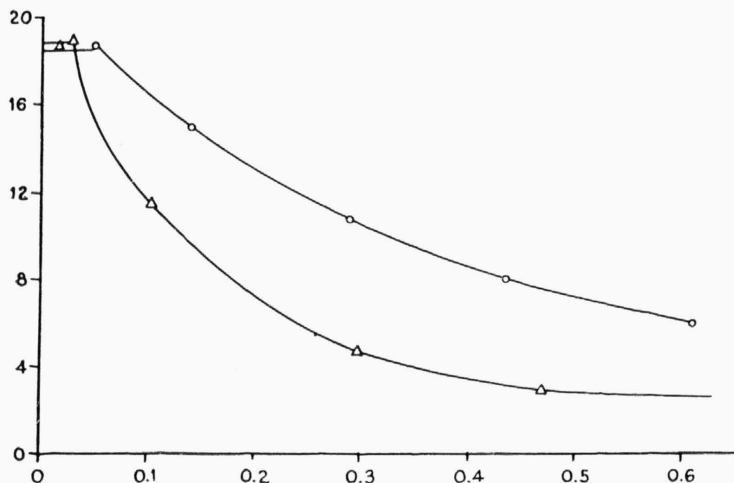


Fig. 3. Efficiency of photosynthesis (percentage of light energy used for photochemical reduction of CO_2 plotted on ordinate) plotted as a function of the incident light energy (abscissa, in $\text{cal./cm.}^2/\text{min.}$) for the same two *Chlorella* cultures of figure 2 (circles for complete nutrient, triangles for nitrogen deficient nutrient). Data from van Oorschot (1955).

2) B: In experiments carried out in the Earhart Laboratory by Dr. S. Dunn, young tomato plants were grown for 6 day periods under artificial lights over a range of 6 different light intensities. The amount of dry matter formed during this period was determined; the results of such an experiment, representative of all others, are shown in figure 5. It shows that up to 1300 ft.-c. dry matter production is exactly proportional to the light intensity; above 1300 ft.-c. a further increase in intensity has no effect at all any more, or in other words, the plants were saturated with light. Many further experiments (Went 1957) have shown that the limiting factor at high light intensity is growth. At any color or type of light, or at any temperature or other growing condition, a certain maximal development of the plant occurs which cannot be surpassed by a higher rate of photosynthesis. This means that the amount of cell material and storage food is strictly limiting; since in this way growth and photosynthesis are entirely independent processes, there is no interaction between them as in chain reactions or mass reactions and there is no transition where these two processes are each partly in control; it is either one or the other.

The same thing appears from the lower curve of figure 2, where up to $0.04 \text{ cal./cm.}^2/\text{min.}$ radiation there is proportionality between growth of the algae and light intensity, whereas a further ten-fold increase in light hardly increases production any further. Therefore it appears that, up to the saturating intensity, light is utilized at full efficiency in the dry matter production of algae and higher plants, and that in both cases the extent to which the photo-

synthates are being used in growth determines the saturating light intensity.

It is possible to influence both CO_2 reduction and growth by changing the external conditions; or in other words, the slope of the first leg of the curve of figure 5 or the level of the second leg can be controlled independently (for details see Went 1957). The angle α represents the efficiency of light utilization; in figure 5 this is 5 and 7% for the two curves. By using other

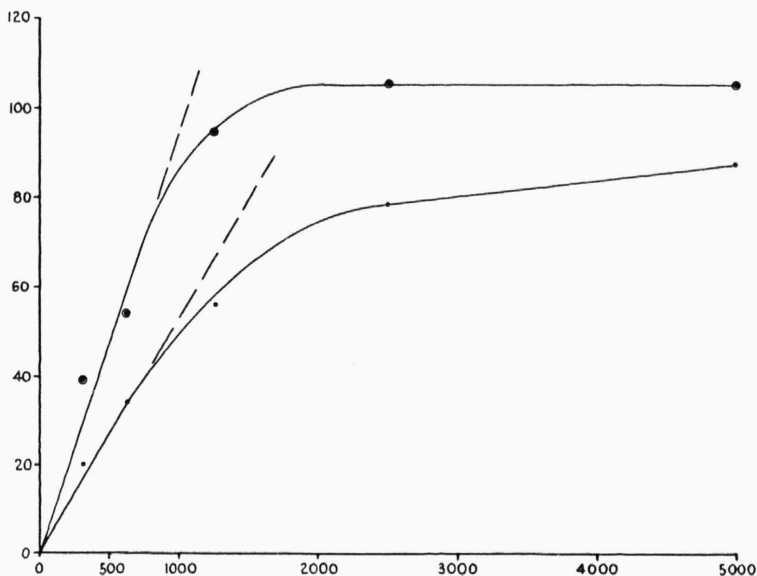


Fig. 4. Rate of CO_2 reduction (ordinate: mg. CO_2 reduced per hour) of 300 cm^2 of *Ulmus* leaves in 4.5% CO_2 , in different light intensities (abscissa: approximate foot-candles). Upper curve: green leaves; lower curve, yellow leaves. From Willstätter and Stoll (1918).

fluorescent lamps (a mixture of equal numbers of blue and of high intensity red tubes, with some incandescent light added) as much as 10% of the incident light can be transformed into chemical energy, harvestable as plant material. By other means, such as by growing the plants in a light-dark cycle which differs too much from a 24-hour period, the efficiency of light utilization can be decreased.

