Summary.—When mice were given the specific antimetabolite of serotonin, viz., 1-benzyl-2,5-dimethylserotonin or BAS, followed by 5-hydroxytryptophan, the serotonin content of their brains was markedly increased. This was reflected in behavioral changes and thus was an indication that the excess serotonin in the brain was pharmacologically active. Some of the effects on peripheral organs, however, were prevented. This was true of the diarrhea, due to intestinal contractions, which 5-hydroxytryptophan caused to a marked degree in unprotected animals. The relationship of these results to experimental psychiatry has been indicated.

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SOME FACTORS INFLUENCING THE LONG-WAVE LIMIT OF PHOTOSYNTHESIS

BY ROBERT EMERSON, RUTH CHALMERS, AND CARL CEDERSTRAND

BOTANY DEPARTMENT, UNIVERSITY OF ILLINOIS, URBANA, ILLINOIS

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There is evidence from several sources that the quantum efficiency of photosynthesis begins to decline at wave-lengths where light absorption by chlorophyll is still strong. Emerson and Lewis[1] found a sharp drop in efficiency beyond 685 mμ for both *Chlorella* and *Chroöcoccus*. Tanada[2] found a similar decline for the diatom *Navicula minima* at about the same wave length. Action spectra measured by Haxo and Blinks[3] for representatives of the green and brown algae also indicate declining photosynthetic efficiency beyond the red maximum of chlorophyll absorption.

It has seemed plausible to Rabinowitch,[4] Duysens,[5] and others that photosynthesis is brought about entirely by the lowest excited electronic state of chlorophyll *a;* yet this appears to conflict with the evidence of declining photosynthetic activity within the red absorption band of chlorophyll. Absorption anywhere within the red band, followed by vibrational equilibration with the medium, should bring the chlorophyll molecule into the same excited electronic state, with the same (temperature-determined) vibrational distribution (cf. Rabinowitch,

op. cit., pp. 1156–1157). In the living cell, the red absorption maximum is close to 680 mμ, and, although the long-wave side of the band is very steep, absorption probably remains appreciable as far as 700 mμ and perhaps somewhat beyond. The sharp decline in efficiency of photosynthesis beginning at or near 685 mμ therefore requires interpretation. A decline in yield of fluorescence on the long-wave side of an absorption band, known for chlorophyll as well as for many other dye molecules, poses a similar problem (cf. Rabinowitch, *op. cit.*, p. 752, and Stepanov[6]).

We reported,[7] for both *Chlorella pyrenoidosa* and the red alga *Porphyridium cruentum*, that at lower temperatures the decline in yield of photosynthesis begins at longer wave lengths and that in the region of the long-wave decline the yield could be improved by supplementary light of shorter wave lengths. We give here the results of additional experiments with *Chlorella* which confirm these effects of temperature and supplementary light in greater detail.

Our manometric technique for measuring photosynthesis was similar to that described by Emerson and Chalmers,[8] except that we used the single-vessel instead of the two-vessel method. We are concerned here with steady rates, which can be measured by the single-vessel method in either carbonate buffer (about pH 9) or in acid culture medium (about pH 5). In the case of single-vessel measurements in acid culture medium, it is necessary to assume a value for γ (the ratio CO_2/O_2). We have used a value of -1, since it has been well established that γ is close to -1 for steady rates of photosynthesis and respiration of *Chlorella*. The two-vessel measurements of Emerson and Chalmers show that this is specifically the case for the conditions of the experiments to be reported here.

The cell material (*Chlorella pyrenoidosa*) was grown at about 23° C., over a combination of fluorescent and incandescent lamps. The inoculum was 30 μl. of cells in 200 ml. of medium, and the harvest (after 3 days' growth) was about 200 μl. of cells. For the measurements of photosynthesis, about 250 μl. of cells were suspended in 8 ml. of liquid. In this high concentration the cells transmitted no appreciable fraction of the light beam used for measuring quantum yields, out to about 700 mμ.

