

Lecture 7: Chromatic Adaptation

Smit, A. J.

University of the Western Cape

Table of contents

1	Introduction: Development of the Theory of Chromatic Adaptation	2
2	Early Observations: Anders Ørsted	3
3	Theodor Engelmann and Chromatic Adaptation Theory	4
4	Engelmann's Experimental Design	5
4.1	Action Spectrum Demonstration	8
5	Implications and Predictions	9
6	Moving Forward	10
7	Revisiting Engelmann's Work	11
8	Green Algae: Action and Absorption Spectra	13
9	The Role of Accessory Pigments in Brown Algae	14
10	Red Algae: Patterns, Anomalies, and the Emerson Enhancement Effect	16
11	From Engelmann to Haxo and Blinks: Confirmation and Caution	17
12	Chromatic Adaptation and Vertical Distribution: Theory and Reality	19
13	Towards an Explanation	20
14	<i>In Situ</i> Experiments on Seaweed Acclimatisation	20
14.1	Experimental Design	21
14.2	Comparing Functional Forms and Light Adaptation	23
14.3	Surface Area to Volume Effects	24
14.4	Transplant Experiments: Shallow vs Deep	25
14.5	Acclimatisation Mechanisms and Plasticity	28
14.6	<i>Codium</i> 's Distinctive Behaviour	29
14.7	Structural and Optical Differences: <i>Ulva</i> vs <i>Codium</i>	30
15	Conclusion	34
	Bibliography	34

💡 Content

- Discuss the importance of light in photosynthesis and the different types of pigments involved.
- Explain the concept of light compensation point and light saturation point.

💡 Aims

The lecture will focus on the importance of light for photosynthesis, exploring the different types of pigments involved and physiological concepts such as the light compensation point and light saturation point.

📘 Reading

- Saffo, M. B. (1987). New light on seaweeds. *Bioscience*, 37(9), 654-664.
- Ramus, J., Beale, S. I., & Mauzerall, D. (1976). Correlation of changes in pigment content with photosynthetic capacity of seaweeds as a function of water depth. *Marine Biology*, 37(3), 231-238.
- Ramus, J., Beale, S. I., Mauzerall, D., & Howard, K. L. (1976). Changes in photosynthetic pigment concentration in seaweeds as a function of water depth. *Marine Biology*, 37(3), 223-229.



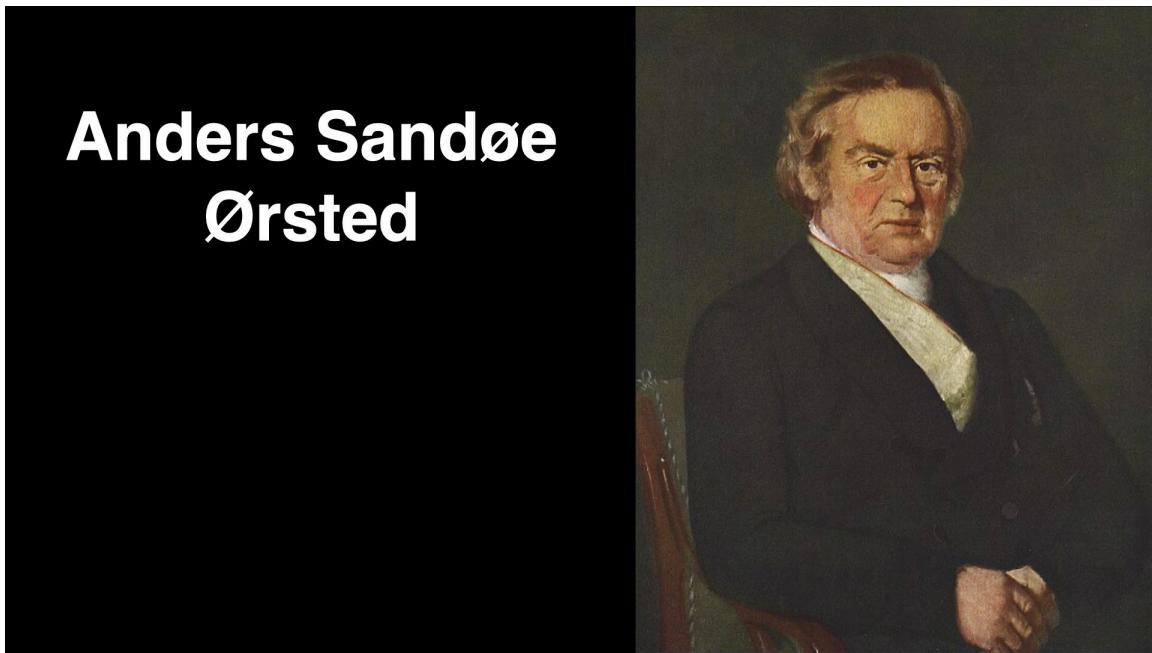
1 Introduction: Development of the Theory of Chromatic Adaptation

Welcome back again. Today, we're going to be talking about the development of the theory of chromatic adaptation. This is an interesting story that offers insight into how science evolves, and it demonstrates that over a span of about 150 to 170 years, our understanding of how plants adapt to a variable light environment—in terms of both quality and quantity of light—has changed significantly. These shifts in thinking resulted from the accumulation of different forms of evidence, the

advent of new technologies allowing for diverse methods of measurement, and the gradual building up of empirical data over the years.

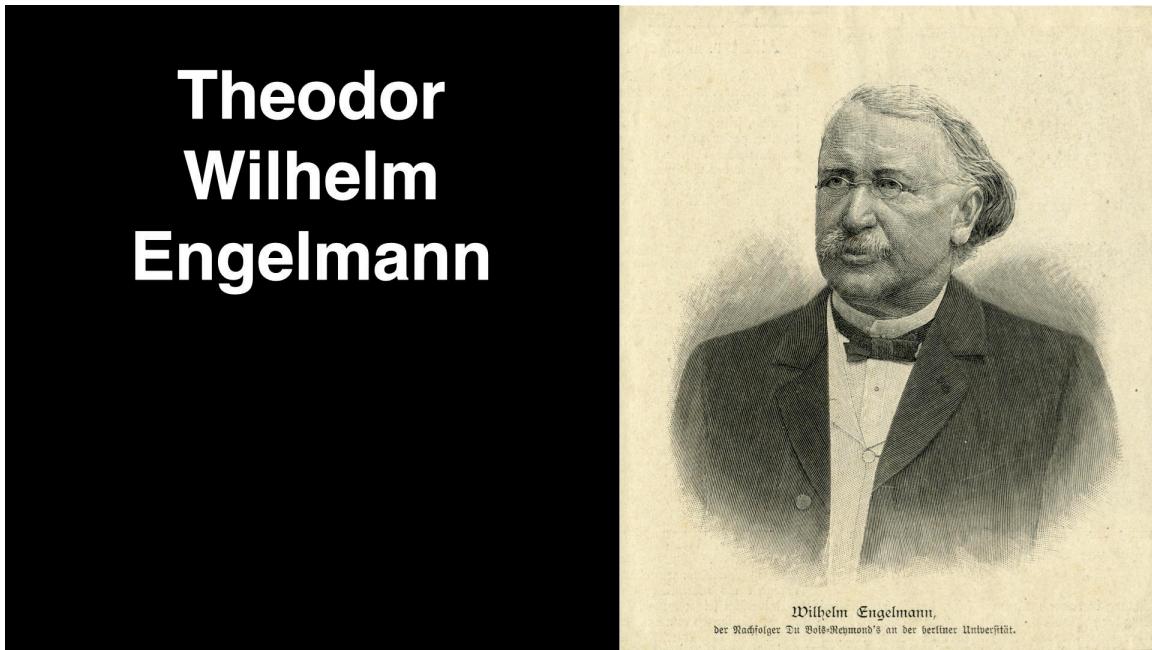
Let us explore some of the key contributors to our theories surrounding chromatic adaptation.

2 Early Observations: Anders Ørsted



The story begins in the mid-19th century with Anders Ørsted. In 1843, Ørsted observed that seaweeds come in different colours: green, brown, and red. Today we refer to these as the Chlorophyta (green algae), Phaeophyta (brown algae), and Rhodophyta (red algae). Ørsted noted this colour variation and postulated that perhaps it was related to where seaweeds live in the ocean—that their colours might correlate with their specific habitats.