The maximal growth rate, or the level of the second leg of the curve of figure 5 can be raised or lowered by different experimental means. By growing the plants in a mixture of red and blue light with the exclusion of green the maximal rate of dry matter production is raised 30% in comparison with white light. By interrupting the daily light period with one or two dark periods of about 2 hours, provided the main dark period has a length of at least 10 to 12 hours, and the total cycle is 24 hours, the saturating light intensity can be raised as much as 50 per cent, without changing the efficiency of light utilization. By decreasing the growth rate through very high or through low night temperatures, or through root pruning, the saturating light intensity is reduced too.

From the preceding analysis we have seen that under different conditions photosynthesis can be limited by different internal factors:

1) The photosynthetic CO_2 reduction as measured over short periods is usually not completely saturated with light up to half or full sunlight intensity; yet, above 1000—2000 ft.-c. the strict proportionality between photosynthesis and light intensity does not hold any more and photosynthetic efficiency drops (figure 3). It is the Blackman reaction, or the biochemical transformation of the light energy, which is limiting here. In this respect there is no difference in principle between algae and higher plants.

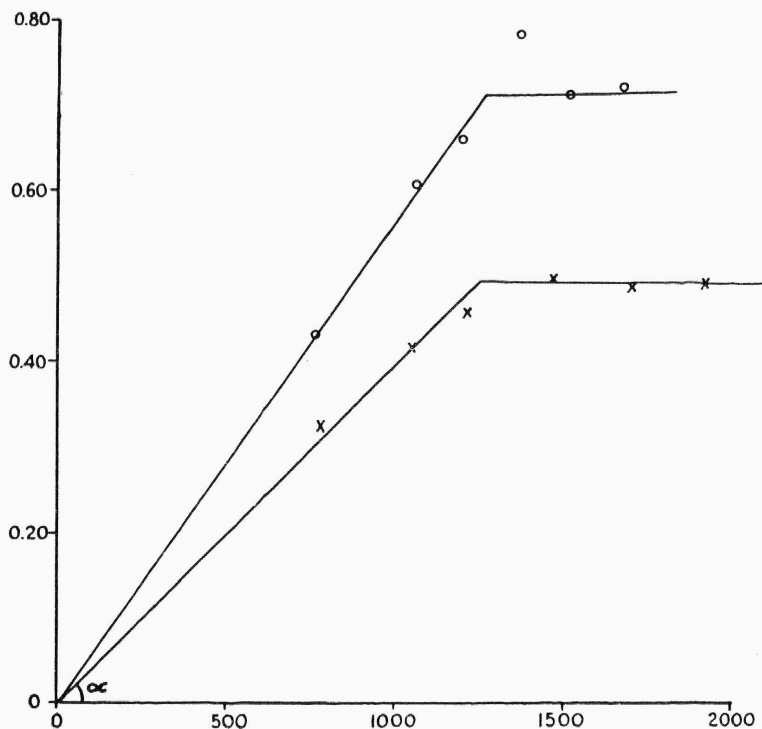


Fig. 5. Dry matter production (ordinate: mg. dry wt. formed per cm.² per 6 days) in tomato plants as a function of light intensity (abscissa, in ft.-c., or 10^{-4} cal./cm.²/min.). Lower curve: warm-white fluorescent lamps only; upper curve, warm-white fluorescent lamps plus 10% light from incandescent bulbs. Data from Dunn, from Went (1957).

2) In long-term experiments (of several days at least) the total yield of plant substance is limited by the rate at which the photosynthates are used or stored. This makes a great potential difference between algae and higher plants in their maximal light utilization. Unicellular algae cannot possibly transform more light energy than is contained in their cell material; since their rate of cell division is limited, their rate of light utilization is equally limited. In higher plants the photosynthates are moved out of the leaf cells (which themselves do not grow any more), and thus it is not the rate of growth of the individual photosynthetic cell, but mainly the growth of the rest of the plant which determines the maximal rate of photosynthesis. In algae it is strictly the amount of growth of the individual cell which limits the maximal yield; in *Chlorella* the potential maximal rate of photosynthesis is twice the maximal rate of growth (Myers 1957). Therefore, theoretically, a higher light utilization is possible in multicellular organisms.

3) It was shown that many different factors increased the maximal light utilization by tomato plants. Further experimental work undoubtedly will extend the range of light intensities which can effectively be used by leaves, such as dark interruptions.

