

PHOTOCONTROL OF DEVELOPMENT IN ALGAE

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CONTENTS

INTRODUCTION	157
PHOTOPERIODIC CONTROL OF ALGAL DEVELOPMENT	158
<i>Types of Algae Exhibiting Photoperiodic Responses</i>	158
<i>Types of Development Controlled by Photoperiod</i>	159
<i>Physiological Contrasts Between Photoperiodism in Algae and in Higher Plants</i>	160
NONPERIODIC PHOTOCONTROL OF ALGAL DEVELOPMENT	161
<i>Types of Algae Whose Development Is Influenced by Light</i>	161
<i>Types of Development Under Control by Light</i>	161
ACTION SPECTRA FOR ALGAL RESPONSES AND POSSIBLE PHOTORECEPTORS	166
<i>Red/Far-Red Reversible Responses—Phytochrome in Algae</i>	166
<i>Responses Activated by Photoreversible Pigment Systems Other than Phytochrome</i>	167
<i>Blue Light (Cryptochrome) Responses</i>	168
<i>Responses Activated by Both Blue and Red Light</i>	169
<i>Responses Activated by Green Light</i>	169
SUMMARY	170

INTRODUCTION

Here the term “development” will be treated with what some may regard as excessive freedom in order to include metabolic development (e.g. greening, enzyme synthesis, etc) as well as the more conventional development of vegetative and reproductive structures. This cavalier use of “development” is necessary since many unicellular algae have little morphology to develop, but their responses to light exhibit many similarities to those of macroscopic algae. In effect, this article covers all effects of light on algae that appear to be

independent of the photosynthetic apparatus, with the exception of orientation responses [i.e. phototaxis, phototropism, and light-induced chromatophore movement—see reviews by Haupt (45) and Häder (42)] and responses to light that are so rapid that they cannot involve synthesis of proteins or other cell constituents (e.g. changes in membrane potential, activation of existing enzymes, etc). The full breadth of this topic, covering all groups of algae, has not been tackled since Lang presented a “synopsis” of the physiology of growth and development of algae in 1965 (59). However, marine macroalgae have sometimes been singled out for attention (photomorphogenesis—26, 65; blue light effects—22, 23), and photoperiodism in algae was reviewed in 1970 (20) and again in 1984 (21).

The objective of this review is to summarize the state-of-play of such photobiological studies among the algae as a whole, and to derive generalizations that will encourage photobiologists (or photomorphogeneticists) to make wider use of algae as experimental tools. A wide range of responses among algae are controlled by light, and a wide range of different photoreceptors appear to be involved. In the algae, we seem to be looking at the early stages in the evolution of the phytochrome system, which is so well known from (and more widely seen in) flowering plants. In addition, algae exhibit a wider range of cryptochrome responses than is found in vascular plants, and a number of other pigment systems, which are as yet poorly characterized—largely because they are known from only one or a few species. This range of photomorphogenetic pigment systems could be regarded as analagous to the range of photosynthetic pigment systems also found among algae, although there is little indication so far that particular photomorphogenetic pigments are correlated with specific photosynthetic systems and, hence, with phylogenetic groupings of the algae.

PHOTOPERIODIC CONTROL OF ALGAL DEVELOPMENT

This topic was reviewed in detail in 1984 (21) and, although a few interesting new responses have been reported (10, 18, 38), there has been only one significant contribution to the physiology of photoperiodism in algae since then (9). The earlier review requires little revision, therefore, and the present account aims to illustrate the range of response types and algal groups represented, and to summarize the features of greatest physiological interest. The photoreceptors involved in these responses are discussed in the final section of this review.

Types of Algae Exhibiting Photoperiodic Responses

At the latest count, about 55 photoperiodic responses had been reported in macroscopic species from three algal divisions (Chlorophyta, Phaeophyta,

Rhodophyta). The green algae (65, 84) are less well represented than the brown and red algae, but this is almost certainly because of the scarcity of macroscopic green algae in the temperate marine flora of the northern hemisphere, which results in their receiving less attention from experimental phycologists. Freshwater algae (51) are also poorly represented among photoperiodic species, but this probably reflects the numerical distribution of macroscopic algae between marine and freshwater habitats rather than any fundamental insensitivity of freshwater algae to photoperiod.

What may be more fundamental, however, is the complete absence of unicellular algae from the lists of photoperiodic species. This does not mean that a macroscopic morphology is essential for a photoperiodic response, because several of the known responses occur in the microscopic phases of the life histories of macroscopic plants (e.g. 9, 65, 81). The apparent absence of photoperiodic responses among unicellular algae may have more to do with the planktonic habitat that many of them occupy. Factors such as irradiance, temperature, and nutrient supply are often thought to have greater ecological significance than daylength in controlling the seasonal behavior of planktonic species.