There is little doubt that, out to this point, absence of transmission implies practically total absorption of the energy of the incident beam by chlorophyll and hence that the number of absorbed quanta equals the number of incident quanta. Visual inspection (the eye remains a sensitive detector nearly to 700 mμ) and tests with an emission-type photocell and amplifier betrayed no appreciable transmission. Beyond 700 mμ, the photocell and amplifier continued to show no evidence of transmission to about 710 mμ, where it became just detectable. In this region, absorption by chlorophyll is probably so small that scattering and reflection begin to contribute appreciably to the quenching of the incident beam, and therefore absence of evidence of transmission becomes an uncertain criterion of totality of absorption. However, our data, presented in this communication, that full efficiency of photosynthesis can be extended to 700 mμ by supplementary light, are strong evidence that we have maintained total absorption to this point. Tests made by Emerson and Lewis[9] with different densities of suspension indicated that total absorption could be maintained to somewhat beyond 700 mμ.

Illumination was from the grating[10] monochromator described by Emerson and Lewis.[11] The light source was a tungsten ribbon filament lamp operated at about

7.5 volts and from 29 to 31 amps. At each wave length the current was adjusted to give equal numbers of incident photons per unit time (about 0.1 μeinstein per minute).

The energy of the incident beam was measured with a bolometer calibrated against radiation standards from the U.S. Bureau of Standards. Appropriate corrections were made for reflection losses at the bolometer window and for differences in optical path to bolometer and to reaction vessel.

The band width was estimated by mounting a Zeiss hand spectroscope at the exit slit of the monochromator and moving the hand spectroscope across the width of the exit slit. The band width did not exceed 10 mμ. This is probably equivalent to the band half-width of 5 mμ specified by Emerson and Lewis[11] for their measurements in the red region. It is more appropriate to specify the full visible width, because the wide slits make the significance of the half-width uncertain.

With dense cell suspensions and low light intensities, respiration exceeds photosynthesis, so that the rate of respiration during light exposures is an important correction term in the calculation of quantum yields. The usual method of estimating this correction (interpolation from respiration measurements made during dark periods before and after light exposures) led to small maxima and minima in the plots of quantum yield against wave length. The positions of these maxima and minima depended on the sequence of exposures to different wave lengths and on the spacing of the dark periods. A new method of estimating the respiration during light exposures eliminated the uncertain maxima and minima, as well as the dependence of yield on the sequence in which the exposures to different wave lengths were made. Instead of interspersing many dark periods among the light exposures, we made only one direct measurement of respiration, in a single dark period at about the middle of the experiment. At this time we determined the difference between the rate of respiration in darkness and the net rate of photosynthesis and respiration at a standard wave length (660 mμ). Other experiments had shown that this difference, D, remained nearly constant during the course of an experiment; hence exposures to a standard wave length (always at the same intensity) could be used as an index of changes in rate of respiration, without repeatedly returning the cells to darkness. The observed net rate at the standard wave length was plotted against time, and the difference D was subtracted from the plot to find the curve for respiration as a function of time. The respiration correction applicable to each measurement of photosynthesis was read directly from this curve.

Figure 1 shows two sets of measurements made in this way. The sequence of observations was first from short wave lengths to long (solid circles and continuous line) and then from long wave lengths to short (open circles and dashed line). The agreement between the two sequences is close, and there is no evidence of systematic differences.

Each curve plotted in Figures 2 and 3 represents an average of two sets of observations like those in Figure 1, first in sequence from short wave lengths to long, then in the opposite sequence.

In experiments with supplementary light no direct measurement of respiration was required, but it was nevertheless necessary to make allowance for changes in respiration. The net metabolic rate during photosynthesis from the supplementary

light varied with changes in respiration. This net rate was measured at intervals, and a smooth curve was drawn through the observations. To find the increment in photosynthesis attributable to the measured energy of the monochromatic beam, we took the difference between the observed rate of supplementary light plus monochromator beam, and the rate for supplementary light alone, read from the smooth curve for the corresponding time.