4) It was shown (Went 1957) that a sufficient rate of air movement past leaves the normal CO_2 concentration of the air of 320 parts per million is not limiting photosynthesis. This was found by van den Honert (1930) with his *Hormidium*, and it is true for tomatoes too.

Reports to the contrary are usually based on experiments with more or less stagnant air, when the diffusion gradient becomes shallow and the CO_2 supply definitely becomes limiting.

5) The work of Willstätter and Stoll (1918) has shown that within a wide range the chlorophyll concentration in leaves does not limit photosynthesis.

Taking all these facts together we come to the conclusion that usually in the first place dry matter production in nature is limited by non-optimal growing conditions, which can obviously be improved, and which can, under optimal light intensities (1000 ft.-c. for most mesophytic leaves), cause 10% of the incident light to be transformed into the chemical energy of the plant body.

In the second place dry matter production seems to be limited by the 1000 ft.-c. saturating light intensity, since the maximal light intensity at noon on a clear day is about 10,000 ft.-c., and the average light intensity over the whole daylight period on a clear day is as high as 5000 ft.-c. On cloudy days this can be very much less. Thus, in parts of England, the average daylight intensity over a whole growing season is less than 2000 ft.-c. Yet, even at that figure, it would seem that a considerable portion of all sunlight would be wasted by plants just because it is well above the saturating light intensity as it reaches a leaf surface.

There is another factor which has to be taken into account while considering light utilization in nature. Work of Emerson and Arnold (1932) has shown that algae can fully use much higher than saturating light intensities provided this light is interrupted by dark periods. Then the dark reactions (Blackman reaction) are able to catch up with the photochemical reaction. Since the dark reaction is completed in a fraction of a second, light flashes of very high intensity can be fully used when they come with a frequency of not more than 10—100 per second, and when they are followed by sufficiently long dark periods.

As mentioned earlier, also long interruptions of an hour or more of the daily light period tend to increase the saturating light intensity. Therefore, light of variable high intensity can be used by plants with greater efficiency than light of constant intensity. This shows that there are other dark reactions than the Blackman reaction involved in photosynthesis.

It has been suggested by several investigators (e. g. Kurssanov 1933) that the rate of photosynthesis does fall off once the leaf cells are filled with photosynthates. Therefore, if light exposure at a supra-saturating intensity is continued only long enough to saturate the mesophyll cells with photosynthates, and then is interrupted by a dark period long enough to decrease their photosynthates significantly, a following light exposure might utilize more light. Such dark interruptions would therefore tend to increase effective light utilization and to increase the saturating light intensity. Examples of such behavior were actually found and described (Went 1957). When tomato plants were given their daily light exposure of 8 or 9 hours all in one stretch, the saturating light intensity was 1000 ft.-c. But when this light exposure was interrupted once or twice with 4 or 2 hours of darkness, light up to 1500 ft.-c. could be used effectively, and total dry weight production was increased.

The results of Allard and Garner (1941) have shown, however, that giving intermittent light at periods much shorter than 24 hours decreases the effectiveness of the light. This seems to contradict the results mentioned in the previous paragraph. In experiments carried out in the Earhart Lab-

oratory both results could be verified. With a 4 hr. light—4 hr. dark—4 hr. light—12 hr. dark cycle total dry matter production was increased over an 8 hr. light—16 hr. dark treatment with a 1400 ft.-c. light intensity (see table 1), but when the same 8 hours of light per day was provided in 60 min., 10 min. or 1.3 min. periods, interrupted by 30, 5 and 0.7 min. dark periods, growth and apparent photosynthesis in tomatoes was significantly decreased. It then increases again with still shorter light-dark cycles.

From the preceding analysis we can conclude, that light at an average intensity above 1000 ft.-c. at the leaf surface is largely wasted, since there is at most only a small increase in yield with an increase in light intensity up to 10,000 ft.-c. This would mean that under field conditions, where the noonday light intensity on a sunny day is about 10,000 ft.-c., most sunlight would be wasted. This can be made even clearer by considering a model, in which a number of leaves of 1 dm.² surface are stacked on top of each other (see figure 6). In this model the second leaf receives only the light transmitted by the first, which for the sake of argument will be assumed to be 20%. This would mean that when the top leaf receives 10,000 ft.-c., (which is equivalent to 100 cal./dm.²/min.), the second gets 2,000 ft.-c., the third 400 ft.-c. $10 + 10 + 4 = 24$ cal. could be effectively used by these leaves; the rest (76 cal.) would be lost.

This situation clearly exists in algal suspensions. Van Oorschot (1955) found that, although at low intensities his algal cultures could transform 19% of the light energy into cell material (see figure 3); under natural light conditions this value was at most 8% because of the ineffectiveness of the higher intensities.