Types of Development Controlled by Photoperiod

The majority of the responses reported involve a change of phase in the life history of a species, although this is not always achieved by the formation of reproductive structures in the conventional sense. In both red and brown algae, the formation of erect thalli from a prostrate system (a crust or branching filaments) is commonly controlled by photoperiod (24, 51, 85), but either gametogenesis (10, 41, 105, 107) or sporogenesis (1, 9, 18, 27, 65, 81) may also occur in response to changes in daylength. Most of these responses have been observed in species with a heteromorphic alternation of generations, but a few are found in isomorphic species (e.g. *Dumontia*; 85) and in species with single-phase life histories (e.g. *Ascophyllum*; 107). It is not possible, therefore, to correlate photoperiodic control with any particular type of life history.

Vegetative responses to photoperiod, analogous to the onset or breaking of dormancy in higher plants, have also been observed in a few algae. The short-day (SD) responses of *Laminaria* and *Constantinea* both result in the initiation of a new blade in the autumn or winter (68, 79), while the rate of growth of the young blades of two kelp species (*Pleurophycus* and *Laminaria*) is stimulated by long-day (LD) conditions (38; K. Lüning, unpublished observations). These vegetative responses may be less complex than reproductive responses and are, therefore, potentially easier to study. So far, however, they have been found only in plants whose large size effectively cancels out the experimental advantages of their responses. Nevertheless, two

responses offer promising approaches to the biochemistry of photoperiodism. The formation of new blades in *Laminaria* under SD conditions (68) is correlated with changes in the activities of key enzymes (62), while the development of *Derbesia* protoplasts under SD contrasts with that in LD (84).

Physiological Contrasts Between Photoperiodism in Algae and in Higher Plants

Although the first algal responses to be investigated in detail (20, 81) showed a remarkable similarity to photoperiodic responses in vascular plants, it has since become clear that other responses do not share all the classical features of photoperiodic control of flowering. It has, therefore, become necessary to redefine the criteria for accepting a response to daylength as a photoperiodic response in the strict sense of the term—i.e. “the control of some aspect of a life cycle by the timing of light and darkness” (47). The main casualty of this process of redefinition has been the night-break as a diagnostic feature of true photoperiodic responses (21).

A few SD responses in algae have been shown to be completely insensitive to night-break treatment (e.g. the red algae *Acrosymphyton* and *Cordylecladia*; 9, 10) even though all other tests (i.e. day extensions, testing different daylengths with the same total daily exposure to light, sharp critical daylengths) show the responses to be controlled by the timing of light and darkness. In another SD red alga (*Rhodochorton*), night-breaks failed to inhibit the response to 8-h days but caused complete inhibition of the response to 10-h days (27). Such insensitivity to night-breaks is unknown among SD flowering plants, although many LD plants show a similar reluctance to respond to night-break treatment (112). Vince-Prue has suggested that such LD plants may be “light-dominant,” responding to the length of the day rather than to the shortness of the night, whereas most SD plants are known to respond primarily to the length of the dark period (“long-night”; 114). However, the LD plants that respond to night-breaks are clearly measuring night length, and a few SD plants may conversely be “light-dominant.” These two categories of photoperiodic plants can be distinguished by exposing plants to an 8-h day-extension either before or after an 8-h main photoperiod. For long-night responses, both treatments have similar effects but, for light-dominant responses, day-extensions before the main photoperiod inhibit the effects of the SD to a greater extent than day-extensions after the main photoperiod (113).

Recent experiments of this type with *Acrosymphyton* (9) have given precisely the latter result, suggesting that this SD plant is measuring daylength rather than night length. In other respects, however, it does not behave in a way similar to that of Vince-Prue’s light-dominant plants. It is far more sensitive to light as a day-extension, and it responds primarily to blue light, with some effect of red but none of far-red (see p. 169; 9). Since phytochrome

does not seem to be the photoreceptor, it is hardly surprising that a working hypothesis based on phytochrome action (114) will not fit. We seem to be facing a range of different types of photoperiodic mechanism in algae, and further quantitative data from more species are needed before we can make much sense of the situation.

NONPERIODIC PHOTOCONTROL OF ALGAL DEVELOPMENT

The intention of this admittedly ambiguous heading is to state, in conjunction with the heading of the previous section, that here will be found examples of algal development controlled by light through attributes other than the length of the day. Some aspects of this topic have been reviewed previously (23, 26, 65), but this is probably the first attempt to cover all types of response in all types of algae. A full discussion of the photoreceptors involved will, however, be postponed to the final section of this article so that they can be considered together with the photoreceptors involved in algal photoperiodism.

Types of Algae Whose Development Is Influenced by Light

Light has been shown to affect some aspect of the development of at least one species from every algal division recognized by Bold & Wynne (7; Tables 1–3). In marked contrast to the case with photoperiodic responses, unicellular species are well represented. The familiar laboratory maids-of-all-work from the Chlorophyta (*Chlorella*, *Chlamydomonas*, *Scenedesmus*) appear rather frequently, but *Euglena*, *Cryptomonas*, and the odd dinoflagellate are also present. It is surprising that no response has so far been reported for a diatom, but a recent study of the growth of *Chaetoceros* in blue light found no effects that could not be attributed to differential absorption by the photosynthetic pigments (40). Two divisions of mainly multicellular algae for which no photoperiodic responses have been reported are the Charophyta and the Cyanophyta (or cyanobacteria). The stoneworts (Charophyta) have the most highly differentiated thalli of any algae containing chlorophyll *b*, and it is no surprise, perhaps, to find photoresponses similar to those in mosses and ferns and apparently mediated by phytochrome (Table 2 a,b). The prokaryotic Cyanophyta are, of course, very different both in the types of response they exhibit and the photoreceptors involved (Table 1 b; 2 a,b). That is the main reason for discussing them here, rather than considering them as bacteria and therefore outside the scope of this volume.