3 Theodor Engelmann and Chromatic Adaptation Theory



Building on Ørsted's observations, Theodor Engelmann published his theories around 1881 to 1883. Engelmann's primary question was: "Does light quality—the colour of light—affect the vertical distribution of different seaweeds in the ocean?" He hypothesised that because red and blue lights are most prevalent in shallow waters, green algae, being able to absorb these wavelengths most effectively, would be abundant there. In contrast, in intermediate water depths where green light predominates, brown algae—capable of absorbing green light—would be found. Deeper down, where only dim blue light remains, red algae, with pigments that can absorb blue light, would become dominant.

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

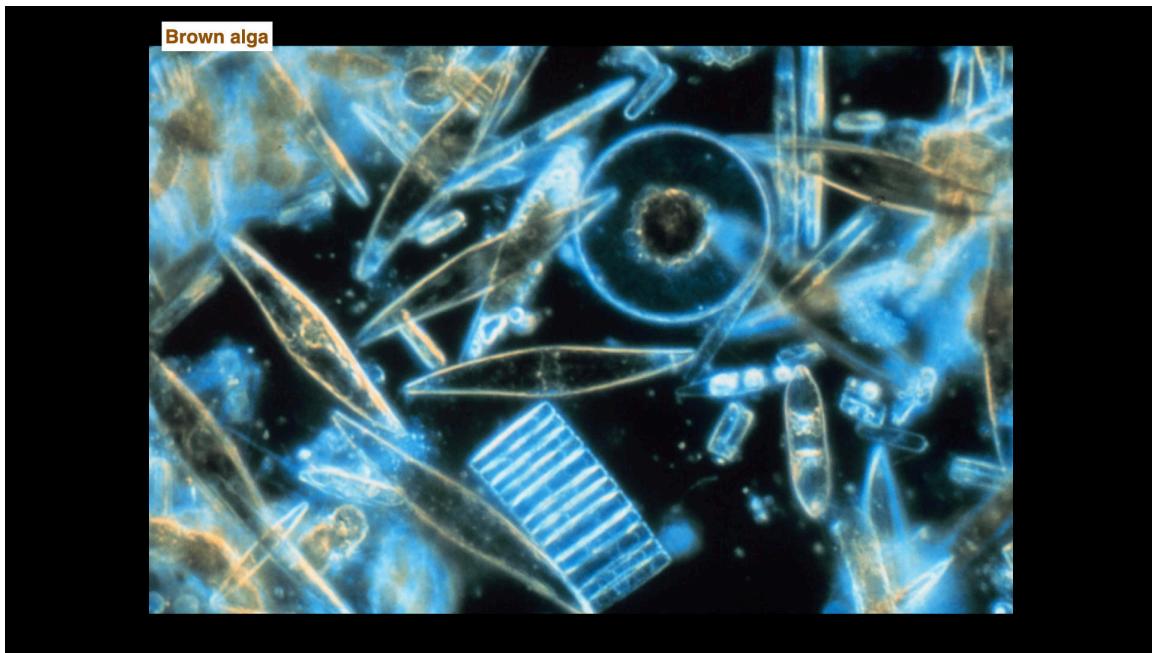
Mary Beth Saffo

- Anders Ørsted (1844): green < brown < red
- Theodore Engelmann noted that light changes in quality, quantity with depth.
- Noted that seaweeds come in different colours, and remembered Ørsted.
- Could light quality affect seaweed distribution?
- Engelmann measured the action spectra of seaweeds (1883).
- Hypotheses:
 - Red light is most abundant at shallow depths, and so the greens would be most abundant in shallow waters.
 - Using similar logic he hypothesised that browns would occur at intermediate depths ...
 - ... and reds the deepest down.
 - This hypothesis seems reasonable.

On paper, this seems a reasonable hypothesis—even today, many might formulate similar conjectures without access to contemporary evidence. Engelmann sought to test this hypothesis experimentally.

4 Engelmann's Experimental Design



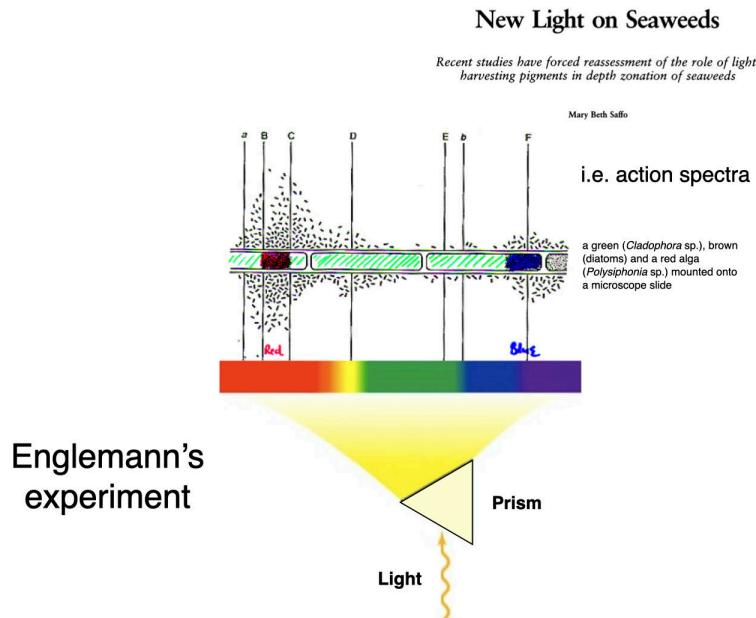


Polysiphonia brodeli (Dillwyn) Sprengel
Killkee, Co. Clare, Ireland; mid-shore rock pools
© M.D. Guiry
[Download](#)

CLOSE X



Engelmann's clever experiment utilised a prism, constructed by Carl Zeiss—a leading figure in optics at the time. Zeiss's company, known for its lenses and microscopes, continues to exist. Engelmann used the prism to split white light into its constituent spectral colours, ranging from red to blue, which he then projected onto a microscope slide.



On this slide, along the gradient of coloured light, he positioned different algae: a green alga (for example, *Cladophora*, though Engelmann used a species within this genus), a brown alga (unicellular

diatoms, known for their xanthophyll pigments and golden-brown hue), and a red alga (such as the filamentous *Polysiphonia*, which contains phycobiliproteins like phycocyanin and phycoerythrin).

In the watery medium surrounding the algae, Engelmann introduced aerotactic bacteria—organisms attracted to regions with the highest oxygen concentration. The premise was that as each type of alga was exposed to a spectrum of light, photosynthesis would occur most efficiently at wavelengths suited to its pigments. The bacteria would congregate where oxygen (a byproduct of photosynthesis) was produced most abundantly, thereby indicating which regions of the light spectrum promoted photosynthesis for each algal type.

4.1 Action Spectrum Demonstration

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

- Results of Engelmann's experiment:
 - The green alga is best at photosynthesising in red (and blue) wavelengths ...
 - The brown alga can photosynthesise better than green algae in the green - yellow wavelengths.
 - Red pigments effectively absorb green light.

Engelmann observed, for example, that in green algae—containing primarily chlorophyll-*a* (and to a lesser extent, chlorophyll-*b*)—the bacteria accumulated at two main peaks along the slide: those corresponding to red and blue light. This demonstrated, for the first time, an action spectrum—the relationship between wavelength and photosynthetic activity—though Engelmann did not yet reference absorption spectra (as you'll see later with the work of Haxo and Blinks).

He also performed this experiment with brown algae and red algae. In these cases, thanks to their accessory pigments (xanthophylls in browns, phycobilins in reds), photosynthesis also occurred in the green gap region where chlorophyll-*a* is ineffective. Bacteria correspondingly accumulated in the wavelengths that these accessory pigments absorb.

5 Implications and Predictions

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

- Therefore Ørsted's predictions seemed to have been explained by Englemann (Case II waters):
 - **Green algae are best at photosynthesising in red (and blue) wavelengths.** Red light is rapidly diminished with depth limiting the alga's occurrence to shallower waters (according to Engelmann's reasoning).
 - **The brown algae can photosynthesise better than green algae in the green-yellow wavelengths.** This is the range that penetrates to the intermediate depths, and brown algae have brown pigments that absorb this wavelength (green) best.
 - **Red algae effectively absorb blue/green light.** The reds should be able to live deepest because they have red pigments which effectively absorb blue/green light which penetrates furthest in coastal water.

Engelmann's results seemed to experimentally confirm Ørsted's reasoning from 1844, stating that green algae photosynthesise most effectively in red and blue light. Consequently, Engelmann argued that green algae should be most abundant in shallow oceanic waters, where red and blue light penetrate deeply. Red light is quickly attenuated with depth, thus restricting green algae to shallower regions.