The purpose of this paper is to analyze this situation with respect to the higher plants. In the following considerations the saturating light intensity for a leaf will be considered 1000 ft.-c. (or 10 cal./dm.²/min.), which is close to the actual value (Went 1957), and the incident light intensity on a horizontal surface will be assumed to be 100 cal./dm.²/min., corresponding with full sunlight on a clear summer day at noon. In the previous paragraphs it was shown that when leaves are stacked, the upper leaf wastes most of the light, whereas the fourth leaf receives less light than required to compensate for its respiration. Thus less than $\frac{1}{4}$ of the total amount of utilizable light energy is actually used by such a stack of leaves, and with a maximal 10% efficiency of the photosynthetic conversion of light into chemical energy, only a maximum of 2.5 per cent of the sun's energy could be captured by higher plants as chemical energy. Such a consideration also suggests that further work on the photosynthetic efficiency of higher plants would be futile; it is very likely that the experimental emphasis on algal cultures is prompted by the subconscious feeling of investigators that the light utilization of higher plants could not be increased anyway.

Against such a pessimistic viewpoint we should weigh evolutionary considerations. When one considers the remarkable achievements of algae to potentially transform 20 per cent, and in higher plants, 10% of the incident light energy into chemical energy (at least below 1000 ft.-c. intensity), it would seem a relatively small evolutionary step to increase the saturating intensity of leaves and algal cells to 10,000 ft.-c. If in this way 4 times as much light energy could be used by plants, such an evolutionary step would give any plant an enormous advantage over all others, and therefore one might expect

it to have occurred during the several hundred million years of evolution of the land plants. Since apparently this step has not occurred, in nature plants must be able to use light more efficiently than would follow from the previous theoretical considerations.

A few simple geometrical considerations will make it evident that the previous analysis is incomplete. The amount of light which falls at an angle on a leaf surface is proportional to the sine of the angle of incidence. Thus, a leaf at a 30° angle with the sun's rays will receive only one half the amount of radiation compared with a leaf normal to the incident rays. At 12° this value is 20% and at 6° only 10% of the light reaches it.

If optically the leaf were homogeneous, the light intensity at any point just below the surface would be decreased proportionally to the sine of the angle of incidence of the light; the absorption within the leaf would be increased in the same proportion, divided by the refractive index of the leaf. Since the leaf is not optically homogeneous, the light relations inside the palisade cells will be more complicated, with occasional chloroplasts being subjected to the full sunlight intensity, when they are placed perpendicular to the incident rays; but the average light intensity in each palisade cell will be again proportional to the sine of the angle of light incidence.

Let us now consider a few different hypothetical geometrical arrangements of leaves. In all cases we make the same assumption as used earlier: leaves of 1 dm.² area, transmitting 20% of the light falling perpendicularly on them, being saturated at 1000 ft.-c., the incident light intensity being 10,000 ft.-c., or 100 cal./dm.²/min. We have already seen that this results in 24 cal./dm.²/min. being available for photosynthesis

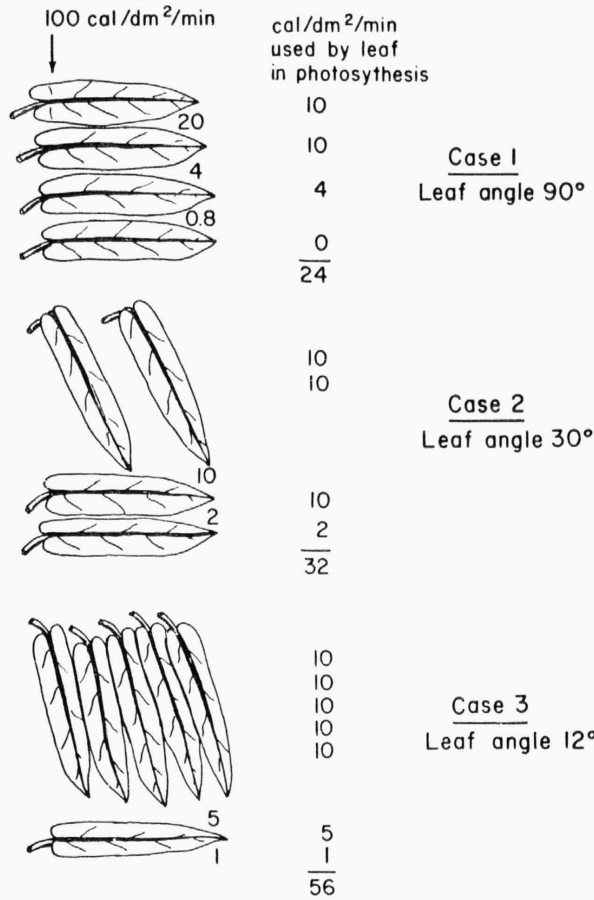


Fig 6. Light utilization by 1 dm.² leaves placed when at different angles with the incident light, which is 100 cal./dm.²/min. Leaves are saturated at 10 cal./dm.²/min. Figures between leaves indicate energy transmitted.

when the leaves are stacked one on top of the other, with the light falling perpendicularly on the leaf surface.