Types of Development Under Control by Light

METABOLIC DEVELOPMENT As is not the case in higher plants, the differentiation of chloroplasts and the synthesis of chlorophyll occur in com-

plete darkness in many algae, but some species or mutants have been found that require light for greening (Table 1 a). *Euglena gracilis* and the mutants of various green algae have received the most attention, and blue light has been shown to precondition the cells so that they respond more rapidly to the wavelengths absorbed by protochlorophyllide (blue and red; 92). The pre-treatment with blue light may simply stimulate respiration and thus supply energy or precursors, but a direct influence of blue light on the formation of enzymes that synthesize amino-levulinic acid is often detectable also (95). Recent studies of greening in *Euglena* have suggested that other photoreceptors absorbing orange (55) or green light (30) may be involved in addition to cryptochrome and protochlorophyll. Since all of the detailed work has been done on algae containing chlorophyll *b*, it will be interesting to learn more about the red alga *Delesseria*, which forms phycoerythrin in complete darkness but requires light for chlorophyll formation (67).

The pigment composition of fully "greened" algae is notoriously plastic, and it is often claimed that changes occur in response to either the irradiance

Table 1 Types of metabolic development in algae controlled by light

Type of development	Genus	Algal group ^a	Effective color(s)	Reference
(a) Greening (i.e. chlorophyll synthesis, chloroplast formation, etc)	<i>Chlorella</i>	Chl.	blue	95
	<i>Scenedesmus</i>	Chl.	blue	95
	<i>Euglena</i>	Eugl.	various	30, 55, 92
	<i>Delesseria</i>	Rhod.	?	67
(b) Pigment composition	<i>Chlorella</i>	Chl.	blue	57
	<i>Scenedesmus</i>	Chl.	blue	49
	<i>Fremyella</i>	Cyan.	green/red	46, 116
	<i>Tolypothrix</i>	Cyan.	green/red	37
	<i>Ochromonas</i>	Chry.	blue-green	53
	<i>Cryptomonas</i>	Cryp	green	53
	<i>Prorocentrum</i>	Pyrr.	green	33
(c) Enzyme synthesis	<i>Chlorella</i>	Chl.	blue	88
	<i>Chlorogonium</i>	Chl.	blue	87, 101
	<i>Acetabularia</i>	Chl.	blue	93
	<i>Acrochaetium</i>	Rhod.	blue	110
	<i>Cyanidium</i>	Rhod.	blue	102
(d) Stimulation of cell division	<i>Chlorella</i>	Chl.	blue	97
(e) Inhibition of cell division	<i>Chlamydomonas</i>	Chl.	blue/yellow	12
	<i>Chlorella</i>	Chl.	blue/yellow	12
	<i>Prototheca</i>	Chl.	blue	32
(f) Cell differentiation	<i>Volvox</i>	Chl.	green	56
(g) Osmoregulation	<i>Chlamydomonas</i>	Chl.	blue	109

^a Chl. = Chlorophyta; Chry. = Chrysophyta; Cryp. = Cryptophyta; Cyan. = Cyanophyta; Eugl. = Euglenophyta; Pyrr. = Pyrrophyta; Rhod. = Rhodophyta.

or the quality of the incident light. Regardless of the outcome of the (possibly never-ending) dispute between "intensity adaptation" and "chromatic adaptation," it is clear that pigment synthesis in algae is influenced by light; and it may be more fruitful to enquire about the mechanisms than to continue the argument about the causes. The situation seems to be simplest in those blue-green algae that can vary the ratio between the two phycobilin pigments (Table 1 b). Red light stimulates the formation of phycocyanin and green light the formation of phycoerythrin (37, 46, 116), and the result is chromatic adaptation in the original sense. Outside the Cyanophyta, the phycoerythrin content of *Cryptomonas* also increases in green light (53), as does the peridinin content of *Prorocentrum* (33), but there is no other experimental evidence for adaptive changes in pigments in response to light quality (see 23). All algal groups show a response similar to that of higher plants when grown in low irradiances of white light (i.e. total pigment increases and the ratio of chlorophyll *a* to accessory pigments decreases). In some freshwater green algae, this response appears to be controlled by cryptochrome (whereas in flowering plants this would be a phytochrome response; 49, 57, 96), but the evidence from other algal groups is far less consistent (23) and there is a need for more critical investigation.

