

HISTORICAL CORNER:

On the 1958 historical lecture of Robert (Bob) Emerson:

Discovery of auxiliary pigments working in synchrony with chlorophyll *a* in algae

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Prelude

In August 1958, the late Robert (Bob) Emerson (1903-1959; see Rabinowitch, 1959) delivered a very important (i.e., of high significance) historical lecture where he presented his speculations concerning the synergistic role of light absorbed by accessory pigments (e.g., chlorophyll *b*, phycobilins, and fucoxanthol) and chlorophyll *a* in diverse groups of algae; it was published in the November, 1958 News Bulletin of the Phycological Society of America, and is reproduced below (see Emerson and Chalmers, 1958; note that his coauthor Ruth Chalmers was his highly talented technical assistant). Emerson had three brief abstracts on this topic, all presented at the annual meetings of the US National Academy of Sciences (Emerson, Chalmers, Cederstrand, and Brody, 1956; Emerson, 1957; Emerson, 1958; see footnote #1), and his key (highly recognized) paper on the synergistic effect of light absorbed in chlorophyll *b* on photosynthesis by light absorbed in chlorophyll *a* in the green alga *Chlorella* was published in the *Proceedings of the National Academy of Sciences* (Emerson, Chalmers and Cederstrand, 1957).

Robert Emerson was already the ‘*Grand Master of Photosynthesis and Related Processes*’ in this World when I knew him during 1956-1958, as my mentor and advisor (see Govindjee and Govindjee, 2021). In his PhD thesis, in Berlin, Germany, Emerson (1927) explored in depth, in several algae, the intriguing absence of inhibition of respiration by hydrogen cyanide (HCN) and carbon monoxide (CO); this phenomenon baffled him, as well as his advisor Otto Warburg; full molecular understanding of this phenomenon still needs attention. [See Lichtenthaler and Bjorn (2020) for the English translation of this 32-page thesis, as well as comments by Govindjee (2020) on Emerson.] Further, Emerson’s famous 1948 Stephan Hales lecture is now available (see: Govindjee, 2018).

In 1932, Emerson, together with his undergraduate student William Arnold (see Govindjee and Srivastava, 2014), discovered the concept that hundreds of chlorophyll *a* molecules ‘cooperate’ in doing photosynthesis (Emerson and Arnold, 1932a,b), which has led to the concept of ‘Photosynthetic Unit’ (i.e., ‘antenna and the reaction center’). In 1943, Emerson, together with Charlton M. Lewis, not only confirmed that the minimum quantum requirement for the evolution of one oxygen molecule was 8-12, not 3-4, as the Nobel Laureate Otto Warburg had insisted, but there was a “Red Drop” in the

long-wavelength region, beyond 685 nm (Emerson and Lewis, 1943)—both were early “teasers” to the current concepts of photosynthesis (see Govindjee, 2001, for Emerson’s contributions; Nickelsen and Govindjee, 2011, for the controversy on the minimum quantum requirement for oxygen evolution; and Govindjee et al., 2017, for the evolution of the current Z-scheme of photosynthesis). It is very unfortunate that Emerson passed away, in a tragic plane crash, long before we showed that different spectral forms of chlorophyll *a* are present in both the photosystems I and II (Govindjee and Rabinowitch, 1960a,b); Emerson’s two light effect is in photosynthesis, not in respiration (see R. Govindjee et al. 1960), and the minimum quanta requirement, even under conditions dictated and insisted by Otto Warburg, are 8-12, not 3-4 (see R. Govindjee et al., 1968) confirming Emerson. Lastly, the two-light effect of Emerson in photosynthesis was confirmed through observations of a two-light effect on chlorophyll *a* fluorescence, also in 1960 (G. Govindjee et al., 1960).

I provide below a brief personal commentary on Emerson’s 1958 lecture, along with full references cited in his lecture (the latter are marked with a *). (For readers unfamiliar with the background and details of photosynthesis, we refer to Rabinowitch and Govindjee (1969), to Shevela et al. (2019), and most importantly to Blankenship (2021) for the thorough and complete current understanding of the mechanism of photosynthesis.