He reasoned that brown algae, with their ability to exploit greenish wavelengths due to xanthophylls, would be most successful at intermediate depths. Meanwhile, red algae—able to use blue light particularly efficiently—would dominate the deeper ocean, where blue and green light are most available.

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

- Experimental evidence for Engelmann's hypothesis:
 - Engelmann's hypothesis was accepted as fact and repeatedly used in textbooks. The work of Haxo and Blinks (1950), who measured algal action and absorption spectra to determine which pigments are active during photosynthesis, provided further 'confirmation' of Engleemann's work. The 'theory' of **complementary chromatic adaptation** was born.

At the time, no one had directly surveyed seaweed distribution by colour at different depths, but the experimental and theoretical framework appeared solid. For decades, Engelmann's work underpinned ecological thinking about seaweed vertical distribution—even as recently as the 1980s and 1990s, some zoologists continued to teach this narrative as fact.

6 Moving Forward

As we shall see in the next lecture, later work by Haxo and Blinks provided further evidence for this mode of thinking. However, more recent research began to challenge this story, signalling the emergence of a different understanding—a topic we will discuss in more detail in due course.

7 Revisiting Engelmann's Work

Jour Pl Sci Res 38 (2) 449-454 2022
Letter to the Editor

Francis Theodore Haxo (March 9, 1921–June 10, 2010): Innovator, Dedicated Biologist, and Grand Master of the Carotenoids in Marine Organisms

Govindjee Govindjee* and Anitra Thorhaug*

*Department of Plant Biology, Department of Biochemistry, and Center of Biophysics, University of Illinois at Urbana-Champaign (UIUC), Urbana, Illinois, USA.
†Greater Caribbean Energy and Environment Foundation, 1359 SW 22 Terrace, Suite 1 Miami, FL, USA.

*Corresponding author e-mail: gov@illinois.edu

Francis Haxo has been known to us as a thoughtful, patient, and dedicated scientist of the highest order. As a genuine scholar, he meticulously mulled over ideas for years before publishing his research. One of us (GG) knew him through three other friends: Barbara B. Przelin, 1948–2021; David (Dave) C. Fork, 1929–2020; Beatrice M. Sweeney, 1914–1989; additionally, Anitra Thorhaug (AT) knew him as she was his last student. Lawrence Blinks, with whom Haxo had worked with, Francis Haxo gave credit to him for his work, but he took no credit for it. He did however, in his will, ensure that all was well. We provide here a glimpse of his research after a brief note on his personal life—remembering him more than a decade after his death. He was an unsung hero and he deserves to be remembered by algal, marine, and plant biologists throughout the world. A thorough and detailed memorial to Francis Haxo and his research, will soon be published by Anitra Thorhaug, Graeme Berlyn, and Synnøve Liane-Jensen (2023).

Keywords: Lawrence Blinks, Algal pigments, Carotenoids, Beatrice Sweeney, Circadian rhythms, *Neurospora*, polarography, Stanford University, Scripps Institution of Oceanography.

PERSONAL LIFE

Francis Theodore Haxo was born on March 9, 1921, in Grand Forks, North Dakota. In 1941, he obtained his BS (Biology) from the University of North Dakota. Francis married Nan Bolander in 1946; they had 2 children, and divorced in the mid-1950s. In 1961, he married Judith McLaughlin, with whom he had 3 children. Francis died of pneumonia on June 10, 2010, in San Diego/La Jolla, California. Figure 1 shows a photograph of F. T. Haxo aged about 50.

ACADEMIC LIFE AND RESEARCH: PRE-1960 PERIOD

In 1937, Francis graduated from Central High School in Grand Forks, North Dakota. In 1941, he obtained his BS (Biology) from the University of North Dakota, the state's oldest and largest university. Then, during

DOI: <https://doi.org/10.32381/JPSR.2022.38.02.1>



Fig. 1: A 1970s photograph of Francis T. Haxo taken at Brewster Hall, the Biological Sciences Building, as a professor at the Scripps Institution of Oceanography. Source: <https://library.ucsd.edu/dc/object/bb12638600/zoom/8>

Figure

1:

130 Photosynth Res (2009) 100:129–141

Lawrence Rogers Blinks

two different pigments, gave higher rates than the sum of photosynthesis in the two beans grown separately (see Emerson and Rabinowitch 1960; Govindjee and Rabinowitch 1960). These were later explained in terms of two separate photosystems and two light reactions. Myers and Packer (1960) also found the same effect as the Emerson effect in the same organism, *Chlorella*, and concluded that both these effects were caused by the same phenomenon, photosynthesis enhancement. (Also see comments on this topic below.) In addition to the Emerson effect, as well as comments by two scientists (not cited) Haxo and Blinks (1950) had earlier found through measuring the action spectra of a number of red algae that light absorbed by phycoerythrin was far more effective in light harvesting for photosynthesis than light absorbed by chlorophyll *a*. Davies (1952) then proposed two forms of chlorophyll *a* fluorescence that received excitation energy from phycoerythrin, and the other that was non-fluorescent. This non-fluorescent chlorophyll *a*, later found to be largely attached to Photosystem I, was active in oxygen evolution only in conjunction with the associated form of chlorophyll *a* that was associated with photosystem II.

In this tribute, we also present Blinks's non-photosynthesis research contributions to science and institution building especially his substantial research contributions to monsoon and ion pumping. For Blinks's non-photosynthesis research, we have cited extensive photochemical reviews by others including an extensive remembrance written for this tribute by Francis Haxo, a colleague and postdoctoral associate of Blinks during the critical action spectra measurements and pigment photosynthetic work.

Figure 1 shows a photograph of Blinks in his later years, whereas Fig. 2 shows him in his early middle years at his algae incubation tanks at the Hopkins Marine Station.

The 2006 symposium in California

During the centennial celebration of the Botanical Society of America in Chico, California (August 1, 2006), a symposium honored Lawrence Rogers Blinks (1900–1989) and his colleagues in algal ecology and physiology. A series of tributes in memory of Blinks were presented at the symposium. Below is a tribute to his work in photosynthesis assessed by his colleagues, which does not fully address his appreciable contribution to algal eophysiology and ion transport systems. The information presented in this tribute to Blinks is obtained partially from the information presented at the Symposium sponsored jointly by the Physiological and the Phycological sections of the Botanical Society of America, "A Tribute to L.R. Blinks," which included substantive



Fig. 1 Lawrence R. Blinks in his later years in his laboratory at the Hopkins Marine Station of Stanford University after his retirement from Stanford (Source: Library of the Hopkins Marine Station of Stanford University, Pacific Grove, CA)



Fig. 2 Lawrence R. Blinks with his alga cultivation tanks at Hopkins Marine Station of Stanford University in Pacific Grove, California (Source: same as that for—Fig. 1)

Continuing with our narrative on chromatic adaptation, let us turn our attention to some of the research undertaken by Haxo and Blinks, which was carried out approximately 50 or 60 years after Engelmann's initial experiments. They were able to repeat similar experiments to those of Engelmann, but with the benefit of more modern technological advancements. Specifically, they had access to laboratory-built devices capable of precisely generating monochromatic spectra of light.

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

- To construct an action spectrum, photosynthetic measurements are taken at equal incident light intensities (photon fluence rates) at different wavelengths (i.e., using monochromatic light). Haxo and Blinks then thought to **correlate these with the cell or thallus absorption spectra** which resulted in their breakthrough.

In their studies, Haxo and Blinks used a variety of red, brown, and green seaweeds—akin to Engelmann's approach. However, they extended the methodology by examining not only the action spectra, but also the absorption spectra of both intact thalli and pigment extracts from the different seaweeds. As a result, they utilised three distinct lines of evidence in tandem: action spectra, absorption spectra from intact tissue, and spectra from pigment extracts. Engelmann had primarily focused on action spectra, whereas Haxo and Blinks introduced this more differentiated and integrated approach.

Based on their accumulating evidence, they drew several novel conclusions.

8 Green Algae: Action and Absorption Spectra

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

- Haxo and Blinks' results (green algae):
 - Thallus absorption best in **blue** (428.5 nm) and **red** (660.5 nm) regions, i.e. the same as that of chl-a (action and absorption spectra correlated).
 - This closely matches the action spectrum determined for green algae, so that photosynthesis is maximal when grown in blue or red light.