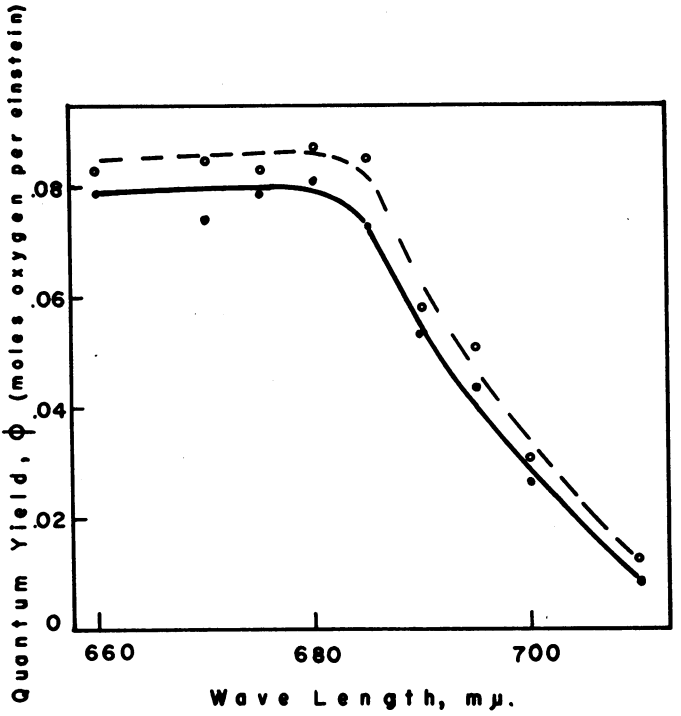
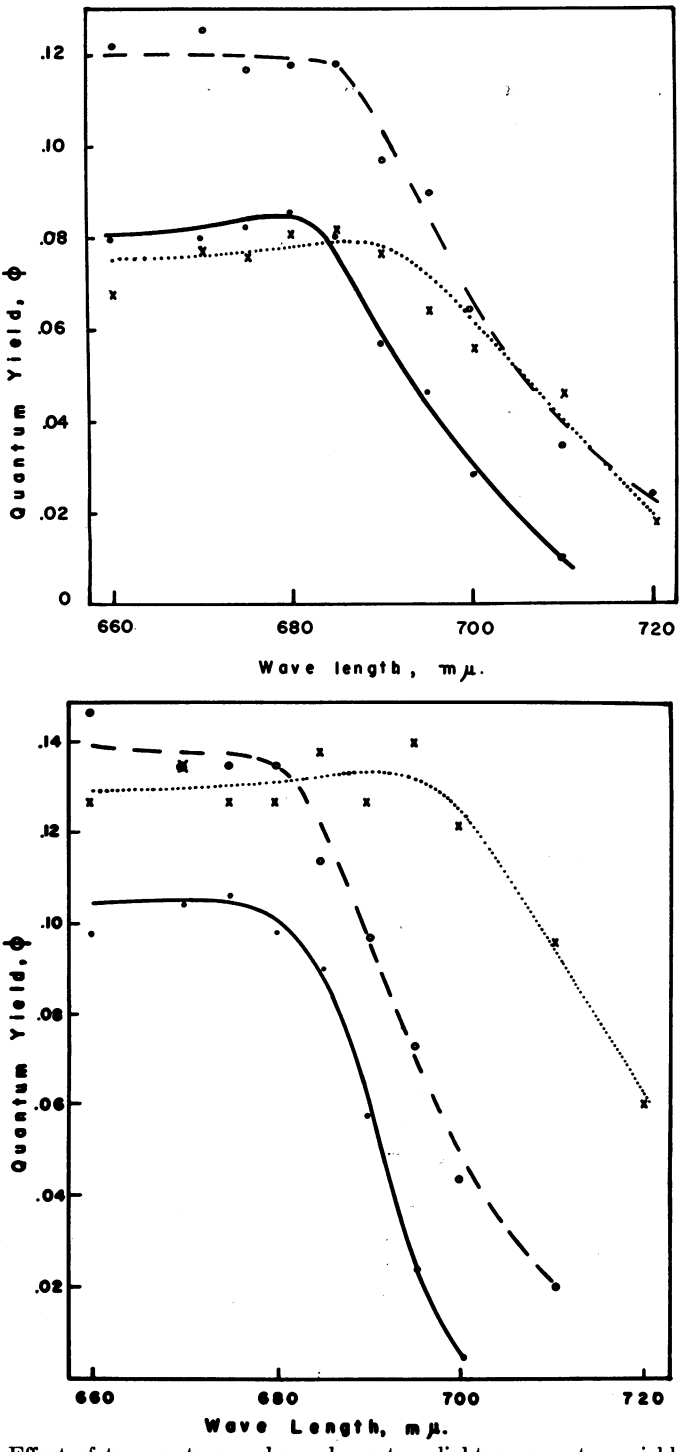


FIG. 1.—A test to show that the method of measuring dependence of yield on wave length gives the same result for opposite sequences of wave lengths. Solid dots and continuous line are for sequence from short wave lengths to long, measured first; measurements in opposite sequence are shown by open circles and dashed line.

