

Highlighting Theodor W. Engelmann's “Farbe und Assimilation” [Color and Assimilation]

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Abstract

In 1883, Theodor Wilhelm Engelmann, a German scientist, wrote his essay “color and assimilation” (Ger.: “Farbe und Assimilation”) describing the state of the art in photosynthesis research, his recent findings, and further assumptions based upon his presented results. Nearly 140 years later, many of his assumptions were proven correct. By his still well-known bacteria experiments using aerotactic, heterotrophic bacteria, he identified the chloroplasts as the location in which photosynthesis and oxygen production takes place. Furthermore, by evaluating the effects of different light spectra, he constructed the first action spectra that demonstrated the implication of the “green gap” of chlorophylls. He further posited that accessory photosynthetic pigments existed to extend the absorption range of chlorophyll. Although infrequently cited, his work was foundational for current ecological research of the vertical appearance of algae species within the underwater gradient in light spectrum due to specific harvesting of different light spectra, hence complementary chromatic adaptation of communities. This short retrospective highlights this piece of literature that represents an early step toward our current understanding of ecological competition for light spectra.

Introduction

Underwater light is highly variable in its spectral quality (i.e., color) due to the selective absorption by water molecules, dissolved substances, nonalgal particles, and algae

themselves (Kirk 2010). During their evolution, phototrophic algae adapted to this heterogeneity by taxon-specific equipment with pigments by which the wavelengths of light can be efficiently exploited (Falkowski and Knoll 2007). Due to the different light absorption of these pigments, the available light spectrum affects photosynthetic yield and drives competition of phototrophs but can also enable coexistence if different parts of the light spectrum can be harvested (Stomp et al. 2004).

Today, researchers are well aware of the physiological complexity of photosynthetic processes, but also of the complex role light, as a multitude of resources, plays in ecology. Nevertheless, our current understanding would not be possible without the long journey of scientific investigations within the past centuries.

Although the involvement of light in the production of oxygen by plants was discovered early by Ingen-Housz (1779), it took various investigations until Daubeny (1836) explored how the light spectrum affects the plant responses of greening and movement of leaves, as well as transpiration and photosynthesis. Eight years later, von Mohl (1844) then characterized the presence and structure of chloroplasts. Despite these advances, the location of photosynthesis was still a matter of debate (Pringsheim 1881). Furthermore, photosynthetic reaction pathways (e.g., light and dark reactions or electron transport), associated cellular components (e.g., chloroplast structure or photosystem architecture), and organic compounds involved in photosynthesis (e.g., adenosine triphosphate) were not yet discovered, hence photosynthesis was roughly described as the assimilation of CO₂, production of a carbohydrate, and release

of O₂ under the use of light energy, without the underlying mechanisms known.

At that time, Theodor Wilhelm Engelmann (Fig. 1), a German scientist and musician who lived from 1843 to 1909, introduced novel ideas and investigational methods to shed light on photosynthesis (Drews 2005). By monitoring aerotactic, heterotrophic bacteria to detect O₂ production of phototrophs, he made substantial contributions to the investigation of the location and process of photosynthesis. Engelmann's bacteria experiments (Engelmann 1881) belong to the very first bioassays and are still well known after 140 years. Notably, the work “color and assimilation” (Ger.: “Farbe und Assimilation”) of Engelmann (1883) summarized his and other's recent findings and presented new insight and concepts on that topic (Fig. 2, online accessible at: <https://www.biodiversitylibrary.org/item/104958>). Despite using rudimentary methods, much of his work proved correct and some of his ecological concepts have been picked up through the years and are presently of major scientific interest. Here, I went back to the roots, by investigating the three parts of “color and assimilation,” deriving their main concepts in photosynthesis research, and set them in context of our modern ecological knowledge.

Part I. Assimilation only takes place within the colorful plasma-particles. Ger.: “Assimilation findet nur in den farbstoffhaltigen Plasmatheilchen statt”

At that time, it was unclear whether the process of CO₂ assimilation of phototrophs via



FIG. 1. Portrait of Theodor Wilhelm Engelmann designated as successor of Emil du Bois-Reymond as the chair of physiology at the University of Berlin (Kamen 1986). Wood engraving from approx. 1897 by an unknown artist. Retrieved from the collection of the Utrecht Archives (catalog no. 104527).