As the second case we will consider the first 2 leaves placed at a 30° angle with the vertically incident sunlight, the next two leaves being stacked as in the first case, perpendicular to the light, and below the other two leaves (see figure 6). Both the slanting leaves would receive a light intensity well

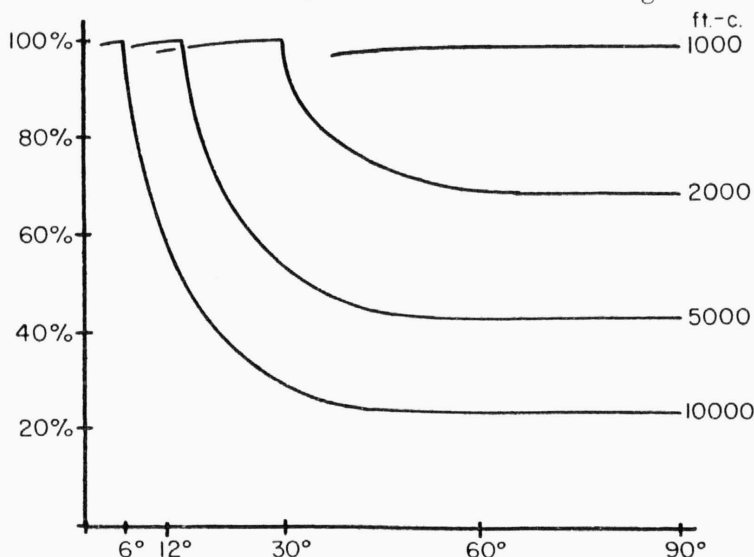


Fig. 7. Percentage utilization of the incident light (ordinate) when leaves are placed at different angles with the incoming light (abscissa), which is of 1000, 2000, 5000 or 10,000 ft.-c. intensity.

above the saturating intensity, and one leaf below it would still get enough light for near-saturation. In this case out of the 100 cal./dm.²/min. falling on this system, 27.5 cal. would be available for photosynthesis (below the saturation point) against 24% for all leaves stacked normal to the incident light.

In the third and fourth cases (figure 6) the leaves are placed at a 12° and a 6° angle with respect to the light; in the third case 5 leaves can then occupy the space of 1, in the fourth case even 11. Light utilization becomes then 50 or 100 cal./dm.²/min.

In figure 7 the light utilization has been plotted as a function of the angle of incidence of the light, for a 10,000, a 5000 and a 2000 ft.-c. light intensity. Obviously, the maximum amount of usable light increases with decreasing angle of incidence. By plotting the same data, using the percentage usable light as the ordinate, another picture emerges (figure 8). At the lowest light intensity (1000 ft.-c.) a leaf perpendicular to the direction of the light is saturated, and this fully utilizes the light falling on it. To get full light utilization the leaves have to have smaller and smaller angles with the incident light, the higher the light intensity.

Two corrections should be made to make this picture applicable to plants growing in nature. The first concerns the compensation point. This is the point where respiration, both in light and during night, uses as much photosynthates

as were formed during day, and in tomatoes is about 100 ft.-c. Leaves receiving less light are usually shed. In this way they do not constitute a nutrient drain on the rest of the plant. Thus when leaves become too closely packed at too small an angle, efficiency of light utilization drops sharply.

The second correction has to do with the reflectance of light from the leaf surface. The smaller the angle of light incidence, the larger the proportion of reflected light. This will not affect the total amount of light which the plant as a whole receives, for the total amount of reflected light for the plant remains the same; there is only more light reflected against the other leaves, causing a more even light distribution within the whole mass of leaves. This will tend to decrease the light gradient inside the leaf which will give greater efficiency of light utilization.

With the previous considerations in mind we will now look at plants under field conditions to see to what extent they place their leaves perpendicular to the strongest light.

There are only few plants in which the leaves are able to move and follow the sun. *Malva neglecta* is one of these (Yin 1938); at any time its leaves are exactly perpendicular to the incident sun rays. Because the leaf surface is corrugated, the leaf surface on the average makes an angle of 60° and the total surface exposed to light is 1.4 times a flat surface of equal dimensions.

In the *Leguminosae*, leaves and leaflets of most members of the family have joints at their base and often at the base of the petiole too, and these joints remain mobile throughout most of the life of these leaves. Much work has been done on the movements of these leguminous leaves in relation to light (for review, see Nuernbergk 1925), and three main facts have emerged:

- 1) in darkness the leaf blades usually place themselves in a vertical plane,
- 2) in low light intensities the leaf blades become oriented perpendicular to the incident light,
- 3) in high light intensities (leaves exposed to full sunlight) the leaflets place themselves parallel with the sun rays. This phenomenon has been called day-sleep (see Nuernbergk 1925).