The supplementary light was from a mercury-cadmium lamp. The intensity was adjusted to maintain photosynthesis in excess of respiration by an amount roughly equal to the respiration itself. The supplementary light entered the reaction vessel from above, and the monochromator beam from below. The cell suspension was transmissive for the yellow and green lines of the mercury-cadmium lamp, so that all cells in the suspension were continuously illuminated, though at varying intensity, as they circulated. On the other hand, the cells were intermittently illuminated by the monochromator beam; the intensity of this light dropped to zero as it penetrated the suspension.

The effects of temperature and supplementary light on the long-wave limit of photosynthesis are shown in Figure 2 for cells in carbonate buffer and in Figure 3 for cells in culture medium. In both figures the curve for 20° (solid circles and continuous line) bends downward at the shortest wave length, the curve for 5° (open circles and dashed line) at a slightly longer wave length, and the curve at 20° with supplementary light (crosses and dotted line) extends horizontally to the



FIGS. 2-3.—Effect of temperature and supplementary light on quantum yield. Fig. 2, cells in carbonate buffer. Fig. 3, cells in acid culture medium. In each figure the solid dots and continuous line are for 20°, the open circles and dashed line for 5°. The dotted curves and crosses are for measurements at 20° with supplementary light.

longest wave length before turning downward. The wave lengths where the curves decline to one-half their maximum level are in the same sequence and can be more precisely specified than the long-wave limits of the horizontal portions. In Figure 2 the halfway points come at 696, 702, and 711 mμ for 20°, 5°, and 20° with supplementary light, respectively. In Figure 3 the corresponding halfway points are at 690, 695, and 718 mμ.

All the curves in Figure 3 are somewhat higher than the corresponding ones in Figure 2. Rieke[12] also found that the quantum yield was higher for cells suspended in culture medium than for cells in carbonate buffer; hence the differences between Figures 2 and 3 with respect to maximum yield are probably significant. Less easy to explain is the difference, to be seen in both Figures 2 and 3, between maximum yields at 5° and 20°. The dashed curve is substantially higher than the solid line, for both carbonate buffer and culture medium. If further work should confirm that the quantum yield is indeed a function of temperature, this would call for revision of current interpretations. Our method, however, was devised to show the dependence of yield on wave length, perhaps at some sacrifice of comparability in regard to the absolute value of the yield. Our derivation of the correction for respiration from only a single dark period in each experiment may lead to differences in precision at different temperatures, and the value of γ may not be quite the same at 5° and 20°. Since at 20° the rate of respiration is higher and is also subject to greater changes, there is greater opportunity for error in quantum yields through error in estimation of respiration correction. Without special attention to these factors, it would not be justifiable to conclude that the quantum yield is a function of temperature or to attach special significance to differences in maximum yield. On the other hand, the effects of temperature and supplementary light on wave-length dependence were confirmed in many experiments over a period of months, and we regard this as evidence that comparability with respect to dependence of yield on wave length was adequately maintained.

Since the intensity of the supplementary light was sufficient to make photosynthesis exceed respiration, the low yield at long wave lengths without supplementary light might have been characteristic of photosynthesis of these cells below the compensation point. Several authors (for example, Kok,[13] Bassham *et al.*[14]) have suggested that the quantum yield of photosynthesis may be different above and below compensation. The difference they reported (higher yield below compensation than above) is opposite to that which would be required to account for our results, but if there are factors which can change the yield in the neighborhood of the compensation point, the change may not necessarily be always in the same direction. We have therefore tested the effect of intensity, above and below the compensation point, both in the region where yield is not changing with wave length (640–670 mμ) and in the region of the long-wave decline (675–700 mμ). It was necessary to use these wide bands in order to attain intensities well above compensation.

Figure 4 shows the results of these measurements. For both wave-length regions the rate of photosynthesis is a linear function of intensity below, through, and above the compensation point. The slope is lower for the longer-wave band, in agreement with the lower quantum yields shown in Figures 1–3 at longer wave lengths. There is no indication that higher intensities alone can raise the yield for

longer wave lengths. On the other hand, supplementary light of shorter wave lengths can improve the yield for the long-wave band, even at the highest intensity shown in Figure 4, just as it does for the very low intensities of long wave lengths used in Figures 1–3. In Figure 4 the point marked with a square represents the yield for the wave band 675–700 mμ at the same intensity as the solid black dot just below, but supplemented by light of shorter wave lengths. It is raised to the same level as the corresponding point on the line for the 640–670 mμ band.