photosynthesis (i.e., their light reaction) takes place within the “colorful” chloroplast granules, or if those chloroplasts would only capture the light and then deflect it toward the cytoplasm where the photosynthetic reaction could take place (Pringsheim 1882). In the first part of his publication, Engelmann determined that if photosynthetic cells of algae (e.g., *Spirogyra* sp., *Mesocarpus* sp., *Zygnema cruciatum*) were illuminated, aerotactic bacteria accumulated only near the chloroplast granules, but not near the “uncolored” parts (e.g., stroma, cytoplasm, and vacuoles) of the cell. When illuminating those uncolored parts of the

cells, no response was visible. Moreover, he let the light of both natural (sun) and artificial (gas lamp) sources transmit through either a leaf or extracted chlorophyll solution to test if that might alter the light, which then could trigger a photosynthetic reaction within the uncolored parts of the cells. As this did not occur, Engelmann concluded that the colored chloroplast granules are not only absorbing the light but are also—and solely—responsible for CO₂ assimilation and subsequent O₂ production.

Today, due to scientific and technical progress, we know that the light reaction pathway is located within the thylakoid

membrane lying free in the cytoplasm of prokaryotes or packed within chloroplasts in eukaryotes, proving Engelmann right. However, examples of a few primitive cyanobacteria are known that do not contain thylakoids as separate organelles, but conduct photosynthesis in their cell membrane (Björn 2008). In any case, there is no alteration of the incident light by chloroplasts, by which the beam of light itself could become accessible to other organelles, proving Engelmann right.

Part II. Closer relationship between absorption of light and assimilation. Ger.: “Näherer Zusammenhang zwischen Lichtabsorption und Assimilation”

In the second part of his publication, Engelmann summarized the relationship of light absorption and assimilation of CO₂ through measuring bacterial accumulation. In previous work, he had projected a variety of light spectra on photosynthetic organisms (Fig. 3). Thereby, he partitioned the used light spectra according to the Fraunhofer lines, which are characteristic dips in the spectrum of sun light, hence often used to describe a light spectrum back then. By assessing the photosynthetic reaction as a response to the incident spectrum of light, he was among the earliest scientists monitoring photosynthetic action spectra (i.e., the photosynthetic response to light ascertained over the wavelength range of light; Kirk 2010). Under green light, he found surprisingly lower bacterial accumulation than under red or blue light, related to what is today commonly known as the “green gap” (i.e., the weak absorption of green light by chlorophylls; Björn 2008). He further assessed these action spectra for a variety of differently colored cells: green (e.g., *Sphagnum* sp., *Cladophora* sp., *Scenedesmus* sp.), yellow-brown (*Meliosira* sp., *Navicula* sp., and *Pinnularia* sp.), blue-green (*Oscillatoria* sp. and *Nostoc* sp.), and red cells (*Callithamnion* sp. and *Ceramium* sp.) (Fig. 4). For those cells he detected that a relationship existed between the photosynthetic response (action spectrum) and color of the cell (absorption spectrum) as plots of both over the wavelength of light roughly accord. Hence, Engelmann concluded the

BOTANISCHE ZEITUNG.

Redaction: A. de Bary. L. Just.

Inhalt. Orig.: Th. W. Engelmann, Farbe und Assimilation. — H. G. Reichenbach, Spirantes euphobia. — Litt.: H. Vöchting, Die Bewegungen der Blüten und Früchte. — Sammlung. — Personalnachricht. — Neue Literatur.

Farbe und Assimilation¹⁾.

Von
Th. W. Engelmann.

I. Assimilation findet nur in den farbstoffhaltigen Plasmatheilchen statt.

Seit Ingenhousz 1779 auf Grund seiner bekannten Versuche den Satz aussprach, dass nur grüne Pflanzentheile im Stande seien, fixe Luft zu dephlogistisiren, d. h. Sauerstoff in einer kohlen säurehaltenden Atmosphäre zu entwickeln, ist die Existenz eines absoluten causaln Zusammenhanges zwischen Assimilation und Chlorophyll nahezu unbestritten geblieben. Einzelne Einwürfe wurden widerlegt. Die Thatsache, dass auch manche nicht grüne Laubblätter assimiliren, fand ihre einfache Erklärung im Resultat der mikroskopischen Untersuchung, dass hier echtes Chlorophyll im assimilirenden Blattgewebe vorhanden, aber durch einen anderen Farbstoff für das unbewaffnete Auge verdeckt ist. Wo, wie bei Diatomaceen, Florideen, Oscillarien u. a. auch bei mikroskopischer Prüfung das assimilirende Protoplasma nur einen, nicht grünen, Farbstoff zu enthalten scheint, gelang es, durch chemische Mittel aus dieser gefärbten Masse einen grünen Farbstoff abzusondern, der mit Chlorophyll die grösste Uebereinstimmung zeigte. Hier meinte man, sei das assimilirende Chlorophyll durch einen oder mehrere beigeunte, assimilatorisch unwirksame Farbstoffe maskirt.