In addition to the 1958 lecture of Emerson (discussed here), his famous 1948 Stephan Hales lecture on the present, past and future of photosynthesis., was also unavailable earlier, now published in Govindjee, (2018). For a history of all aspects of photosynthesis research, see different chapters in the book edited by Govindjee et al. (2005).

Commentary on Emerson and Chalmers (1958)

The major discovery, presented here for the first time, is the very first action spectra, in different algae, of what we now call the ‘Emerson Enhancement Effect’ (i.e., enhancement in the yield of oxygen in far-red light), by adding supplementary light absorbed by various accessory pigments. This included: chlorophyll *b* (peaks at 480 nm and 655 nm) in *Chlorella* (a green alga), phycoerythrin (peak at 546 nm) in *Porphyridium* (a red alga), phycocyanin (peak at 600 nm) in *Anacystis* (a cyanobacterium), and a carotenoid fucoxanthin (fucoxanthol; peak at 540 nm) and chlorophyll *c* (peak at 645 nm) in the diatom *Navicula*. Although shown in the lecture, the 1958 paper has no figures, and Emerson died on February 4, 1959. They were published only 2 years later by Eugene Rabinowitch (Emerson and Rabinowitch, 1960). We must point out that Emerson missed the action band of a short-wavelength absorbing form of chlorophyll *a* along with that of accessory pigments because he had used Hg-Cd lines for his supplementary light and not a monochromator, providing all wavelengths of light. I have always regretted that I could not have his name on my paper when we observed (Govindjee and Rabinowitch, 1960a,b) that chlorophyll *a* 670 was in the same system as chlorophyll *b* (in *Chlorella*) and fucoxanthol (in *Navicula*).

Emerson began his lecture by talking about the function and phylogenetic significance of so-called accessory (or auxiliary) pigments in algae (1) by pointing out that the older ideas in the book by Josephine Elizabeth Tilden (Tilden, 1935) needed to be reexamined, and (2) by stating that there was a real need to understand the physiological significance of different combinations of pigments present

in algae. He then talked about the “Red drop” in the yield of photosynthesis (Emerson & Lewis, 1943) and the Enhancement by Supplementary light he had just observed (Emerson et al., 1957, not 1956 as in the paper); he also mentioned his earlier presentation at a conference (e.g., Emerson, 1957). Then, he talked about his unusual data with yellow-green algae: *Polyhedriella helvetica* and *Tribonema aequale*. We mention this so that someone may reexamine the available literature and even engage in doing new experiments to find the reasons why Emerson had failed to find the ‘Enhancement effect’ in these organisms. I regret that I did not pursue it then (or even later) because this is what Emerson wanted me to do for my PhD and I did not – yes, I grew these two algae during 1958 but was frustrated with their slow growth! Emerson also mentioned in his lecture that he had not yet tested *Ochromonas* (see Myers & Graham, 1956). Tanabe et al. (2011) have now published as to how some *Ochromonas* species use the xanthophyll cycle to their advantage. However, further research is needed on the “two photosystems” of this alga.

Emerson ended his lecture by relating his observations to the evolution of the combination of pigments. He cited Oparin (1957). He speculated that the earliest organisms contained not only chlorophyll *a*, but carotenoids, but may have had limited photosynthesis as in *Ochromonas*. The rest of Emerson’s talk dealt with how the accessory pigments helped in the evolution of efficient photosynthesis – not only for capturing light not absorbed by chlorophyll *a* but in a different way, as we know now -- through their use in capturing light for the two distinct photosystems I and II. Lastly, Emerson noted that he had not done any experiment on anoxygenic photosynthetic bacteria (see Chapter 6 in Blankenship, 2021, for further information on the mechanism of photosynthesis in such bacteria).