From figure 6 it can be seen that leaves, saturated at 1000 ft.-c. surface intensity, will use most of the sun light energy if they make an angle of less than 10° with the incident light; therefore, since leaves are not perfectly flat and are moved back and forth even by slight air currents the average light intensity inside the cells of leaves placed parallel with the light rays will probably be close to saturation. In this way the day-sleep movements of leguminous leaves cause them to intercept the minimum amount of light for maximal photosynthesis, leaving much light to reach lower leaves. When these receive a low enough light intensity, they will remain placed perpendicularly to the incident light and thus something like case 4 of figure 6 obtains (only with a higher intensity on the horizontally placed leaf).

Leaves without joints usually show leaf movements as long as their petioles are elongating, but once their leaf stalks are full-grown, they have a fixed position which, at most, changes slowly through epinasty. What is this position?

In shade plants we usually find all leaves in one layer, all placed perpendicularly to the incident light, and arranged in a more or less perfect mosaic pattern. In textbooks the examples of leaf mosaics shown are usually shade plants such as ivy, or young *Acer* growing in deep shade. Exceptions are plants

with leaves floating on water, such as water lilies or especially *Trapa natans*. These mosaics are usually caused by differential growth of petioles. Since it is known (F u n k e 1938) that petioles of water lilies grow as long as part of the leaf blade is submerged, any young leaf overlying an older one will make the petiole of the latter elongate until the older leaf has moved out from under the younger.

In sun plants or on branches of plants exposed to full daylight, I never have seen leaf mosaics in which leaves have spread out perpendicularly to the highest light intensity. On the contrary, leaves usually make a sharp angle with the incident light. This is most clearly seen in pine needles which generally are pointing upward. Even if they were placed normal to the incident light, the average intensity at the surface directed towards the light source would be only two thirds of a flat surface intercepting the same amount of light.

In desert regions we often find leaves placed parallel with the incident light. Most typical in this respect are the *Eucalyptus*-like leaves, which hang down, intercepting little light, yet receiving enough for very effective photosynthesis, as their rate of dry-matter production shows. In Australia this *Eucalyptus*-type leaf is common in shrubs in the semi-arid regions. Once we have seen that in trees and shrubs leaves do n o t place themselves perpendicular to the incident light, it is not surprising any more, that in herbs the same thing is true. In a cornfield we see all leaves inserted at a sharp angle with the stem; somewhere halfway the leaf blade hangs vertically down. Thus the average angle of incidence of the light on the leaf lamina is not more than 15° . The same is true for wheat and other cereals. And it certainly holds for most pasture grasses, except a few, like crabgrass (*Eleusine indica*), which we try to keep out of lawns.

In sugar cane, which has in the field the highest light-conversion potential, the average light incidence angle is also small with most leaves pointing upward, each receiving only a fraction of the light which a horizontally spread leaf would obtain. Thus each leaf gets an average surface light intensity many times less than full sunlight and thus is about saturated with light, not wasting much light above the saturation point.

The next highest efficiency in light conversion is found in the sugar beet. Experiments with young plants in the Earhart Plant Research Laboratory have shown that their leaves are light-saturated at about 1000 ft.-c. surface intensity (W e n t 1957). In the early stages of growth the leaves are not covering each other as yet. In mature plants the center-most leaves are all pointing upward; the older leaves which stand out more horizontally are largely shaded by the younger more upright ones. Thus the same situation holds as in sugar cane, and all leaves receive near-saturation light intensities.

There are some special cases of herbs whose leaves place themselves parallel with the most intense noon sunlight. These are so-called compass plants, *Sylphium laciniatum* and *Lactuca scariola*. Their leaves turn themselves strictly in a north-south plane, parallel with the stem. Thus in early morning and late afternoon they receive full intensity sunlight; the surface intensity remains approximately the same throughout the day. These compass plants are steppe or prairie plants, where they extend well above the other plants without taking away much of the noon sunlight. When they are growing near shading structures they do not place their leaves in a north-south plane, but parallel to the average highest light intensity.

In all these cases it has been claimed that the position of these leaves was an adaptation to reduce excessive transpiration. Although this is a by-product, the main function of reducing light intensity at the leaf surface seems to be to keep the average surface intensity near the light saturation point. Any more light not only is wasted, but heats the leaf which thus transpires more, using the excess light energy for water volatilization.

In regions with high light intensities, such as in deserts or in alpine regions, many plants have their leaves covered with hairs which are strongly reflective. This will reduce the light intensity in the chlorophyll-containing cells, and most of the incident light is reflected so that other, surrounding, leaves are benefitted. Therefore, the hair-covering of leaves may not be associated with a reduction in transpiration, as was suggested, e. g. by Schimper, but may be a mechanism by which a greater percentage of the sunlight can be used in photosynthesis. Let us assume that hairs will give a 50% reflectance of the incident light. Then only half the incident amount of light will reach the leaf interior, which is then still saturated. If the leaves are placed at an angle with the incident light, a large part of the light reflected from them will reach the lower leaves, which in this way receive considerably more light than in case 2 and 3 of figure 6, and thus the total light utilization can be actually more than if less light reflection occurred.