Da auch niemals Sauerstoffausscheidung bei farbstofffreien Pflanzen oder Pflanzentheilen hatte nachgewiesen werden können, war man

¹⁾ Weitere Ausführung eines am 27. Juni 1882 in der Sitzung der naturwiss. Abtheilung des „Provinciaal Utrechtsch Genootschap“ gehaltenen Vortrags sowie eines unter obigem Titel in den „Onderzoekingen“ des physiologischen Laboratoriums zu Utrecht VII, p. 209f. 1882 publicirten Aufsatzes.

somit gewiss berechtigt, zwischen Assimilation und Farbstoff, speciell Chlorophyll, einen absoluten Zusammenhang anzunehmen.

Erst in letzter Zeit sind, aufs neue Bedenken gegen diese Annahme erhoben worden. Wie man weiss, glaubt Pringsheim, dass das Chlorophyll nur als Lichtschirm wirke. Es soll durch Absorption der Strahlen, die sonst (nach Pringsh.) eine heftige Oxydation im Protoplasma hervorrufen würden, diese Oxydation hemmen und dadurch der Sauerstoffausscheidung das Uebergewicht verschaffen, die auch ohne den Chlorophyllfarbstoff statthaben könne.

In seiner ersten grossen Abhandlung¹⁾ erklärt sich Pringsheim noch nicht vollkommen deutlich darüber, ob er auch das ungefärbte Protoplasma ausserhalb der Chlorophyllkörper für einen Sitz der Kohlen säurezerlegung halte. Seine Worte können in diesem Sinne aufgefasst werden und sind in der That von vielen in diesem Sinne aufgefasst worden. Auch von mir, der ich alsbald in den mittels der Bacterienmethode inzwischen erhaltenen Ergebnissen eine Widerlegung der Pringsheim'schen Hypothese sehen zu müssen glaubte²⁾. Niemals hatte mit dieser unerhört empfindlichen, die genaueste mikroskopische Localisation gestattenden Methode Sauerstoffentwicklung an anderen als den chlorophyllhaltigen Stellen des Zellenplasmas entdeckt werden können.

In einer unlängst erschienenen Abhandlung³⁾ leugnet nun Pringsheim die Beweiskraft

¹⁾ Ueber Lichtwirkung und Chlorophyllfunction in d. Pflanze. Jahrbücher f. wiss. Botanik, herausg. v. N. Pringsheim. XXI, 1851, S. 285.

²⁾ Neue Methode zur Untersuchung der Sauerstoffausscheidung pflanzlicher und thierischer Organismen. (Bot. Ztg. 1851, Nr. 28. — Onderzoek. etc. VI, 1851, p. 315. — Pflüger's Archiv. XXV, S. 258.

³⁾ Ueber Chlorophyllfunction und Lichtwirkung in der Pflanze. Offenes Schreiben u. s. w. Berlin 1852, S. 101. — Jahrb. f. wiss. Botanik. XIII, Heft 3, 1852.

absorption and photosynthesis (Engelmann 1884). With improved equipment, today's research has turned away from roughly adjusting prismatically dispersed light to Fraunhofer lines and toward the use of higher resolution radiation per respective wavelength (e.g., by high-intensity monochromators; Björn 2008). The measurement of the photosynthetic response does not rely on bacterial aerotaxis anymore, but can be directly measured (e.g., by real-time imaging of photosynthetic O₂ development; Kasai et al. 2019). Yet, the concepts of action spectra, the exemplary “green gap” of chlorophyll absorption, and dependency of photosynthesis on the specific light absorption are still valid.