Footnote #1: Experiments on the two-light effect were done by Emerson only after he had failed to understand the “red drop” in the action spectrum of the quantum yield of photosynthesis, as in Emerson and Lewis (1943). Emerson et al. (1956) was his first attempt in *Chlorella* and *Porphyridium*; together with his assistant Ruth Chalmers (who grew algae and did manometry), Carl Cederstrand (who managed the instruments), and Marcia Brody (a graduate student), he explored the “red drop” at 5° C and 20-26° C, and at different light intensities. We recognize that it was here that the first experiments on the use of supplementary light and enhancement of photosynthesis is mentioned. Further, it was here that he suggested that the conclusion of Haxo and Blinks (1950) about inactive chlorophyll (Chl) *a*, in the red region, may have been due to temperature effects and that Chl *a* was fully active and normal at shorter wavelengths! Emerson’s (1957) presentation is a preliminary summary of the (Emerson) Enhancement Effect in *Chlorella* that was published soon thereafter by Emerson et al. (1957) – and led later to provide background for the two-light reaction-two-pigment system concept of photosynthesis. The last presentation (Emerson, 1958) was mainly to show that the “two-light effect” he had discovered had nothing to do with the catalytic blue-light effect Warburg et al. (1957) had reported on—it was a totally different phenomenon.

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Speculations Concerning the Function and Phylogenetic Significance of the Accessory Pigments of Algae

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Special interest attaches to the accessory pigments of algae for two reasons. First, the natural occurrence of the pigments in certain combinations, each peculiar to a phylum or group of phyla, is accepted as evidence that the pigments are taxonomically and phylogenetically significant, but there seems to have been no serious attempt to provide a plausible and comprehensive explanation for the development and survival of the existing combinations of pigments since Tilden (J. E. Tilden, *The Algae and Their Life Relations*, Univ. of Minnesota Press, Minneapolis, 1935). The scheme she devised was in accord with information then available, but there have been important advances in our knowledge of the algal pigments which call for a fresh look at the problem. Second, it is now well established that light absorbed by the accessory pigments can be contributed to photosynthesis with high efficiency, and something is known of the manner in which this contribution is made, but the physiological significance of the different pigment combinations is not clearly understood.

Chlorophyll *a* is common to all autotrophic algae and higher plants. It is always accompanied by other plastid pigments, some of which have been shown to contribute the light energy they absorb to photosynthesis. These include chlorophylls *b* and *c*, the carotenoid fucoxanthol, and the phycobilins phycoerythrin and phycocyanin. We refer to these as accessory pigments. Various carotenoids other than fucoxanthol always accompany chlorophyll, β carotene apparently being as universally distributed among photosynthetic plants as chlorophyll *a* itself. The extent to which light energy absorbed by carotenoids other than fucoxanthol can be contributed to photosynthesis is uncertain, so for the present we are not including them among the accessory pigments.

The primary role as sensitizer of photosynthesis is now usually assigned to chlorophyll *a*, both because of its universal distribution in photosynthetic plants above the bacteria and because of the evidence (from observations on fluorescence) that excitation energy acquired by the accessory pigments through absorption of light can be transferred to the chlorophyll *a*, thus leading to the same excited state of the chlorophyll *a* as that which results from direct absorption of light by the chlorophyll *a* itself. The accessory pigments are believed to act only indirectly in photosynthesis, by absorbing light in various parts of the spectrum and transferring the excitation energy thus acquired to the chlorophyll *a*.

Our measurements of the quantum yield of photosynthesis in longer wave lengths of red light have suggested that the accessory pigments may play a more direct part. Emerson and Lewis showed in 1943 (*Amer. J.*

Bot. 30: 165) that longer wave lengths of red light are utilized for photosynthesis with a relatively low quantum yield. This was surprising, because these wave lengths, being within the red absorption band of chlorophyll *a*, must be expected to bring about the same excited state of chlorophyll *a* as would result from the absorption of shorter wave lengths. The yield of photosynthesis should not depend upon the wave of light which produced the excited state, if the excited state is the same in all cases.

We found (Emerson *et al.*, Proc. Nat. Acad. Sc. 43: 133, 1956) that the range of wave lengths where the yield of photosynthesis is low was different for the red alga *Porphyridium cruentum* and the green alga *Chlorella pyrenoidosa*. *Porphyridium* showed a diminished yield beginning at about 650 m μ . For *Chlorella*, the yield did not begin to decline until about 685 m μ . We thought it possible that the difference might be correlated with the accessory pigments characteristic of these algae.