There have been numerous reports of blue light affecting (usually stimulating) enzyme activity (see 88, 89), and many of these refer to algal species (Table 1 c). Unicellular green algae are, as usual, favorite subjects, but the giant-celled *Acetabularia* has also been intensively investigated (14, 15, 93). The only non-green algae to appear on these lists so far are the red algae *Acrochaetium* (110) and *Cyanidium* (102). In most of these studies, plants were grown in monochromatic light for an extended period, and enzyme activity was then measured in cell-free extracts under optimal conditions. Higher activity in an extract from a blue-grown plant was usually, therefore, taken to imply that more enzyme had been synthesized in blue light, although direct proof of this interpretation (e.g. through the use of inhibitors) has rarely been obtained. Also, since plants had to be grown for long periods in the different wavelengths, it was not often possible to investigate the action spectrum in detail; and the commonly accepted idea that they are all due to cryptochrome may be questioned.

Almost all of the enzymes investigated (88, 89) control rate-limiting steps in respiratory or photosynthetic pathways, and such photocontrol of enzymes is the probable primary cause of the contrasting patterns of growth and chemical composition of algae cultivated in blue and red light (e.g. 11, 14, 15, 33, 50, 73, 117). The various effects of blue light on cell-cycle events (Table 1 d-f) may also be the indirect result of light affecting enzyme synthesis or activity. Similarly, the swelling and subsequent rupture of a wall-less mutant of *Chlamydomonas* is prevented in blue light, possibly

because the cellular components required for osmoregulation are not produced in other wavelengths (109).

DEVELOPMENT OF VEGETATIVE MORPHOLOGY Studies of the control of seed germination by light provided the basis for much early work on photomorphogenesis in flowering plants, and the development of photomorphogenetic studies on algae may have been delayed by the apparent rarity of similar responses among algal spores. A few exceptions to the rule that algal spores do not require light for germination are now appearing (Table 2 b). These include two charophytes, which have larger and more elaborate spores than many other algae; phytochrome has been implicated in one of these responses (103). There is also some evidence that phytochrome controls akinete germination in *Anabaena fertilissima* (80), although a more detailed action spectrum for the same process in *A. variabilis* (8) indicated phycocyanin as the photoreceptor. Since germination was only slightly reduced by DCMU (dichlorophenyl-dimethyl urea), photosynthesis was not apparently essential for the response; but the opposite result was obtained (and the opposite conclusion reached) in a study of the control of spore germination in *Bangia* by green light (13). The induction of germination in *Scrippsiella* cysts by green light is clearly a photomorphogenetic response, however, since less

Table 2 Types of vegetative development in algae under nonphotoperiodic control by light.

Type of development	Genus	Algal group ^a	Effective color(s)	Reference
(a) Growth responses	<i>Nostoc</i>	Cyan.	red/green	60, 86
	<i>Fremyella</i>	Cyan.	red/green	17
	<i>Spirogyra</i>	Chl.	red/far-red	115
	<i>Chara</i>	Char.	red/far-red	82
	<i>Nereocystis</i>	Phae.	red/far-red	28
	<i>Vaucheria</i>	Chry.	blue	54
(b) Spore germination	<i>Anabaena</i>	Cyan.	red(/far-red)	8, 80
	<i>Chara</i>	Char.	red/far-red	103
	<i>Nitella</i>	Char.	red	100
	<i>Scrippsiella</i>	Pyrr.	green	3
	<i>Bangia</i>	Rhod.	green	13
(c) Two-dimensional development	<i>Petalonia</i>	Phae.	blue	69
	<i>Scytosiphon</i>	Phae.	blue	25
(d) Hair formation	<i>Acetabularia</i>	Chl.	blue	94
	<i>Desmotrichum</i>	Phae.	blue	63
	<i>Dictyota</i>	Phae.	blue	73
	<i>Scytosiphon</i>	Phae.	blue	25
(e) Rhizoid formation	<i>Spirogyra</i>	Chl.	red/far-red	74

^aChar. = Charophyta; Phae. = Phaeophyta; other abbreviations as in Table 1.

than 1 s at the standard culturing irradiance was sufficient to induce a 50% response (3). Other dinoflagellates also require light for cyst germination (2), so we may soon be on the trail of other green-light effects in algae.

Up to now, blue-light effects have been most prominent, and a common response to blue light is the formation of hairs (Table 2 d). *Scytosiphon* and *Acetabularia* have been most fully investigated (25, 94), and the responses of both species appear to be typical of cryptochrome, as does the induction of two-dimensional growth in *Scytosiphon* (25). The latter response closely parallels the transition from filamentous to two-dimensional growth in fern gametophytes (48); but there is no obvious parallel to the hair-formation responses among other plants, possibly because hairs of this type only form in aquatic plants. The control of both types of response by blue light may have some ecological significance (see discussion in 23, 26).