Part III. Further conclusions. Ger.: “Weitere Folgerungen”

In his final part, Engelmann made several conclusions of his presented work. As he found that the light spectrum has different effects on cells depending on their color, he concluded that there must be more light absorbing substances besides chlorophyll that have a role in photosynthesis. At the time of his work, the function and presence of other photosynthetic (accessory) pigments within a single cell was a matter of debate. In particular, the involvement of phycoerythrin as the predominant red color of *Florideophyceae* and their greenish discoloration after dieback due to presence of chlorophyll was highly disputed (Kylin 1911). Engelmann added to this discussion by claiming that multiple “chromophylls” (Ger.: “Chromophylle,” i.e., pigments) need to be present and involved in photosynthesis. The close relationship of absorption and action spectra indicates their active involvement in photosynthesis rather than simply being present to color the cell. If not involved in photosynthesis, accessory pigments would still attenuate the light reaching the chlorophyll; hence, Engelmann's experiments could never show these specific photosynthetic activities. Furthermore, he highlighted that the high variety of natural cell colors indicted these chromophylls exist as a mixture within the chloroplast granules. In a mixture of green and nongreen chromophylls, the latter ones would then act as “optical sensitizing agents” (Ger.: “optische Sensibilatoren”) and extend the absorption spectrum of the cell. However, this

FIG. 2. Title page of “Farbe und Assimilation” within the journal “Botanische Zeitung” (Engelmann 1883). Printed volume in possession of the Mertz Library of the New York Botanical Garden's collection, retrieved online from the Biodiversity Heritage Library (<https://www.biodiversitylibrary.org/item/104958>).

photosynthetic activity would increase the better the light could be absorbed by the cell. However, this pattern did not hold for red cells, whose absorption differed from their action spectra. The presence of chlorophyll absorption but lower action under blue and red light was revealed decades later by the discovery of photosystem II and I (Fromme and Mathis 2004).

One problem in Engelmann's experimental series was the incomparable application of different light spectra. He aimed to

correct these differences in light intensities by adjusting the lighting's slit width and further ascertained the loss of light due to scattering by comparing colored and uncolored cells. However, due to technical restrictions, it can be assumed that the light spectra treatments were not run under consistent intensities, neither in terms of energy nor quanta. Especially for the adjustment of far-red light under the usage of gas lamps, he discussed problems arising due to its low intensity, as well as a steep increase in

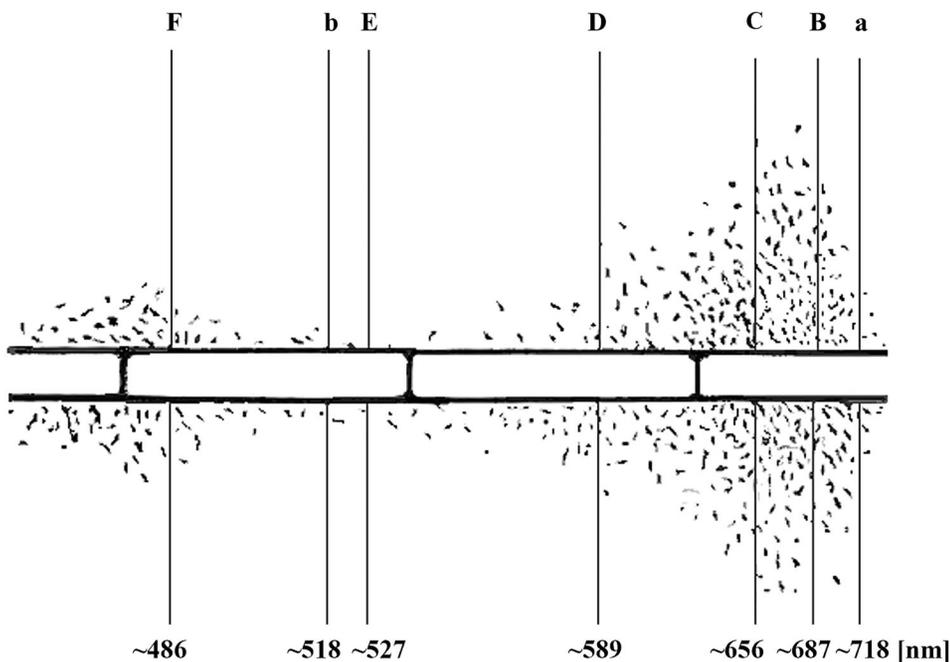


FIG. 3. Engelmann's bacterial experiment on a filamentous chain of *Cladophora* sp. cells. The cells were illuminated with light dispersed using a Zeiss's microspectral apparatus (Engelmann 1888) across the chain according to the Fraunhofer lines (be aware, that the notation of Fraunhofer line *a* as used by Engelmann does not accord to the line *a* referred to today). As the cells were uniformly filled with chloroplasts (not illustrated), aerotactic bacteria accumulated to regions where O_2 was produced, hence photosynthesis must have taken place. Modified after Engelmann (1882).

would not explain the photosynthetic activity of cells of low or nongreen colors. Hence, he concluded all chromophylls are related in the same manner to the photosynthetic reaction.