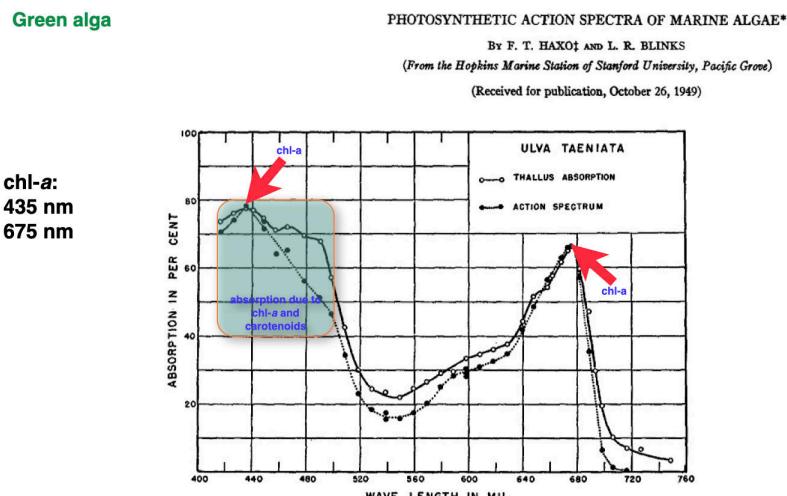


FIG. 8. Absorption spectrum of the green alga *Ulva taeniorhiza* (taken in the apparatus shown in Fig. 5). The photosynthetic action spectrum, corrected to relative rates for equal incident quanta, has been made to coincide with the former at 675 $m\mu$; the correspondence through the rest of the spectrum is then good. Deviations suggest inactive absorption.

When conducting experiments on green algae, Haxo and Blinks found that the thallus absorbs light most efficiently in the zones of blue light, approximately 430 nanometres, as well as in the red light region. The absorption spectrum of the thallus closely resembled that obtained from a chlorophyll-*a* extract.

Additionally, the absorption spectrum in the thallus matched very closely the action spectrum established for green algae. Whereas Engelmann's methods relied on the movement of aerotactic bacteria as an indirect measure of photosynthesis, Haxo and Blinks directly measured photosynthetic rates.

For green algae, their findings were represented on a graph: the absorption peak for chlorophyll-*a* appears in the blue light region, as well as in the red. The solid line, marked with open circles, depicts the absorption spectrum, i.e., the extent to which the thallus absorbs light at the tested wavelengths. The dotted line illustrates the action spectrum—the rate of photosynthesis across those wavelengths. Strikingly, at the peaks of chlorophyll-*a* absorption—in both the blue and red regions—the action and absorption spectra are almost identical.

However, there exists a significant discrepancy in the region from approximately 460 to 500 nanometres. In this region, carotenoids, principally beta-carotene, play a key role by absorbing light inaccessible to chlorophyll-*a* alone, passing that energy to chlorophyll-*a*, and thus facilitating photosynthesis at those wavelengths. This effect highlights the vital function of accessory pigments such as carotenoids, enabling photosynthetic activity in spectra where chlorophyll-*a* would otherwise be ineffective.

9 The Role of Accessory Pigments in Brown Algae

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Sallo

- Haxo and Blinks' results (**brown algae**):
 - The main accessory pigment is the xanthophyll, fucoxanthin, resulting in this group's characteristic brown colour.
 - Having fucoxanthin improves the alga's ability somewhat to absorb light in the green to yellowish region (500 - 560 nm). The presence of chl-*c* helps with absorption in the 630 nm region.
 - Some members are also optically black.

Brown alga

PHOTOSYNTHETIC ACTION SPECTRA OF MARINE ALGAE*

By F. T. HAXO† AND L. R. BLINKS

(From the Hopkins Marine Station of Stanford University, Pacific Grove)

(Received for publication, October 26, 1949)

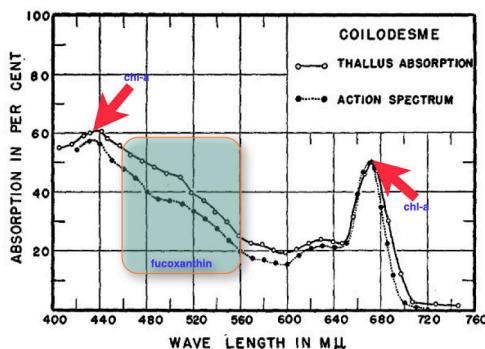


FIG. 11. Absorption and action spectra of the brown alga *Coelodesme californica*. The curves, having been made to coincide at 675 m μ , show only minor divergences elsewhere. The high activity in the region 500 to 560 m μ suggests the participation of fucoxanthin.

Similar experiments with brown algae showed that the dominant accessory pigments are xanthophylls, particularly fucoxanthin, which give these seaweeds their distinctive colour. Fucoxanthin enhances absorption in the green to yellowish part of the spectrum—between 500 and 560 nanometres. The presence of chlorophyll-c also contributes to absorption at around 630 nanometres.

Some brown algal species accumulate so much chlorophyll-c that they appear almost “optically black,” meaning they are nearly opaque to all light—a phenomenon we will discuss in more detail later.

In summary, peaks persist in both the blue and red regions (where chlorophyll-a absorbs maximally). However, in the so-called “green gap” region—which would otherwise show limited absorption were it not for accessory pigments—the presence of fucoxanthin allows light capture, thereby enabling chlorophyll-a to drive photosynthesis in the green to yellowish region. Xanthophylls, primarily fucoxanthin in this context, expand the functional spectral range available to brown algae.

10 Red Algae: Patterns, Anomalies, and the Emerson Enhancement Effect

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

- Haxo and Blinks' results (**red algae**):
 - Absorption in the green gap region is filled by the presence of phycobiliproteins. These pigments give reds their red colour.
 - Notice that the action/absorption spectra for *Scizymenia pacifica* differ markedly from that of *Ulva* and *Colloidesme* in that maximal photosynthesis occurs in the area between 500 - 570 nm (absorbed by the phycobiliproteins), and that chl-a is 'inactive' in the red and blue parts (the red drop and blue drop). Why? Basically, because photosynthesis takes place in two photosystems, the Emerson enhancement effect, etc. (there's a lot more to this explanation...).

Figure

2:

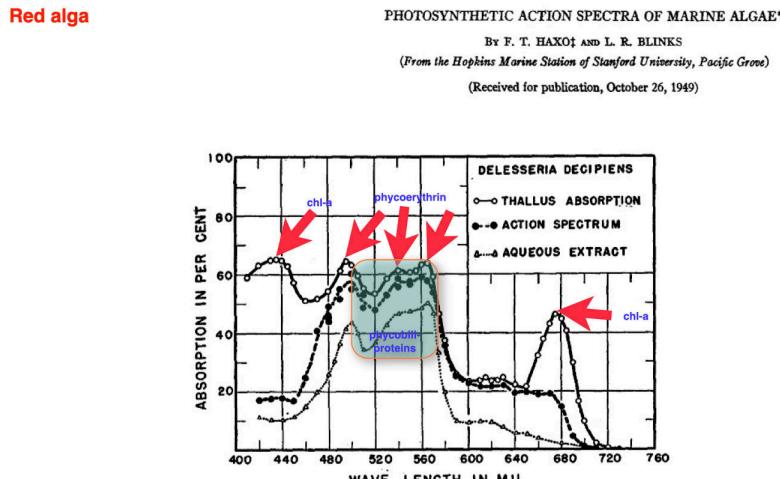


FIG. 20. Absorption and action spectra of *Delesseria decipiens*. This is a very red thallus, with a minimum of phycocyanin, and a somewhat low chlorophyll peak in the red. The action spectrum rather closely parallels the absorption of the aqueous extract (largely phycoerythrin).

Red seaweeds demonstrate a broadly similar pattern, with absorption and action spectra matching closely except for a notable anomaly between 500 and 570 nanometres. An explanation for this only surfaced later, and you are not expected to master it at this stage. This is known as the Emerson enhancement effect: a complex photophysiological response observable primarily in red algae.

Emerson Enhancement Effect in Chloroplast Reactions^{1, 2}

Rajni Govindjee³, Govindjee,

Department of Botany, University of Illinois, Urbana

and George Hoch

RIAS, Baltimore, Maryland

Plant Physiol., 1964; 39(1): 10–14.

“We depend upon photosynthesis and photosynthesis depends upon Govindjee.”