The "growth responses" (Table 2 a) are a heterogeneous group. Perhaps their only common feature is that they deserve more detailed investigation. The growth rate of the blue-green alga *Fremyella* (17) and the transition from amorphous to filamentous growth in *Nostoc* appear to be controlled by a red/green photoreversible pigment system (60, 86, 91) similar to that implicated in the chromatic adaptation of pigment composition in other cyanophytes (Table 1 b). Tip growth in the coenocytic chrysophyte *Vaucheria* is stimulated by blue light (54), and this response may be the primary cause of phototropic bending in this species—also a blue-light response. Two very different algae—*Chara* sporelings and the large kelp *Nereocystis*—both show an elongation response to end-of-day treatment with far-red light (28, 82). The response of *Chara* can be reversed by subsequent treatment with red light, but reversal was not convincingly demonstrated for *Nereocystis*. Elongation of cells in *Spirogyra* filaments is also affected by red and far-red light (115), and another apparent phytochrome response is seen in rhizoid formation in this alga (74).

DEVELOPMENT OF REPRODUCTIVE STRUCTURES The nonphotosynthetic and nonphotoperiodic effects of light on the reproduction of algae may be exerted on the formation of reproductive structures or on the release of propagules from them. In one species of unicellular green algae, zoospore production is inhibited by light, whereas reproduction in another green unicell (*Trebouxia*, the algal symbiont of a lichen species) and in several macroscopic algae is stimulated by light (Table 3 a,b). Release of spores is also more commonly stimulated than inhibited by light (Table 3 c,d). Even in *Laminaria*, which is an apparent exception to this generalization, release is merely delayed for a few hours by blue light and the circadian rhythm of release is inhibited (66). However, keeping ripe receptacles of *Pelvetia* in light prevented release of eggs for up to 450 h, but transfer to darkness for as little as 3

Table 3 Types of reproductive development in algae under nonphotoperiodic control by light.

Type of development	Genus	Algal group ^a	Effective color(s)	Reference
(a) Induction of gamete or spore formation	<i>Acetabularia</i>	Chl.	blue	106
	<i>Dictyota</i>	Phac.	red	73
	<i>Laminaria</i>	Phae.	blue	64, 70
	<i>Macrocystis</i>	Phae.	blue	71
	<i>Trebouxia</i>	Chl.	red/far-red	39
(b) Inhibition of spore formation	<i>Protosiphon</i>	Chl.	blue/yellow	29
(c) Induction of gamete or spore release	<i>Bryopsis</i>	Chl.	blue	98
	<i>Monostroma</i>	Chl.	blue	99
	<i>Desmotrichum</i>	Phae.	blue	63
	<i>Dictyota</i>	Phae.	blue	58
(d) Inhibition of gamete or spore release	<i>Laminaria</i>	Phae.	blue	66
	<i>Pelvetia</i>	Phae.	?	52

^a Abbreviations as in Tables 1 and 2.

min resulted in egg release within 10 min (52). This unusual observation should be followed up.

ACTION SPECTRA FOR ALGAL RESPONSES AND POSSIBLE PHOTORECEPTORS

This section brings together information on the action spectra for all types of nonphotosynthetic effect of light on algae, including where appropriate those nondevelopmental responses (i.e. orientation and rapid effects) excluded from detailed discussion in the rest of this review.

Red/Far-Red Reversible Responses—Phytochrome in Algae

The first indication that phytochrome occurs in algae was obtained when chloroplast movement in the filamentous green alga *Mougeotia* was found to be reversibly influenced by red and far-red light (43). This species has figured prominently in the phytochrome literature ever since. The desmid *Mesotaenium* was soon shown to have a similar response (44), and phytochrome was extracted from this species in 1967 (104). Since the absorption peaks of the two forms of phytochrome from *Mesotaenium* were at slightly shorter wavelengths than those of phytochrome from higher plants, it is possible that green algae possess a different (more primitive?) form of the pigment. There is recent evidence, however, that at least part of the molecule is similar in angiosperms, mosses, and green algae. Three species of green algae gave a positive result when tested with a monoclonal antibody directed to phytochrome from peas (16). The species included *Chlamydomonas* as well as

Mougeotia and *Mesotaenium*, but there is as yet no indication of what phytochrome might do in *Chlamydomonas*.

The evidence for phytochrome in green algae is thus based on action spectra, extraction, and molecular biology. It is surprising, therefore, that only three other species among the Chlorophyta (*Dunaliella*, 61; *Spirogyra*, 74, 115; *Trebouxia*, 39) have been shown to respond to red and far-red light. The stoneworts are included in the Chlorophyta by many authorities, and so the two responses of *Chara* in which red/far-red reversibility has been shown (82, 103) can perhaps be added with reasonable confidence to the list of phytochrome effects. However, the remaining red/far-red effects—all in non-green algae (i.e. from outside the Chlorophyta)—must be treated with more caution.

Such effects have been reported for various types of response in algae from widely separated evolutionary lines—photoperiodic responses (19, 81, 83) and absorbance changes (111) in red algae; growth responses in a brown alga (28), a diatom, a dinoflagellate, and a coccolithophorid (61); a behavioral response in another dinoflagellate (31, 34, 35); and germination in a blue-green alga (80). For many of these responses, red and far-red light were the only wavelengths tested and, in green plants, this is all that would be needed (according to Mohr's operational criteria; 72) to establish phytochrome involvement. As phytochrome has not yet been extracted from a non-green plant, however, better evidence than simple red/far-red reversibility is required, because antagonistic effects of red and far-red light could result from differential absorption by photosystems I and II (5). This possibility can be ruled out, however, if other wavelengths that activate photosystem II have a different morphogenetic effect from red light. Such evidence is available for *Gyrodinium* (31) and for the photoperiodic response of *Porphyra tenera* (19, 81).