Today, we know that numerous accessory pigments belong to the chlorophylls, carotenoids and biliproteins (Kirk 2010). Their organization in light harvesting complexes (LHC), often referred to as light harvesting antennae, can be interpreted as a mixture of pigments, but clearly being more complex and indeed taxon-specific. Accessory pigments extend the range of absorption, but further can transport excitation energy, or dissipate excessive energy (Rowan 2011). Yet, they do not play the same role in photosynthesis, and despite obviously different cell colors, chlorophyll *a* takes a ubiquitous role in oxygenic photosynthesis (Croce and van Amerongen 2014). Therefore, even cells without a visible green color can have chlorophyll. Furthermore, there are pigments absorbing the light, hence shaping the cells visible color, which are not actively involved in light harvesting for photosynthesis. Prominent examples are photoprotective pigments within the LHC, such as those involved in the xanthophyll cycle that perform

nonphotochemical quenching, as well as pigments or other light absorbing compounds which (sun-)screen the cell and LHC within (Sinha et al. 1998). Therefore, in part contradicting Engelmann's conclusion, today we know of several other light absorbing substances not involved in photosynthesis, which partly explain the deviations between the absorption and action spectrum.

Finally, Engelmann's findings relate to current research on the vertical distribution of algae, and how this is influenced by their ability to harvest the underwater light spectrum. Within a clear water column, the absorption of light by water molecules themselves shifts the available light spectrum toward becoming bluish (less red and green) with depth (Stomp et al. 2007). According to this gradient in availability of light of certain wavelengths, Engelmann hypothesized that the color of algae (primarily referring to macrophytes) and hence their specific absorption of and photosynthetic response to the color of light, drives their vertical arrangement. Based on findings of Berthold (1882), who investigated macrophyte distribution near Naples (Italy), he compared the estimated light spectrum at a given depth to the species dominating at that depth.

Contrary to Berthold, who suspected that this was driven by the intensity of light at depth, Engelmann found agreement in the species light absorption and spectral gradient with water depth. Therefore, he synthesized that green and blue-green cells were dominant at the surface, yellow-brown cells below and red cells at the bottom of the euphotic zone. By drawing this conclusion, Engelmann initially stated the theory of "complementary chromatic adaption" of photoautotroph communities, in which a local community is shaped and can be predicted by the available spectrum of light in a water column.

Today, we know that not only the intensity of light alone but also its spectral quality drives ecological competition. Thus, the growth of a population of photoautotrophs depends on how efficiently they use the available light spectrum (Kirk 2010). Stomp et al. (2004) found that when in direct competition for light with another species, the spectrum can determine competitive outcomes, whereas spectrum partitioning among species can allow coexistence. However, neither the light's intensities nor their spectrum are the only factors or (co-)limiting resources affecting performance and competition of phototrophs. In this regard, especially nutrient availability (Harpole et al. 2011) but also taxon-specific thermal performances are highly important (Eppley 1972). Furthermore, complexity arises by the phenotypic plasticity of organisms to ontogenetically acclimate to the available light. This was later investigated by Engelmann's student Gaidukov, who observed the acclimation of cyanobacteria toward a complementary absorption of the projected light spectrum (Gaidukov 1903). Hence, the relationship of light spectrum and species occurrence is not trivial to examine and was attempted by various researchers leading to different outcomes (Ramus 1982). Yet, with improved monitoring techniques the relationship of available light spectrum and community composition was specifically observed by Hickman et al. (2009), and can further be related to several observations on taxonomical distribution (Kirk 2010). Finally, it was shown that the underwater light spectrum does not gradually shift with depth, but creates specific gaps and peaks according to the vibrational nodes of water molecules (Stomp et al. 2007, Holtrop et al. 2021). These were found to form ecological niches captured complementary-wise by cyanobacteria and by which the presence of phototrophs can be predicted (Holtrop