Overall, the major divergence between the absorption and action spectra at particular peaks is attributable to this phenomenon. For deeper exploration, seminal literature exists, such as the 1964 publication by Govindjee (often cited simply as “Govindjee”), one of the preeminent figures in photosynthesis research. If you wish to read further on the Emerson enhancement effect, consult works by Rajni Govindjee and Govindjee.

11 From Engelmann to Haxo and Blinks: Confirmation and Caution

Conclusion of Haxo and Blinks' work:

“Further, there was a general correspondence between light absorption and photosynthetic rate at a given wavelength. In green and brown algae, for instance, the action spectrum of photosynthetic rates mimicked closely the absorption spectrum across the entire visible spectrum—the greater the absorption at a particular wavelength, the greater the photosynthetic rate. The action spectra of red algae mimicked absorption spectra at 500–675 nm, but not at the outermost reaches (400–500 nm and 675–750 nm) of the visible spectrum. While the incomplete correspondence between action spectra and absorption spectra in red algae was puzzling (an anomaly that ultimately served as evidence for a two-photosystem electron transfer mechanism in photosynthesis), the work of Haxo and Blinks was generally interpreted as a definitive, modern confirmation of Engelmann's hypothesis.”

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

BioScience, Vol. 37, No. 9. (Oct., 1987), pp. 654–664.

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

Haxo and Blinks draw more cautious conclusions about the consequences for vertical distributional trends seen in seaweeds, but state:

"In view of the photosynthetic effectiveness of the phycobilins it would seem logical to assume that the present vertical distribution of red algae has been influenced, at least in part, by this capacity and that some species have been thus enabled to extend their distribution to depths not readily penetrated by other algae. The fact that other algae may also be found at great depths or that red algae are also to be found in shallower waters in no way alters this possibility. Obviously the distribution of algae is influenced by many factors each of which must be considered."

Fundamentally, the work of Haxo and Blinks provides modern and more definitive confirmation of Engelmann's earlier findings, as noted in subsequent review papers by authors such as Mary Beth Saffo . However, the conclusions drawn by Haxo and Blinks are somewhat more measured regarding the vertical distribution of seaweeds.

In the case of red algae, where phycobilins function as accessory pigments, they conclude that it is logical to assume the current vertical distribution of red algae is influenced, at least in part, by the photosynthetic effectiveness conferred by phycobilins. This enables some species to extend their distribution to depths inaccessible to other algae. Essentially, red algae—by virtue of their red pigment, which can absorb blue light—are able to survive further down the water column. Nevertheless, they note that other algal groups, such as greens and browns, are also located at considerable depths, and red algae are present even in shallow waters.

12 Chromatic Adaptation and Vertical Distribution: Theory and Reality

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

- But are Engelmann's conclusions valid?
- Engelmann's hypothesis attracted its first criticism in 1905 when Oltmanns noted that "*Engelmann's Hypothesis is very plausible, and the water colour may affect the struggle for existence under certain conditions, but I know of no certain observations which really prove it*".
- Mounting empirical evidence also suggests that Engelmann's hypothesis is generally not true.

This real-world evidence introduces a measure of doubt to the hypothesis that green algae occupy shallow waters, red algae deep waters, and brown algae intermediate depths. Observational data show substantial overlap among all three groups regarding both minimum and maximum depth ranges. For instance, even though red algae are documented as extending down to roughly 160 metres (as per a 1974 publication), more recent discoveries have shown a green alga at what is currently the deepest recorded distribution for any seaweed [attention].

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

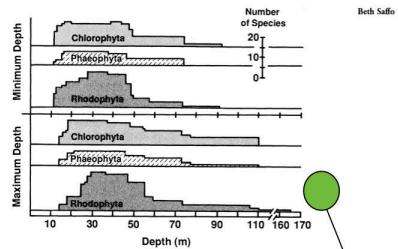


Figure 5. Comparison of the depth distributions of chlorophyte, phaeophyte, and rhodophyte species collected off the coast of the Hawaiian Islands, at 10–165-meter depths. There is no significant difference in the overall depth distribution of the 101 species of chlorophytes, phaeophytes, and rhodophytes studied. Although in this case the two deepest-dwelling seaweeds (at 120–165 m) were rhodophytes, earlier collections from Hawaii also yielded two species of green algae from such depths [Dosty et al. 1974].

The deepest occurring alga is *Cladophora* sp. which was found attached to bedrock at a depth of 212 meters off Hawaii and it is indeed a green alga (Cladophoraceae).

Such empirical data suggest that the theoretical framework of chromatic adaptation—namely, that a seaweed's pigment determines its depth distribution—does not hold up against actual observations. Instead, pigmentation seems not to be reliably indicative of environment, nor a sole determinant of where a species is found.

13 Towards an Explanation

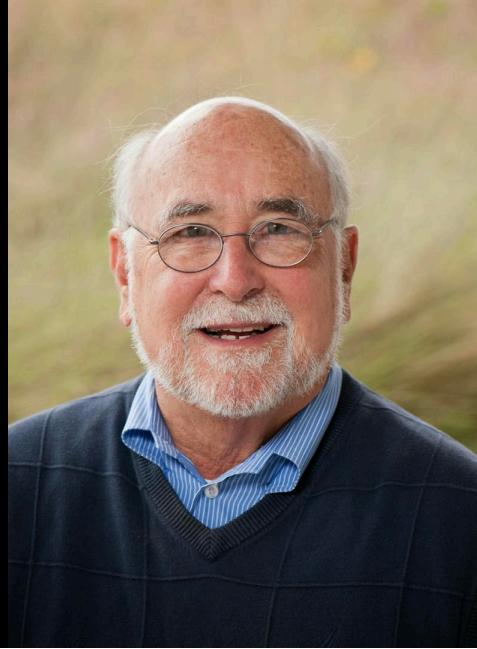
Thus, the chromatic adaptation theory does not adequately explain the actual vertical distribution of seaweeds. To gain a clearer understanding of what does underlie these patterns, we must examine further research, especially the work of Rosenberg and Ramus, which will form the subject of our next lecture.

14 In Situ Experiments on Seaweed Acclimatisation

Right, so now we're going to look at the third part of our series of lectures on chromatic adaptation and, this time, we're going to examine some *in situ* experiments that explore how seaweeds adapt—or more accurately, acclimatise—to different light regimes within the ocean. This is a very different approach compared to the earlier studies by Engelmann, Haxo, and Blinks, all of whom relied on laboratory studies, isolating seaweeds from the ambient environment and failing to explore how they respond adaptively or acclimatise to changing environmental conditions. This is where Rosenberg and Ramus's work is quite distinct.

Joseph S. Ramus

with G. Rosenberg (no image)



Specifically, we will focus on experiments by John Ramus from the late 1970s, which are rather fascinating in their design. Ramus investigated acclimatisation as a process whereby seaweeds, irrespective of their colour, become suited to different light regimes found in the marine environment.

14.1 Experimental Design

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

- So, what is the explanation for the distribution of seaweeds? Is there a general rule that can help explain how seaweeds are distributed?
- The answer should be sought by finding a physiological explanation.
- Initial work done by Ramus et al. (1976a, b); later developed into the ‘functional-form’ model. This is discussed in Saffo (1987) in the section ‘Physiological relations of pigmentation and light’.

Ramus et al. Mar. Biol. 37: 231-238 (1976a).
Ramus et al. Mar. Biol. 37: 223-229 (1976b).

The method they used was as follows: Seaweeds acclimatised to shallow water—the surface, say, for a couple of weeks, so that their photophysiological machinery and pigment profiles had the chance to

adapt—were compared to seaweeds that had, during the same period, been grown in deeper water, at approximately 10 m depth, and allowed to become acclimatised to those conditions.