Phytochrome, therefore, remains the best candidate for these responses, but its presence and activity outside the Chlorophyta cannot be regarded as proven without more detailed action spectra or successful extraction of the pigment from one of the species that shows a physiological response. There are good reasons why these requirements have not been satisfied already. The photoperiodic responses cannot be conveniently or sensitively quantified (see 21), and it is difficult to grow up sufficient material for extraction. Perhaps we should look to the molecular biologists of the phytochrome world (e.g. 16) to provide us with a probe to identify phytochrome in small quantities and in situ.

Responses Activated by Photoreversible Pigment Systems Other than Phytochrome

In the absence of unequivocal evidence for the occurrence of phytochrome in non-green algae, it is of interest that two distinct photoreversible pigment

systems other than phytochrome have been detected in algae. The effects of red light on both the pigment composition (Table 1 b) and the growth responses (Table 2 a) of blue-green algae can be reversed by green light. For a time, there was intense interest in identifying what might prove to be a prokaryotic equivalent of phytochrome (91). One approach has been to fractionate aqueous extracts of the algae and to isolate new pigments (a series of "phytochromes") with photoreversible absorbance properties (4–6). Other workers have attempted to show that the familiar phycobiliproteins (in particular, allophycocyanin) could account for these responses unaided (76, 77). Since none of the absorption spectra exactly matched the action spectra for the physiological responses (6), however, it has not proved possible to settle the claims of the rival pigments, and an uneasy truce exists at present. The structural similarity between phytochrome and allophycocyanin is well known, and it will be valuable to have more information about the role of allophycocyanin or the phytochromes in photomorphogenesis.

A second photoreversible pigment system responding to blue (430 nm) and yellow (580 nm) light has been isolated from three green algae (108), in which it controls zoospore formation (*Protophycopsis*; 29) or cell division (*Chlamydomonas*, *Chlorella*; 12). As is not the case with phytochrome (and, possibly, phytochrome), the photoreversibility of this system appears to result from the interaction of two separable components—a flavoprotein that absorbs blue light, and a plastocyanin that is converted to a form absorbing yellow light after oxidation by the activated flavin (78).

Blue Light (Cryptochrome) Responses

More of the responses in Tables 1–3 are controlled by blue light than by any other waveband. Some of the responses are similar to blue-light effects in higher plants (e.g. enzyme effects, tropic responses, induction of two-dimensional growth), while the induction of reproductive activity (Table 3) is comparable to blue-light-induced sporulation in fungi. Other responses of algae to blue light (e.g. potentiation of greening; pigment changes in low irradiances) are analogous to responses controlled by phytochrome in higher plants (95, 96), but a few responses (e.g. photoperiodic effects, hair formation) appear to be controlled by blue light only in algae.

Perhaps because so many responses have been reported, there are more detailed action spectra available than for other types of response. Those for a wide range of brown algae (24, 25, 58, 66, 70) have many of the characteristic features of cryptochrome spectra from green algae, higher plants, and fungi (see 23 for discussion). It seems reasonable to conclude that cryptochrome—if this really is a single pigment—must be widespread in the Phaeophyta and, possibly, among chromophyte algae in general. However, the situation is far less clear for the Rhodophyta. Although blue light affects

enzyme synthesis (110), photoperiodic control (9), and tropic responses (23) in red algae, neither of the two action spectra available (9, 75) is really similar to that of cryptochrome. Large question marks, therefore, hang over both the phytochrome and the cryptochrome of red algae. It is hoped that someone will soon take up the challenge that they pose.

Responses Activated by Both Blue and Red Light

The SD response of *Porphyra tenera* was inhibited only by red light as a night break (19, 81) and that of *Scytosiphon* only by blue light (24), but the SD responses of four other algae (three red algae and one brown) were inhibited to similar extents by blue and red light (27, 79, 85, 107). In two of these species, the effects of red light could not be reversed by far-red (27, 79) so that phytochrome (or its equivalent in red algae) did not appear to be involved; but far-red was not tested on the other species. Blue and red light also seem to be responsible for stimulating dark respiration and starch breakdown in *Dunaliella* (90). The best-known pigment with absorption in blue and red is, of course, chlorophyll, but a simple photosynthetic function of the light can be ruled out for the photoperiodic responses because the same exposure given at a different time would not be inhibitory. The SD response of another red alga, *Acrosymphyton*, could not be inhibited by night-breaks, but day-extensions with low irradiances ($0.05 \mu\text{mol m}^{-2} \text{s}^{-1}$) of white light were completely inhibitory (9). Blue (420 nm) was the most effective wavelength for day-extensions, but 563, 600, and 670 nm were moderately effective. Only far-red (710 and 730 nm) was completely ineffective. These results are also inconsistent with either phytochrome or cryptochrome action, and prompt the suggestion that photoperiodic responses in algae may be controlled by a variety of pigment systems analogous to the variety of pigments involved in algal photosynthesis. There seems, however, to be little correlation between photosynthetic pigments and photoperiodic pigments.