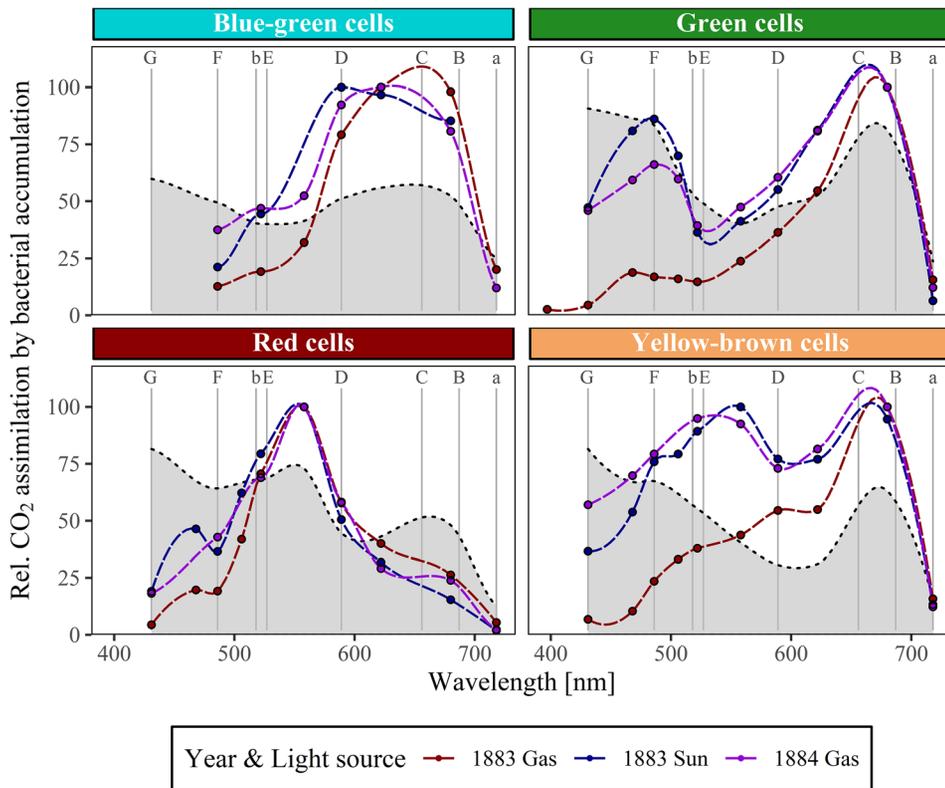


FIG. 4. Action spectra by Engelmann, retrieved from normalized data published in Engelmann (1883, pp. 7–8) as well as Engelmann (1884, p. 91). Gray area displays the absorption spectra of cells. Colored points are the originally measured data points, the dashed lines are fitted by polynomial local regression. Two different light sources were used (gas lamp and sunlight) and dispersed to distinct spectra using a Zeiss’s microspectral apparatus (Engelmann 1888) according to the Fraunhofer lines (be aware, that the notation of Fraunhofer line *a* as used by Engelmann does not accord to the line *a* referred to today). For red cells, the response to sunlight in 1883 was calculated by Engelmann based on gas lamp results, due to a lack of sunlight. There, and additionally in the experiment series of 1884, no sunlight measurements were available due to the “constant disfavor of the Dutch sky.” The description of Engelmann (1884) was used for conversion of Fraunhofer lines to wavelengths.

et al. 2021). Therefore, ecological outcomes and community structures in natural ecosystems are inextricably governed by various environmental factors and resources, other species traits, and trophic interactions, but Engelmann’s nearly 140 years old concept of complementary chromatic adaption is still a veritable prerequisite for our current ecological understanding.

Conclusion

Theodor Wilhelm Engelmann had a substantial impact on the investigation of photosynthesis. He not only concluded where this process takes place within photosynthetic cells, but further found that due to the taxon-specific equipment with accessory pigments, photosynthetic activity depends on its complementarity to the wavelengths of available light. Nearly 140 years ago and long before the description of the competitive exclusion principle and the

concept of ecological niches (Pocheville 2015), and without knowing physiological details of the photosynthetic apparatus (Croce and van Amerongen 2014) concomitant to specific underwater light absorption (Stomp et al. 2007, Holtrop et al. 2021), Engelmann was the first to predict the occurrence of species under different light spectra. This highlights not only the advance of Engelmann’s work, but further the importance for today’s scientists to be aware of the foundational studies in their field to provide context for future research.

Acknowledgments

I thank the Biodiversity Heritage Library (<https://www.biodiversitylibrary.org>) for the conservation and provision of historical scientific work. Without their efforts, most of the sources used in here would become inaccessible and forgotten in today’s internet-era.

I also thank the editors for their constructive comments on the manuscript.

Open access funding enabled and organized by Projekt DEAL.

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