These measurements showing no departure from linearity above and below compensation ("Kok effect") are in agreement with similar measurements[15] with the red cadmium line (644 mμ). In the course of many measurements under a wide range of conditions, we have never observed significant changes in yield in the region of compensation.

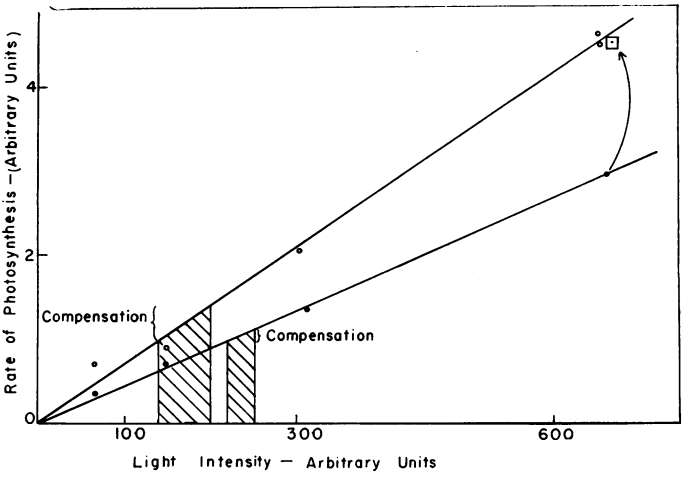


FIG. 4.—Dependence of rate of photosynthesis on intensity. The upper line (*open circles*) is for a band of wave lengths from 640 to 670 mμ. The lower line (*solid dots*) is for 675–700 mμ. The point marked by a square is for the 675–700 band, supplemented by light of shorter wave lengths.

These experiments with higher intensities of light show that the effects of supplementary light on the yield in the far-red region cannot be attributed solely to the higher rate of photosynthesis in the supplementary light. The shorter wave lengths of the supplementary light must be significant. We mention here the results of some preliminary experiments with different wave lengths and intensities of supplementary light, although our work on these factors is incomplete.

By means of colored glass filters, we have isolated groups of lines from the blue, green, or red regions of the spectrum, from the mercury-cadmium source of supplementary light. We found positive effects (i.e., improvement in yield from long-wave red) with all three spectral regions when we used intensities of supplementary light sufficient to give photosynthesis somewhat above compensation of respiration. Intensities too small to give measurable photosynthesis showed no effect on the yield from long-wave red. It seems particularly interesting that effects were obtainable with supplementary red light. This was chiefly the cadmium line at

644 mμ, a wave length still appreciably shorter than the band of long-wave red (680–700 mμ) which, according to Figure 4, gave no improvement in yield at higher intensities. Somewhere between 644 and 680 mμ there must be a limit beyond which the supplementary light is no longer effective.

These exploratory experiments indicate that the effect of supplementary light on the yield from long-wave red differs in important respects from the action of supplementary light described by Warburg *et al.*[16] They reported effects of supplementary light on the yield of photosynthesis from a band of red light centering at about 644 mμ. This is a region of wave lengths appreciably shorter than the long-wave band where we found effects of supplementary light. Our Figure 2 shows no effect for wave lengths shorter than 680 mμ. The dotted line and solid line represent yields at 20° with and without supplementary light. The corresponding curves in Figure 3 show some difference in level for wave lengths shorter than 680 mμ, but the difference is small compared to the effect at longer wave lengths. The measurements in Figures 2 and 3 start at 660 mμ, a wave length longer than the red band at 644 mμ used by Warburg *et al.* However, we have done a number of experiments starting at 640 and 650 mμ and have failed to find significant effects of supplementary light except at wave lengths longer than 680 mμ.

Warburg *et al.* also report that intensities of supplementary light too low to give measurable photosynthesis were effective in increasing the yield for red light and that there was a sharp maximum in effectiveness of supplementary light at 460 mμ. Wave lengths longer than 500 mμ gave very small effects. Our measurements, on the other hand, indicated that intensities of supplementary light sufficient to give measurable photosynthesis were necessary in order to show improvement in the yield from long-wave red light and that all regions of the visible spectrum were effective, at least out to 644 mμ.