Another mechanism by which the light intensity inside the leaf is reduced so that a larger proportion of the total light can be used, is by having the leaf surface corrugated. Many plants normally growing in full sunlight have plicate leaves, such as palms and *Veratrum*. Although most orchids are shade-plants, some have plicate leaves, but these (like *Phajus*) grow mostly in strong light.

In the previous descriptions we have seen how many plants have arrangements by which their leaves receive only a fraction of the full light intensity of the sun and thus do not waste much light which the light intensity on a horizontal plane exceeds the saturating intensity, which is 1000 ft.-c. for most species.

In the introduction it also was mentioned that fluctuating or intermittent light of super-saturating intensity is used more efficiently than light of a constant intensity. In nature we find that the daily movement of the sun provides frequent changes from shade to full sunlight on the leaves located below the upper layer of leaves. Inside a lath house the total light intensity, and consequently total heating is reduced, but through the succession of sunlight and shade falling on leaves a higher proportion of the sunlight can be used. By measuring the optimal lengths of light and shade periods the best width of lath could be determined.

Wind will also cause fluctuations in light intensity on all leaves. There are a number of plants of which the leaves have special arrangements to move freely in the wind. The leaf stalks of the quaking aspen (*Populus tremula* and *P. tremuloides*) are flattened, allowing the hanging leaves to sway in even weak air currents.

In addition to all these purely physical considerations which show that a high degree of light utilization by plants is possible through proper leaf position, or through leaf movements, there are many physiological factors which influence the efficiency of light utilization. Full knowledge of them might lead to better light utilization in the field, if by simple means the effi-

ciency of photosynthesis could be increased. Many of the following facts are discussed and experimentally supported in Went (1957).

1) The first of the physiological factors affecting net photosynthesis is growth. Under poor growing conditions the photosynthates may not be used up or stored at the rate at which they can be produced. Thus the whole plant soon becomes filled up with photosynthates and further CO_2 reduction decreases

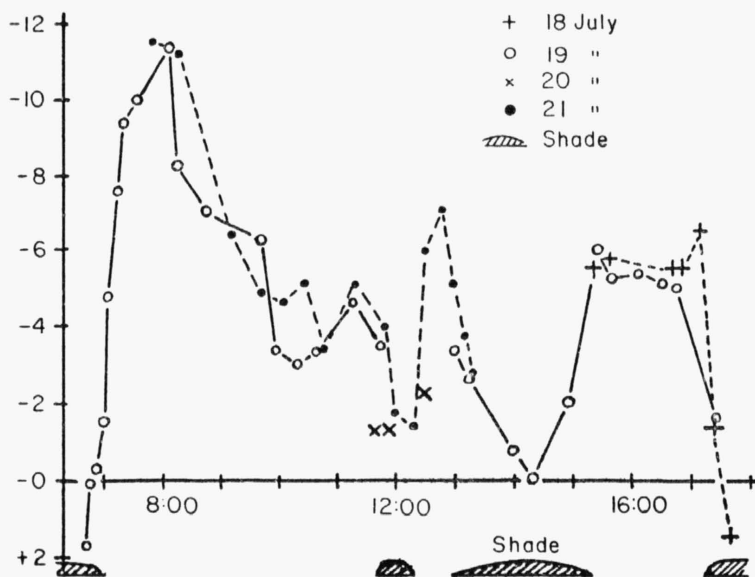


Fig. 8. Rate of photosynthesis (in arbitrary units of CO_2 absorbed or given off, on ordinate) for a branch of *Quercus chrysolepis*, attached to the tree, from sunrise (at 6 : 00) to sunset (at 18 : 00), on 4 successive days.

to the rate at which the carbohydrates are moved out of the photosynthesizing cells. By improving the growing conditions it is conceivable that growth and transformation of sugars proceeds at such a pace that they can be produced at a maximal rate. Thus the efficiency of light utilization can be raised by proper growing conditions.

2) Optimal rate of CO_2 reduction occurs only at a certain sugar level inside the chlorenchyma cells. This is proven by experiments in which photosynthesis in plants kept in darkness for over 24 hours is raised to the maximal rate by previous sugar sprays. From the slow rate of sugar formation in tomato leaves during the first few hours of light exposure (Went and Engelsberg 1946) it is likely that the first formed sugar is needed for priming of the photosynthetic system. From this we might hypothecate that the first one or two hours of daylight are needed for priming the photosynthetic system. That does not require such high light intensities, and thus the whole photosynthetic mechanism is adjusted to a slowly rising light intensity in the morning, then a limited number of hours at saturating light intensity, and then a period of darkness to empty the leaf cells of photosynthates.