Responses Activated by Green Light

Green light has been reported to affect pigment composition in a cryptomonad (53) and a dinoflagellate (33) as well as chloroplast development in *Euglena* (30), but detailed effectiveness spectra have been determined only for cyst germination in another dinoflagellate (3) and for the differentiation of somatic and reproductive cells in synchronized *Volvox* cultures (56). Both of these spectra show a broad peak around 550 nm. Rhodopsin, which has recently been tentatively identified in *Chlamydomonas* (36), has been proposed as the photoreceptor for the *Volvox* response (56); but the various forms of this pigment all have absorption maxima in the blue-green region (470–510 nm; 36) and so would not fit the effectiveness spectra available so far. However, the appearance of a new candidate for photoreception in plants will certainly

revitalize attempts to match action spectra with absorption spectra. This is particularly welcome at a time when the algae are revealing such a variety of new photoresponses.

SUMMARY

Critical points in the life histories of many macroscopic marine algae are controlled by photoperiod, but the physiological mechanisms of their responses are more varied than among flowering plants. At least three pigment systems (responding to red/far-red, blue, or blue + red) appear to be involved, and the variability of other features of the responses (especially their sensitivity to light outside the main photoperiod) may be related to the different photoreceptors. Apart from its photoperiodic effects, light also controls aspects of metabolic, vegetative, and reproductive development in species from every algal division. These include unicellular algae, which appear not to respond to daylength. The commonest photoreceptor found to control algal development is cryptochrome, which is responsible for a wide range of response types. Reversible responses to red and far-red light have been reported for a few species in most algal groups, but phytochrome has been positively identified only in green algae. There is at present no satisfactory alternative explanation for the antagonistic effects of red and far-red light in non-green algae, but the presence of phytochrome in these plants has yet to be confirmed. The action spectra for other responses suggest that at least four other photoreceptors may be found among the algae, including the red/green reversible system of the Cyanophyta. Photobiologists who are saturated by phytochrome and cryptochrome research may, therefore, derive further excitement from the developmental responses of algae.

Literature Cited

1. Abdel-Rahman, M. H. 1982. Photo-périodisme chez *Acrochaetium asparagopsis* (Rhodophycées, Acrochaetiales). Influence de l'interruption de la nyctipériode, par un éclairage blanc ou monochromatique, sur la formation des tetrasporocystes. *C. R. Acad. Sci. Paris, Ser. III* 294:389-92.
2. Anderson, D. M., Taylor, C. D., Armbrust, E. V. 1987. The effects of darkness and anaerobiosis on dinoflagellate cyst germination. *Limnol. Oceanogr.* 32:340-51.
3. Binder, B. J., Anderson, D. M. 1986. Green light-mediated photomorphogenesis in a dinoflagellate resting cyst. *Nature* 322:659-61.
4. Björn, G. S., Björn, L. O. 1976. Photochromic pigments from blue-green algae: phycochromes a, b, and c. *Physiol. Plant.* 36:297-304.
5. Björn, L. O. 1979. Photoreversibly photochromic pigments in organisms: properties and role in biological light perception. *Q. Rev. Biophys.* 12:1-23.
6. Björn, L. O., Björn, G. S. 1980. Photochromic pigments and photoregulation in blue-green algae. *Photochem. Photobiol.* 32:849-52.
7. Bold, H. C., Wynne, M. J. 1985. *Introduction to the Algae*. Englewood Cliffs, NJ: Prentice-Hall. 720 pp. 2nd ed.
8. Braune, W. 1979. C-phycoyanin—the main photoreceptor in the light dependent germination process of *Anabaena* akinetes. *Arch. Mikrobiol.* 122:289-95.