In *Chlorella*, chlorophyll *a* is accompanied by chlorophyll *b*. Light absorption by chlorophyll *b* probably does not extend as far toward long wave lengths as absorption by the *a* component. Direct observation of the limit of the red absorption band of chlorophyll *b* in live cells is not possible, but estimates based on comparison of the absorption spectra of chlorophylls *a* and *b* in solvents suggest that the wave lengths where the yield of photosynthesis is low are probably beyond the absorption band of the *b* component, and in a region where the *a* component accounts for all the light absorption.

In *Porphyridium*, chlorophyll *a* is accompanied by phycobilins, and there is no chlorophyll *b*. The zone where absorption is attributable to chlorophyll *a* alone must begin where absorption by the phycobilins terminates. The most prominent phycobilin of *Porphyridium* is phycoerythrin. Its absorption probably does not extend beyond 600 m μ . Some phycocyanins are present, but since their concentration is low, they probably do not contribute much to absorption beyond 650 m μ . At wave lengths longer than this, absorption of light must be attributable almost entirely to chlorophyll *a*. This is also the beginning of the region where *Porphyridium* shows a declining yield of photosynthesis.

We speculated that the yield of photosynthesis might be low in long wave lengths because these wave lengths were exciting chlorophyll *a* alone, and that maximum yield of photosynthesis might require excitation not only of the chlorophyll *a*, but also of some accessory pigment having an absorption band on the short-wave side of the red band of chlorophyll *a*. In the case of *Chlorella*, this requirement could be met by chlorophyll *b*, and in *Porphyridium*, by either phycocyanin or phycoerythrin.

We tested this hypothesis by measuring the yield of photosynthesis in two beams of light, to which the cells could be exposed either separately or simultaneously (Emerson, Science 127: 1059, 1958). We found that as long as the wave lengths of both light beams were within the range of absorption by accessory pigments, the yield of photosynthesis for the two wave lengths together was equal to the sum of the yields for the two wave lengths taken separately. But if one of the beams was limited to long wave lengths

of red light which could only be absorbed by chlorophyll *a*, and the other beam provided shorter wave lengths which could be absorbed at least partly by accessory pigments, then the photosynthesis for the two beams given simultaneously exceeded the sum of the yields of the two beams given separately.

We interpreted this to mean that the shorter wave lengths increase the yield from the beam of longer wave lengths. The alternative possibility, that the long wave lengths increase the yield from the shorter wave lengths, seems to us unlikely because in general the yields for the shorter wave lengths alone appear to be maximal, while the yield from the long wave lengths alone is lower than the maximum. By treating the increase due to combination of long and short wave lengths as an increase in the yield from the long wave lengths only, it can be shown that the yield from the long wave lengths approaches the maximum attainable with shorter wave lengths, while interpreting the increase in the opposite way, as an effect of long wave lengths upon the yield from short wave lengths, would lead to yields above the maximum, making this the less probable alternative.

We then compared the effects of different wave lengths upon the yield from a beam of long-wave red of fixed wave length and intensity. To do this, we adjusted the intensity of the beam of shorter wave lengths so that at each wave length setting, this beam by itself gave the same rate of photosynthesis. We found that the effectiveness of the shorter wave lengths in improving the yield from the beam of long-wave red corresponded approximately with the absorption spectrum of the accessory pigment or pigments of the alga being tested. More precisely, the effectiveness varied with the fraction of the absorption of the short-wave beam which could be attributed to the accessory pigment or pigments.