Warburg *et al.* report that in red light without supplementary blue, γ for photosynthesis approaches zero, while the supplementary blue restores the normal value of about -1 for γ. Although we have made many measurements of γ for photosynthesis in the red cadmium line (644 mμ), we have never observed γ values approaching zero for steady rates of photosynthesis. In our experience,[8] γ is close to -1, except during periods of transient changes in rate.

We note that Warburg *et al.* measured the effects of supplementary light by the two-vessel manometric method, which can sometimes lead to large errors through inattention to details. We are not prepared to offer a quantitative explanation of how the method might produce the results they describe, but we refer to our earlier analysis[8] of the sensitivity of the two-vessel method to small differences between the vessels. Possibly small differences in light absorption may have contributed to the effects of supplementary light which appear in their results.

Our provisional conclusion is that the effects of supplementary light described by Warburg *et al.* are so different from the effects we have observed that the prospect of a common interpretation is unpromising.

Our results show that for *Chlorella* the effect of temperature on the long-wave limit is not conspicuous. According to Figures 2 and 3, a drop in temperature from 20° down to 5° extends the limit only about 5 mμ. Emerson *et al.*[7] mentioned measurements with the red alga *Porphyridium cruentum* which showed a greater dependence on temperature. The long-wave limit of full efficiency was about 650

mμ at 20° and about 670 mμ at 5°. Besides being farther apart, these limits are at considerably shorter wave lengths than the corresponding limits for *Chlorella* (cf. Figs. 2 and 3).

Haxo and Blinks[3] noticed a similar difference between red and green algae. Instead of measuring quantum yields under conditions of total absorption, they used thin (translucent) pieces of thallus and compared action spectra with absorption spectra. Their figures show that for green and also for brown algae the action spectrum of photosynthesis parallels the absorption spectrum through the red maximum of chlorophyll, while for red algae the action spectrum begins to fall sharply away from the absorption curve at about 650 mμ and drops practically to zero in the red absorption maximum of chlorophyll. They made their measurements at room temperature (probably about 20°), and the wave lengths where their action spectra begin to fall below their absorption spectra correspond reasonably well with the wave lengths where we found declining yields of photosynthesis in our experiments at 20° with *Chlorella* and *Porphyridium*.

Haxo and Blinks concluded that in red algae the light absorbed by chlorophyll is of minor value for photosynthesis and that phycoerythrin plays the major photochemical part. Our measurements at 5° show, however, that in the case of *Porphyridium* the range of full efficiency may extend to 670 mμ, or well into the red absorption band of chlorophyll. If this effect of low temperature proves to hold for red algae in general, there will then be no need to suppose that their chlorophyll is necessarily less efficient than that of green algae. Taking the effect of temperature into consideration, we may say that the analogy between the red and green algae is close. In both cases the range of full efficiency can extend well into the red absorption band of chlorophyll, and the long-wave limit of full efficiency falls appreciably short of the long-wave limit of the red absorption band. It may be possible to find a common interpretation.

A comparison of the limits of absorption and photosynthesis shows that for both red and green algae the yield is low in the region where absorption is attributable to chlorophyll *a* alone. For *Chlorella* the yield remains high to about the wave length where we may expect absorption by chlorophyll *b* to terminate. The long-wave limit of absorption for the *b* component in living cells cannot be directly observed, but it may be estimated from the limit for the *a* component. With proper correction for scattering, measurements with living cells show that at 705 mμ the absorption is close to zero and dropping steeply (Latimer and Rabinowitch[17]). This is the long-wave side of the chlorophyll *a* band. If the distance between the red maxima of the *a* and *b* components is a correct index of the difference between their long-wave margins, then at 690 mμ the absorption due to chlorophyll *b* must be close to zero. Beyond this, absorption must be attributed to chlorophyll *a* alone. Red algae lack the *b* component but are believed to contain small amounts of chlorophyll *d*. Since the concentration of the *d* component is probably so small that it makes a negligible contribution to absorption even in the region of its maximum, we shall overlook it for the moment and consider that the beginning of absorption by chlorophyll *a* alone will coincide with the end of absorption by phycobilins. We may expect this to be variable because red algae contain varying amounts of phycocyanins as well as phycoerythrin, but at least we can say that the zone where chlorophyll *a* alone accounts for practically all the absorption will generally extend

toward shorter wave lengths than for green algae. This is in qualitative correspondence with the observed long-wave limits of full efficiency.