New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

Acclimation

- Ramus *et al.* (1976a, b):
 - *In situ* and lab physiological experiments on photosynthetic abilities, pigment production, and growth rates in same light regimes at different water depths
 - Transplant experiments



10cm

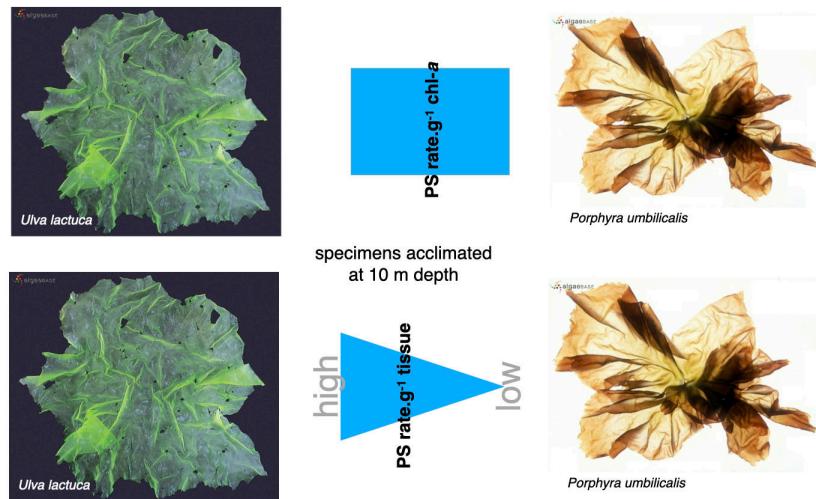
Noting that seaweeds come in a range of colours, they included red and green seaweed species. The red algae possess phycobilins as accessory pigments, along with some β -carotene, while green algae predominantly have chlorophyll-*a* with a bit of β -carotene, but absolutely no phycobilins in the greens.

They selected four species:

- *Chondrus crispus* (red)
- *Porphyra umbilicalis* (red)
- *Codium fragile* (green)
- *Ulva lactuca* (green)

You'll notice these represent two functional forms: the coarsely branched type (*Chondrus* and *Codium*) and the membranous group (*Porphyra* and *Ulva*). By spanning both different pigment groups and functional forms, Ramus and colleagues devised a transplant experiment to address how various algae types acclimatise to different oceanic light levels.

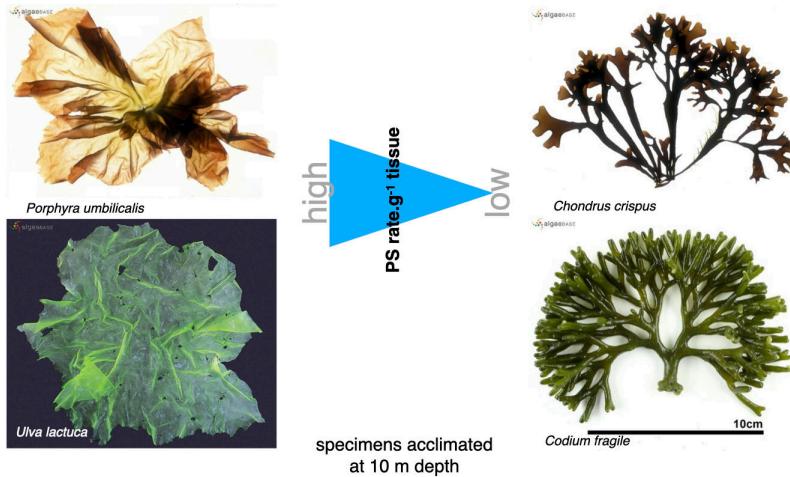
14.2 Comparing Functional Forms and Light Adaptation



So, focusing on comparisons within the same functional form, particularly the membranous group—*Ulva* and *Porphyra*, green and red respectively—let's consider specimens acclimatised to 10 m depth for a couple of weeks. Examining the photosynthetic rate per gram of chlorophyll-*a*, it was found that *Ulva lactuca* and *Porphyra umbilicalis* exhibited precisely the same rate of photosynthesis. This equality, however, only exists when expressing the photosynthetic rate on a per gram of chlorophyll-*a* basis. For every gram of chlorophyll-*a* present in either *Porphyra* or *Ulva*, the amount of photosynthesis driven is exactly the same—chlorophyll-*a*, irrespective of the species, performs identically as the primary photosynthetic pigment.

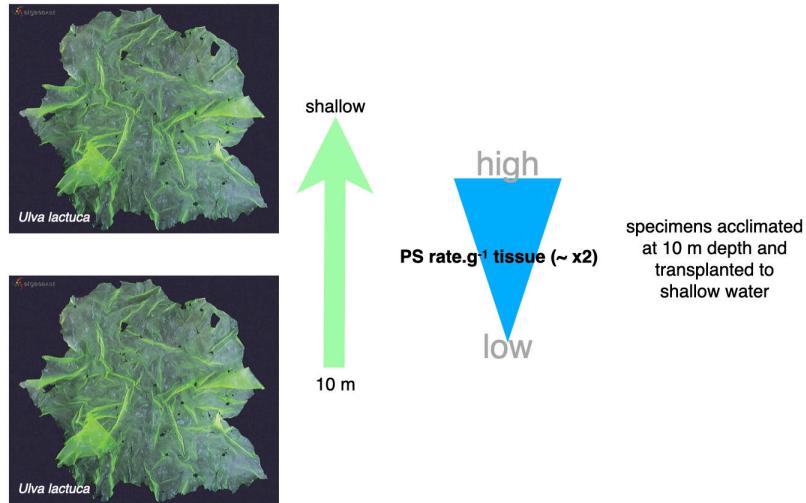
However, when expressing photosynthetic rate per gram of tissue (*i.e.*, per gram of *Ulva* or *Porphyra*), *Ulva* outperforms *Porphyra*. The underlying reason is simple: one gram of *Ulva* contains more chlorophyll-*a* than one gram of *Porphyra*. This makes sense, since *Ulva* is mainly composed of chlorophyll-*a*, whereas in *Porphyra*, much of the pigment content consists of accessory pigments (principally phycobilins), rather than chlorophyll-*a*.

14.3 Surface Area to Volume Effects

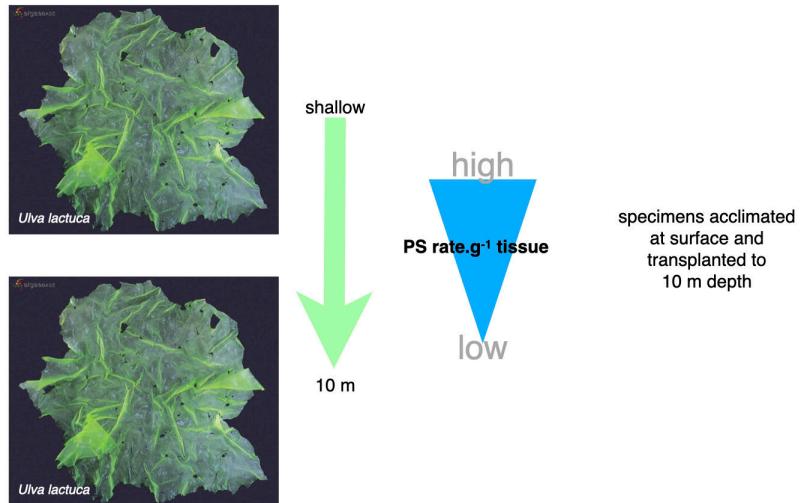


Additionally, when comparing red and green seaweeds at 10 m depth among different functional forms—contrast a flat membrane (high surface area to volume ratio) with something more robust (low surface area to volume ratio)—it is clear that tissues with a *high* surface area to volume ratio show a greater photosynthetic rate *per gram of tissue* than those with a *low* ratio. This is easily predicted using the functional form model: per unit tissue, species with higher surface area to volume ratios can sustain higher photosynthesis rates.

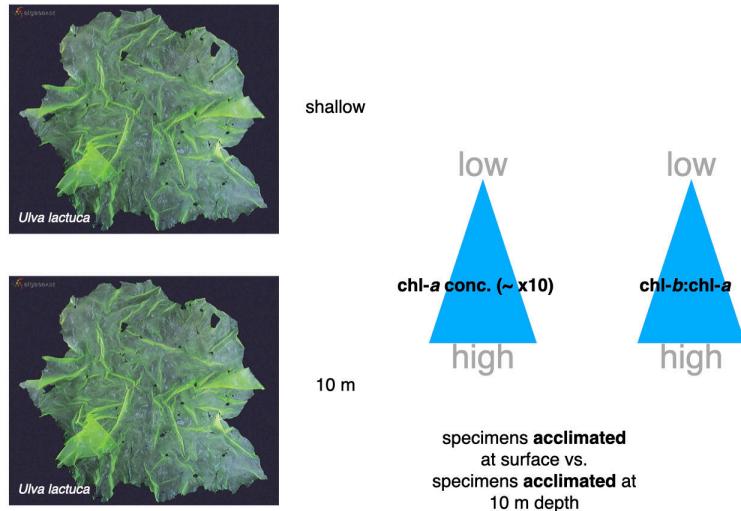
14.4 Transplant Experiments: Shallow vs Deep



For the transplant experiments, they took seaweeds acclimatised to 10 m and moved them to the immediate subsurface (zero metres), where light is both more abundant and richer in red wavelengths. Photosynthetic rate per gram of tissue at the surface approximately doubled compared to specimens kept at depth. The reasoning is straightforward—we'll elaborate on the mechanisms shortly, but increased light availability at the surface supports higher rates of photosynthesis.