This fraction can be only roughly estimated for live cells, but the regions where it is obviously large are clearly identifiable with maxima in the effectiveness of supplementary light. With *Chlorella*, we found maximum effectiveness of supplementary light at about 480 $m\mu$, a region where absorption by chlorophyll *b* is at its maximum and absorption by chlorophyll *a* is very small. The fraction absorbed by chlorophyll *b* attains its largest value here. There is a lower peak of effectiveness of supplementary light at about 655 $m\mu$, coinciding approximately with the red maximum of chlorophyll *b*. Here absorption by chlorophyll *a* is also considerable, so that the fraction absorbed by the *b* component is much less than at 480 $m\mu$. For *Navicula*, the maximum effectiveness of supplementary light is at about 540 $m\mu$, where fucoxanthol contributes most to absorption, and there is a second smaller maximum in the neighborhood of 645 $m\mu$, probably attributable to the contribution of chlorophyll *c* to the absorption of light. *Anacystis* and *Porphyridium* each show single peaks in effectiveness of supplementary light, near where phycoerythrin and phycoerythrin contribute most to light absorption (at about 600 and 546 $m\mu$, respectively).

The evidence seems clear that at least at long wave lengths of light, full efficiency of photosynthesis is not sustained by excitation of chlorophyll *a* alone, and that simultaneous excitation of some second pigment, with an ab-

sorption band or bands at shorter wave lengths, serves to restore to normal the efficiency of the long wave lengths absorbed only by chlorophyll *a*.

Inevitably, this raises a question in regard to the Chrysophyceae and Xanthophyceae. These algae contain chlorophyll *a*, but lack the common accessory pigments clearly identifiable as photochemical contributors to photosynthesis. Strain (*In* Smith, G. M., ed., *Manual of Phycology*, Waltham, Mass., 1951, chapter 13) lists *Tribonema bombycinum* as containing a new chlorophyll which he designates chlorophyll *e*, but it remains to be seen whether this component will prove to be generally characteristic of the Xanthophyceae and whether it occurs in amounts sufficient to account for an appreciable fraction of the light absorbed. Some of the Chrysophyceae are reported to contain small amounts of fucoxanthol, and it may be present in all members of the group, but it is not yet known whether this pigment can contribute to photosynthesis when it is not accompanied by chlorophyll *c*.

We have tested two Xanthophyceae supplied to us through the kindness of Professor Starr of the University of Indiana (*Polyedriella helvetica* and *Tribonema aequale*) and have failed to find any evidence of effects of supplementary light upon the yield of photosynthesis from longer wave lengths of red. Provisionally, we attribute this to absence of accessory pigments. In the case of *Tribonema*, the quantum yield of photosynthesis seems to be low throughout the spectrum, as if the chlorophyll *a* without accessory pigments were incapable of sustaining a high yield of photosynthesis, either in long wave red or at shorter wave lengths. Many more comparisons must be made with a wider range of algal types before we can have confidence that such a generalization is valid.

We have not yet tested any Chrysophyceae for their response to supplementary light, but we consider it significant that at least one representative of this group (*Ochromonas malhamensis*) seems to show only a limited capacity for photosynthesis (Myers and Graham, *J. Cell. Comp. Physiol.* 47: 397. 1956).

On the basis of the effects of supplementary light which we have described here, we are tempted to sketch a possible sequence of evolution of the combinations of pigments to be found in algae. In agreement with Oparin's premises concerning the origin of life (A. I. Oparin, *The Origin of Life*, Edinburgh, 1957), we suppose that when organisms containing chlorophyll first appeared, organic substances were available in abundance, and evolution of heterotrophic forms of life must have been well advanced. Because of the universal presence of chlorophyll *a* in all photosynthetic plants except bacteria, it is likely that all are derived from a common ancestor containing the *a* component. Since none of the accessory pigments is to be found in all the phyla of photosynthetic algae and higher plants, we may suppose that chlorophyll *a* appeared first without accessory pigments. Throughout the phyla of plants, chlorophyll *a* is always accompanied by β carotene and also by other carotenoids, so that in all probability the earliest organisms containing chlorophyll *a* also contained carotenoids, perhaps exclusive of fucoxanthol. These organisms may have been capable of limited photosynthetic activity such as we can see in the chrys-

ophycean *Ochromonas*. Organic nutrition may have made up for the low photosynthetic efficiency which we suppose to be characteristic of chlorophyll *a* when it is unaccompanied by other active pigments.