For both red and green algae, supplementary light extends the range of full efficiency into the region of exclusive absorption by chlorophyll *a*, and perhaps to the limit of the *a* absorption band. This is shown for *Chlorella* by the dotted curves in Figures 2 and 3. Marcia Brody is preparing for publication the results of similar measurements with *Porphyridium* which show that, for this alga also, supplementary light extends the long-wave limit to near 700 mμ.

Since the supplementary light must be of shorter wave lengths than those which by themselves give diminished yield, the significance of the supplementary light may be that it adds excitation of other pigments besides chlorophyll *a*. The maintenance of maximum efficiency may require the excitation of some pigment with an absorption band corresponding to an energy level higher than the first excited state of chlorophyll *a*. In the green algae this could be chlorophyll *b*, while in red algae it could be one of the phycobilins. Since the red maximum of chlorophyll *d* is to the long-wave side of chlorophyll *a*, it would not fill the requirement, and this is the primary reason we omitted it from consideration.

The brown algae and diatoms also lack chlorophyll *b* but contain a *c* component in sufficient concentration to contribute appreciably to absorption. According to Tanada,[2] the long-wave limit of full efficiency of the diatom *Navicula minima* is at about 675 mμ (temperature of 10°), or slightly toward shorter wave lengths than the long-wave limit for *Chlorella*, and we may suppose that the limit of chlorophyll *c* absorption is also on the short-wave side of the chlorophyll *b* limit, since this is true of their maxima.

For blue-green algae, which also lack chlorophyll *b*, we would expect the phycocyanins to fill the role we have suggested for chlorophyll *b* in *Chlorella*. Different phycocyanins probably have different long-wave absorption limits. As in the case of red algae, we might anticipate a range of limits for full efficiency. Emerson and Lewis[18] found that for *Chroöcoccus* full efficiency extended to about 680 mμ. Their Figure 1 indicates that absorption by phycocyanin remains appreciable about to this point. Haxo and Blinks, on the other hand, mentioned preliminary experiments with other blue green algae which indicated termination of full efficiency at shorter wave lengths.

We look forward to testing the effect of supplementary light on the long-wave limits for brown and blue-green algae, to find whether they fit the interpretation we have suggested. It is in conflict with the widely accepted view that transfer of excitation energy to chlorophyll *a* from other pigments takes place with practically 100 per cent efficiency (cf. Duysens[5]). It also fails to account for the reduced yield of fluorescence on the long-wave side of the absorption band of chlorophyll *a*. However, if further work should confirm our suggestion that photosynthesis requires excitation of two different pigments, we can hardly expect to find a common interpretation for the long-wave decline in yield of fluorescence and photosynthesis.

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THE SYMMETRY OF DENDRITIC SNOW CRYSTALS

BY DAN MCLACHLAN, JR.

STANFORD RESEARCH INSTITUTE, MENLO PARK, CALIFORNIA

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Snow crystals are of interest in two major respects: (*a*) meteorologically and (*b*) artistically. The meteorological interest in snow crystals was greatly enhanced by the work of Langmuir[1, 2] and Schaefer,[3–6] who have done such extensive pioneering work on the seeding of clouds with material having a structure similar to that of ice, with the object of gaining some control over rainfall throughout the country. Their most effective seeding materials are frozen carbon dioxide and silver iodide. From the artistic standpoint the interest in the beauty of snow crystals goes back to the most primitive times, but we know that as early as 1555 Olaus Magnus, Archbishop of Upsala, published a woodcut of a snow crystal in a book on the general subject of "Natural Phenomena." The most authentic early drawings of snow crystals were made by Scoresby[7] in 1820. One of the first to use photography for the study of shapes of snow crystals was Hellmann[8] in 1893. The most extensive work on the photography of snow crystals was carried out by W. A. Bentley, of Jericho, Vermont, who apparently spent a good portion of his life at this task, judging from his publications between 1901 and 1927.[9] In 1931 W. J. Humphreys assisted Bentley in compiling about 2,400 of Bentley's most interesting photographs