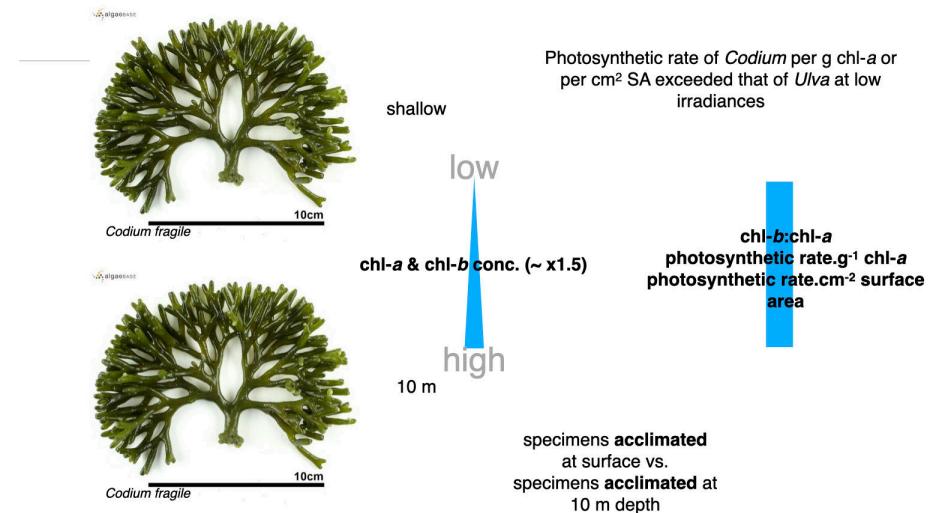
Executing the reverse—transplanting from the surface to 10 m—resulted in a drop in photosynthetic rate, reflecting the reduced light availability at depth. This is simply a consequence of photosynthetic response to less light.



Comparing pigment concentrations, seaweeds acclimatised to 10 m displayed chlorophyll-*a* concentrations around ten times higher than conspecifics from the surface. Not just that, the ratio of chlorophyll-*b* to chlorophyll-*a*—chlorophyll-*b* being an accessory pigment—increases markedly in deeper-grown specimens. Thus, seaweeds in lower-light environments boost both primary and accessory pigments, augmenting their light-harvesting capacity.



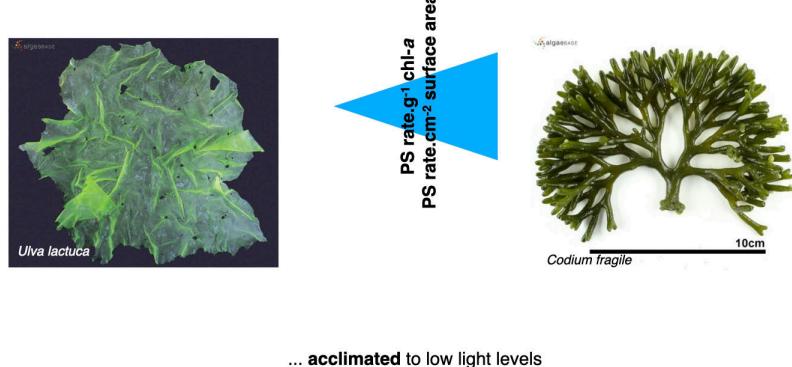
Codium, the coarsely branched green alga, however, presented a different case. Regardless of being grown shallow or deep, the rate of photosynthesis per gram of tissue remained nearly identical, even after transplantation.



Looking into pigment concentrations for surface versus deep-acclimatized *Codium*, the difference was marginal—only about 1.5 times higher chlorophyll-*a* and *b* at depth. Moreover, neither the ratio of chlorophyll-*b* to chlorophyll-*a*, nor photosynthetic rates per chlorophyll-*a* or per surface area, differed much between environments.

In summarising all these results, many types of comparisons arise, helping test numerous hypotheses concerning seaweed acclimatisation and adaptation to varying environments.

14.5 Acclimatisation Mechanisms and Plasticity



Once seaweeds were acclimatised to low light, they found that the photosynthetic rate per gram of chlorophyll-*a* in *Codium*—the coarsely branched green alga—was higher, and likewise, rate per unit surface area was greater compared with *Ulva*.

Interpretation of the *Ulva* results:

- Moved from high to low light: drastic drop in photosynthetic rate because there is less light for photosynthesis
- After some time *Ulva* acclimates to the low light level and manufactures more chl-*a* and even more chl-*b* (incr chl-*b*:chl-*a*); light capture increases, resulting in about a x10 faster rate of PS (compared to those acclimated at the surface and transplanted to 10 m)
- chl-*b*:chl-*a* increases - accessory pigments enhances light absorption under low light
- The opposite is true for transplanting *Ulva* acclimated to 10 m to the surface

For all of these, the chemical energy yield per quantum remains the same

So, what's happening? This mountain of data reveals several important adaptive responses. For seaweeds like *Ulva*, this can be understood via the plasticity of their photophysiological mechanisms. *Ulva*, for instance, can modify its physiology, pigment composition, and growth responses in reaction to prevailing environmental conditions—a demonstration of physiological plasticity.

So, as *Ulva* is transplanted from high to low light (surface to depth), an immediate reduction in photosynthetic rate occurs—less light equals less photosynthesis. This represents the organism being placed at a lower segment of its PI (photosynthesis–irradiance) curve. However, left at depth for several weeks, *Ulva* gradually manufactures more chlorophyll-*a* *and* invests more energy into accessory pigment production (chlorophyll-*b*). The increased chlorophyll content raises light-harvesting capability, bringing the photosynthetic rate back up—sometimes reaching up to ten times greater than for non-acclimatised specimens moved directly from the surface to depth.

The ratio of chlorophyll-*b* to *a* rises too, signifying compensatory synthesis of accessory pigments under dim conditions.

The opposite holds when moving from deep to shallow: photosynthesis rates spike instantly, but over time, pigment concentrations (particularly chlorophyll-*b* relative to chlorophyll-*a*) decrease, as high irradiance makes accessory pigments unnecessary. But across all conditions, the photosynthetic rate per gram of chlorophyll-*a* remains constant, because chlorophyll-*a*'s physiological efficiency as a light-harvesting molecule does not change with acclimatisation.

14.6 *Codium*'s Distinctive Behaviour

Interpretation of the *Codium* results:

- Something very different happens here...
- We need to seek an alternative explanation, because clearly the same physiological responses do not take place in *Codium*

- *Codium* and *Ulva* have the same pigments, and the ability of their pigments to absorb light should not differ
- Yet their results clearly show a difference...?!
- Published absorption spectra of pigments are made *in vitro*, but algae absorb light by pigments packaged in chloroplasts, which are arranged in cells (and which varies by spp.), the cells are arranged differently in differently shaped thalli, etc.
- Functional-form model

Codium, however, does not behave the same way. Despite having similar pigments to *Ulva*, its internal architecture is markedly different, which underpins its dissimilar responses.

14.7 Structural and Optical Differences: *Ulva* vs *Codium*

- An *Ulva* specimen acclimated to surface condition absorbs about 19% of the light
- Its thallus absorptance spectrum resembles that of chl-a (i.e. very little green light absorbed)
- Deep-acclimated *Ulva* can absorb up to 83% of incident light because it has more chl-a and chl-b, and a higher chl-b:chl-a; this allows it to absorb more green light relative to those acclimated to surface conditions
- Nevertheless, the green gap remains

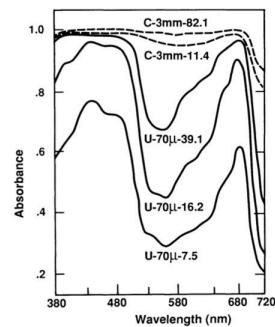


Figure 6. Absorptance spectra of seaweed thalli. C = *Codium fragile*. U = *Ulva lactuca*. Numbers give thallus thickness (in mm or μm), followed by concentration of photosynthetic pigment (nmoles/cm 2). Even at photosynthetic pigment concentrations lower than those of some *Ulva* specimens, *Codium* shows a greater absorptance of green light (Ramus 1978).