We may suppose that organisms containing various pigments in addition to chlorophyll *a* appeared in the course of geologic time and that some of these were capable of supplementing the activity of chlorophyll *a* in such a way that efficient photosynthesis, with production of organic material and oxygen from carbon dioxide and water, could sustain a fully autotrophic mode of life. The various combinations of pigments may have initiated parallel lines of evolution, the end results of which we see today in the different classes of algae.

Our suggestion, that the accessory pigments may endow the photosynthetic system with an effectiveness which it could not have if chlorophyll *a* were the only photosynthetic pigment, seems to offer a plausible explanation for the success of the combination of chlorophylls *a* and *b*. We see that light absorbed by the accessory pigments can extend efficient photosynthesis to longer wave lengths. Possibly, all the light absorbed by chlorophyll *a*—at long and also at short wave lengths—must be supplemented by light absorbed by some accessory pigment in order to sustain maximum yield of photosynthesis. If this is the function served by the accessory pigments, then the farther the absorption of light by the accessory pigment extends towards the red absorption band of chlorophyll *a*, the greater will be the range of wave lengths which can sustain maximum efficiency for the light absorbed by chlorophyll *a*. From this standpoint, chlorophyll *b* should be superior to the other accessory pigments, because the red absorption band of the *b* component is about as close as it can be on the short-wave side of the corresponding band of the *a* component. (We assume that any pigment, such as chlorophyll *d*, with its absorption band on the long-wave side of the *a* component, would be ineffective, because its excited state would be lower than that of chlorophyll *a*). Phycoerythrin, on the other hand, with its absorption extending only to about 600 $m\mu$, makes available the smallest range of wave lengths for sustaining efficient use of red light absorbed by chlorophyll *a*, and phycocyanin is in an intermediate position. Of all the algal groups, the Rhodophyceae are abundant over the smallest part of the earth, while the widespread occurrence of the Myxophyceae, particularly in highly specialized environments, is probably due to broad physiological tolerances not related to pigmentation. The fucoxanthol might offer no greater spectral range than the phycoerythrin were it not for the fact that chlorophyll *c* usually accompanies fucoxanthol, making a combination with chlorophyll *a* which may be as good as, or perhaps better than, the combination of chlorophylls *a* and *b*. Certainly these are the two combinations which are most outstandingly successful—fucoxanthol-chlorophyll *c*-chlorophyll *a* in the oceans, and chlorophyll *a*-chlorophyll *b* on land and in fresh water.

If the carotenoid peridinin of dinoflagellates serves the same function as the fucoxanthol of brown algae and diatoms, then the combination of chlorophylls *a* and *c* with peridinin may be as effective as the combination of fucoxanthol with these two chlorophylls and may contribute to the competitive success of the dinoflagellates.

In contrast, the classical outlook that the value of accessory pigments lies in their capacity to increase absorption of light in parts of the spectrum poorly covered by the absorption bands of chlorophyll *a* does not seem to account for the outstanding success of the combination of chlorophylls *a* and *b*. The *b* component, with its absorption bands closely overlapping those of chlorophyll *a*, hardly increases the range of absorption at all. The combination of chlorophyll *a* with the phycobilins looks most promising from the standpoint of maximum coverage of the visible spectrum with pigment absorption bands, but the more specialized distribution of the organisms for which this pigment combination is characteristic leaves room for doubt whether coverage of the spectrum has been the primary factor in determining the survival value of the accessory pigments.

We have omitted the photosynthetic bacteria from our discussion because the biochemical changes brought about by their photosynthesis seem to be fundamentally different from the biochemistry of photosynthesis as we encounter it in the algae and high plants. The bacteria produce no free oxygen and require hydrogen donors from which hydrogen can be separated at much smaller energy cost than from water—the hydrogen donor for algae and higher plants. The evolutionary position of the photosynthetic bacteria seems to have no direct bearing on the problem of the evolution and function of the accessory pigments of algae and higher plants.

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The Physiological Society of America has instituted a Legacy Society to help individuals make a lasting impact on the Society by including it in their estate planning. If you are interested in arranging a bequest to the PSA Legacy Society, please contact our treasurer, Julie Koester.