3) It is conceivable that translocation of the photosynthates out of the

leaf cells is limiting the rate of CO_2 reduction. This indicates the importance of more knowledge about food translocation inside the plant, as a possible basis for improvement of light utilization. This gives higher plants a possible advantage over algae in the utilization of higher light intensities. They can develop storage space at a rate which is independent of the leaf development. In an algal cell sugar can be produced only up to the limit of the individual cell's storage capacity and its rate of division, except when the sugar formed in excess is excreted into the culture medium, where it is not available any more to the algae itself. It is interesting to note that Tam y i a et al. (1953) have concluded that over longer periods of light exposure the dry matter production of algal cultures is limited by their growth rate, and that this in turn is a function of the illumination.

4) There are indications that green light at high intensity is inhibitory for growth. Further exploration of this phenomenon might also improve light utilization in the field.

5) If photosynthesis occurs at such a rate, that before noon the leaves are already filled with sugar, CO_2 reduction will be curtailed as has been observed by many investigators (K o s t y t c h e w). An interruption of photosynthesis by a dark period during the middle of the day can serve to partially empty the leaves of photosynthates. This will then result in an increased rate of CO_2 reduction during the afternoon. Laboratory experiments have shown that one or two dark interruptions of the daily photoperiod can increase the total amount of photosynthesis as much as 50% (fig. 66 from W e n t 1957). And photosynthesis measurements in the field show that a period of shade reverses the downward trend in CO_2 production at noon (see figure 8). Thus the planting pattern in a field, causing periodic shading of plants, might be used to increase the photosynthetic yield.

Conclusion

In the previous discussion we have seen, that even though leaves of higher plants are saturated with light at about one-tenth full sunlight intensity, when exposed over continuous periods of 8 hours, the rest of the sunlight is not necessarily lost for the photosynthetic process. If at most, in a light intensity of 1000 ft.-c., 10% of the incident light can be transformed into chemical energy, then to many scientists the observed maximal light utilization in the field by higher plants of slightly over 2% (W a s s i n k 1948) seemed to be the maximum obtainable. There are, however, physiological, mechanical, and geometrical reasons why we can expect in future to reach a much higher conversion of sun energy in the field.

References

- Allard, H. A., and W. W. Garner (1941): Responses of some plants to equal and unequal ratios of light and darkness in cycles ranging from 1 hour to 72 hours.—*J. Agric. Res.* 63 : 305—330.
- Emerson, R., and W. Arnold (1932): A separation of the reactions in photosynthesis by means of intermittent light.—*J. Gen. Physiol.* 15 : 391—420.
- Funke, G. L. (1938): Observations on the growth of water plants.—*Botanisch Jaarboek*, deel XXV.
- Honert, T. H. van den (1930): Carbon dioxide assimilation and limiting factors.—*Rec. trav. bot. neerl.* 27 : 149—286.
- Kurssanow, A. L. (1933): Über den Einfluss der Kohlenhydrate auf den Tagesverlauf der Photosynthese. — *Planta* 20 : 535—548.
- Myers, J. (1957): Suppression of carbon dioxide assimilation by glucose in *Chlorella*.—*Plant Physiol.* 32 : XVI—XVII.
- Nuernbergk, E. (1925): Beiträge zur Physiologie des Tagesschlafs der Pflanzen. — *Bot. Abhandl.* 8 : 1—138.

- O o r s c h o t, J. L. P. v a n (1955): Conversion of light energy in algal cultures.—Meded. Landb. hoges. Wageningen 55 : 225—276.
- T a m i y a, H., E. H a s e, K. S h i b a t a, A. M i t u y a, T. I w a m u r a, T. N i h e i, and T. S a s a (1953): Kinetics of growth of *Chlorella*, with special reference to its dependence on quantity of available light and on temperature.—In: Algal Culture, Carn. Inst. Wash. Publ. 600 : 204—232.
- W a s s i n k, E. C. (1948): De lichtfactor in de fotosynthese en zyn relatie tot andere milieu-factoren. — Meded. Dir. Tuinbouw 11 : 503—513.
- W e n t, F. W. (1957): The Experimental Control of Plant Growth.—Chronica Botanica 17 : XVII + 343.
- W e n t, F. W., and R. E n g e l s b e r g (1946): Plant growth under controlled conditions. VII. Sucrose content of the tomato plant.—Arch. Biochem. 9 : 187—200.
- W i l l s t ä t t e r, R., and A. S t o l l (1918): Untersuchungen über die Assimilation der Kohlen-säure. — Springer, Berlin, 448 pp.
- Y i n, H. C. (1938): Diaphototropic movements of the leaves of *Malva neglecta*.—Am. J. Bot. 25 : 1—6.