To clarify, let's examine *Ulva*. Surface-acclimatised *Ulva* absorbs only 19% of available light, as the abundance of light means only a fraction need be harvested for optimal photosynthetic function. Its thallus is just 70 μm thick, with a minimal amount of photosynthetic pigment per square centimetre.

At high light, absorption is reduced—the organism is inefficient at harvesting all incident light, since what it does capture is ample for its needs. Its high surface area to volume ratio allows rapid translation of harvested light into growth.

Transplanted to depth, the same thin *Ulva* thallus ramps up its pigment content—notably chlorophyll-*a*—and thus absorbs more light across the spectrum, especially when blue and red light dominate at depth. Absorption in the green region (the “green gap”), as well as across the spectrum, increases because accessory pigments like chlorophyll-*b* accumulate.

- *Codium* from shallow and deep habitats (the latter having somewhat more chl-*a*) absorbs 97 - 99% of the light falling on it; i.e. the absorbance pattern changes little with chl-*a* concentration
- It also absorbs green light, and the green gap is effectively gone
- *Codium* is optically black
- The cause of this has nothing to do with pigmentation. Thallus construction is important here, because it can determine the efficiency with which it can harvest light

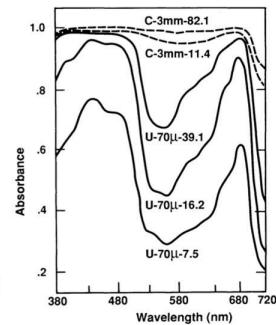


Figure 6. Absorptance spectra of seaweed thalli. C = *Codium fragile*. U = *Ulva lactuca*. Numbers give thallus thickness (in mm or μm), followed by concentration of photosynthetic pigment (nmoles/cm^2). Even at photosynthetic pigment concentrations lower than those of some *Ulva* specimens, *Codium* shows a greater absorptance of green light (Ramus 1978).

But even with increased pigment content, there's always a green gap, as *Ulva* lacks the accessory pigments required to efficiently absorb green wavelengths. Interestingly, *Codium* also lacks such accessory pigments, yet it is able to absorb significant amounts of light even in the green gap.

Codium: coenocytic, interwoven filaments; spongy; filaments terminate in utricles arranged around the periphery; large vacuoles in utricles, with cytoplasm and chloroplasts along the sides; optimised for light capture

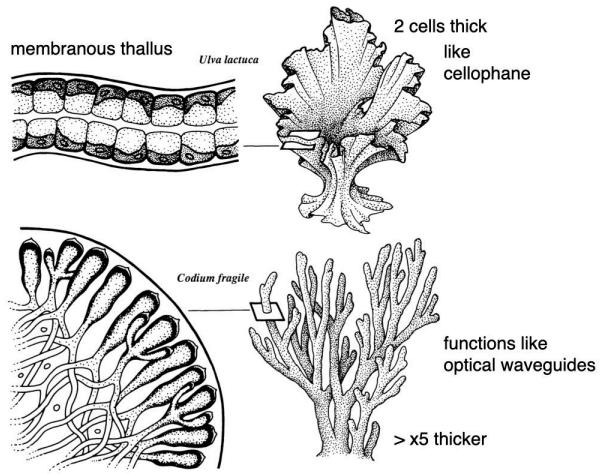


Figure 7. Internal and external anatomies of *Codium fragile* and *Ulva lactuca*. After Abbott and Hollenberg (1976), Bold and Wynne (1985), and Ramus (1978).

The reason is that *Codium* is *optically black*. That is, its tissues are so densely packed with pigment, particularly chlorophyll-*a*, within a very thick (3 mm) thallus, that they are entirely opaque. The pigment is predominantly positioned at the periphery of the coarsely branched utricles (the outward-pointing structures on the thallus). Structurally, *Codium* is a multinucleate, syncytial organism with an internal mesh of filaments but no individual cell walls separating cells as in *Ulva*.

i The “paradox” of chlorophyll-*a* becoming optically black

In an optically black seaweed, chlorophyll-*a* molecules retain their intrinsic absorption spectrum: they are “green” pigments, so they reflect and transmitting green light near 550 nm. How, then, can an alga, composed substantially of these same pigments, appear optically black and absorb almost the entirety of the incident spectrum (including the green light that individual chlorophyll-*a* pigments reflect)? The answer lies in the convergence of several mechanisms, *i.e.*, **complementary pigment absorption profiles, structural light scattering, and path length enhancement** within the thallus architecture. These factors interact to suppress reflectance and transmittance across the visible range to produce near-total absorptance despite the spectral limitations of chlorophyll-*a* alone.

The first and most direct contributor is **accessory pigment composition**. While chlorophyll-*a* dominates absorption in the red and blue regions of the spectrum, its absorption coefficient near 550 nm drops to roughly 10–15% of peak values. This is a substantial reduction but it never reaches absolute zero. In *Codium*, as in other chlorophytes, chlorophyll-*b* and carotenoids provide spectral coverage beyond chlorophyll-*a*’s reach. Siphonaxanthin and siphonein, the predominant carotenoids in *Codium*, absorb in the blue-green portion of the spectrum (approximately 450–550 nm), and this partially fills the chlorophyll-*a* “green gap.” The cumulative absorption spectrum of the pigment complement therefore exhibits greater breadth than chlorophyll-*a* in isolation, and reduces the transmission window that would otherwise produce a green appearance. The degree to which carotenoids alone account for the dark phenotype depends on their concentration relative to chlorophyll-*a* (which varies with species, light environment, and physiological state) but their contribution cannot be dismissed. In many visibly dark algae, accessory pigments provide the primary mechanism for broadband absorption; red algae and cyanobacteria, for instance, rely on phycobilins that absorb intensely in the green, causing them to appear brown, red, or nearly black depending on pigment ratios.

Pigment chemistry alone does not fully explain the optical behaviour of structurally complex tissues. Even with residual chlorophyll-*a* absorption and supplementary chlorophyll-*b* and carotenoids, a sparse distribution of pigments in an optically thin medium would still permit significant reflectance and transmittance of green wavelengths. What transforms this accessory pigment cocktail into a near-perfect absorber is the **optical organisation of the thallus**, *i.e.*, the three-dimensional arrangement of pigments within a scattering matrix that dramatically alters the internal light field.

When photons enter a densely pigmented, structurally heterogeneous tissue such as *Codium*, they encounter multiple refractive index discontinuities: cell walls, cytoplasm-vacuole interfaces, chloroplast membranes, and potentially air-water boundaries in the tubular, siphonous thallus structure characteristic of the genus. Rather than crossing the tissue in a direct path, photons undergo repeated scattering events which redirect their trajectories through the pigment-dense cytoplasm. This process extends the **effective optical path length** far beyond the physical thickness of the tissue. Wavelengths that would be poorly absorbed in a single encounter with chlorophyll-*a* (green photons, for instance) are subjected to tens or hundreds of absorption opportunities as they ping-pong through the scattering medium. Over many scattering events, the cumulative probability of absorption approaches unity even for wavelengths with modest absorption coefficients, provided those coefficients are non-zero.³³

This effect is captured by the concept of **optical thickness**, a dimensionless parameter relating the physical depth of a medium to the mean free path of photons within it. A medium is optically thin when photons typically escape before absorption; it is optically thick when the probability

The concentration of chlorophyll-*a* at the periphery means that any incident light is almost certainly absorbed before it can penetrate far, or it becomes trapped and wave-guided by the internal filaments, ensuring maximal light capture. This is why *Codium* maintains consistently high photosynthetic efficiency and pigment concentrations independent of depth, and thus shows little acclimatory response.

Ulva, by contrast, with its thin, “cellophane” membrane, allows much light to pass through, relying on every cell receiving direct illumination, but cannot match *Codium*’s absorptive efficiency in the green region or at depth.

15 Conclusion

So, to summarise: *Ulva* demonstrates remarkable plasticity in pigment and physiological responses, allowing acclimatisation to new light regimes—and does so primarily by increasing pigment concentrations at depth. *Codium*, by virtue of its dense, optically black construction and peripheral pigment placement, absorbs much more light and shows less need for physiological adjustment. Light absorption and photosynthetic rate per chlorophyll-*a* remain steady, but overall structural and anatomical properties, plus pigment arrangement, explain differences in adaptive responses between these two types of green algae.

That covers the key findings and interpretations you need to understand regarding light capture strategies and chromatic adaptation in seaweeds.

Bibliography