9. Breeman, A. M., ten Hoopen, A. 1987. The mechanism of daylength perception in the red alga *Acrosyphyton purpuriferum*. *J. Phycol.* 23:36-42
10. Brodie, J., Guiry, M. D. 1987. Life history and photoperiodic responses in *Cordylecladia erecta* (Rhodophyta). *Br. Phycol. J.* 22:300-1
11. Brown, T. J., Geen, G. H. 1974. The effect of light quality on carbon metabolism and extracellular release of *Chlamydomonas reinhardtii* Dangeard. *J. Phycol.* 10:213-20
12. Carroll, J. W., Thomas, J., Dunaway, C., O'Kelley, J. C. 1970. Light induced synchronisation of algal species that divide preferentially in darkness. *Photochem. Photobiol.* 12:91-98
13. Charnofsky, K., Towill, L. R., Sommerfeld, M. R. 1982. Light requirements for monospore germination in *Bangia atropurpurea* (Rhodophyta). *J. Phycol.* 18:417-22
14. Clauss, H. 1968. Beeinflussung der Morphogenese, Substanzproduktion und Proteinzunahme von *Acetabularia mediterranea* durch sichtbare Strahlung. *Protoplasma* 65:49-80
15. Clauss, H. 1970. Effect of red and blue light on morphogenesis and metabolism of *Acetabularia mediterranea*. In *Biology of Acetabularia*, ed. J. Brachet, S. Bonotto, pp. 177-91. London: Academic
16. Cordonnier, M.-M., Greppin, H., Pratt, L. H. 1986. Identification of a highly conserved domain on phytochrome from angiosperms to algae. *Plant Physiol.* 80:982-87
17. Diakoff, S., Scheibe, J. 1975. Cultivation in the dark of the blue-green alga *Fremyella diplosiphon*. A photoreversible effect of green and red light on growth rate. *Physiol. Plant.* 34:125-28
18. Dickson, L. G., Waaland, J. R. 1985. *Porphyra nereocystis*: a dual-daylength seaweed. *Planta* 165:548-53
19. Dring, M. J. 1967. Phytochrome in red alga, *Porphyra tenera*. *Nature* 215: 1411-12
20. Dring, M. J. 1970. Photoperiodic effects in microorganisms. In *Photobiology of Microorganisms*, ed. P. Halldal, pp. 345-68. London: Wiley
21. Dring, M. J. 1984. Photoperiodism and phyiology. In *Progress in Physiological Research*, ed. F. E. Round, D. J. Chapman, 3:159-92. Bristol: Biopress
22. Dring, M. J. 1984. Blue light effects in marine macroalgae. In *Blue Light Effects in Biological Systems*, ed. H. Senger, pp. 509-16. Berlin: Springer-Verlag
23. Dring, M. J. 1987. Marine plants and blue light. In *Blue Light Responses: Phenomena and Occurrence in Plants and Microorganisms*, ed. H. Senger, 2:121-40. Boca Raton, Fla: CRC Press
24. Dring, M. J., Lüning, K. 1975. A photoperiodic effect mediated by blue light in the brown alga *Scytosiphon lomentaria*. *Planta* 125:25-32
25. Dring, M. J., Lüning, K. 1975. Induction of two-dimensional growth and hair formation by blue light in the brown alga *Scytosiphon lomentaria*. *Z. Pflanzenphysiol.* 75:107-17
26. Dring, M. J., Lüning, K. 1983. Photomorphogenesis of marine macroalgae. In *Encyclopedia of Plant Physiology*, Vol. 16B, *Photomorphogenesis*, ed. W. Shropshire, H. Mohr, pp. 545-68. Heidelberg: Springer-Verlag
27. Dring, M. J., West, J. A. 1983. Photoperiodic control of tetrasporangium formation in the red alga *Rhodochorton purpureum*. *Planta* 159:143-50
28. Duncan, M. J., Foreman, R. E. 1980. Phytochrome-mediated stipe elongation in the kelp *Nereocystis* (Phaeophyceae). *J. Phycol.* 16:138-42
29. Durant, J. P., Spratling, L., O'Kelley, J. C. 1968. A study of light intensity, periodicity and wavelength on zoospore production by *Protosiphon botryoides* Klebs. *J. Phycol.* 4:356-62
30. Eberly, S. L., Spremulli, G. H., Spremulli, L. L. 1986. Light induction of the *Euglena* chloroplast protein synthesis elongation factors: relative effectiveness of different wavelength ranges. *Arch. Biochem. Biophys.* 245:338-47
31. Ekelund, N. G. A., Björn, L. O. 1987. Photophobic stop-response in a dinoflagellate: modulation by preirradiation. *Physiol. Plant.* 70:394-98
32. Epel, B., Krauss, R. W. 1966. The inhibitory effect of light on growth of *Prototheca zopfii* Kruger. *Biochim. Biophys. Acta* 120:73-83
33. Faust, M. A., Sager, J. C., Meeson, B. W. 1982. Response of *Prorocentrum mariae-lebouriae* (Dinophyceae) to light of different spectral qualities and irradiances: growth and pigmentation. *J. Phycol.* 18:349-56
34. Forward, R. B. 1973. Phototaxis in a dinoflagellate: action spectra as evidence for a two-pigment system. *Planta* 111:167-78
35. Forward, R., Davenport, D. 1968. Red and far-red light effects on a short-term behavioural response of a dinoflagellate. *Science* 161:1028-29
36. Foster, K. W., Saranak, J., Patel, N., Zarilla, G., Okabe, M., et al. 1984. A

- rhodopsin is the functional photoreceptor for phototaxis in the unicellular eukaryote *Chlamydomonas*. *Nature* 311: 756-59
37. Fujita, Y., Hattori, A. 1960. Effect of chromatic lights on phycobilin formation in a blue-green alga, *Tolypothrix tenuis*. *Plant Cell Physiol.* 1:293-303
 38. Germann, I. 1986. Growth phenology of *Pleurophycus gardneri* (Phaeophyceae, Laminariales), a deciduous kelp of the north east Pacific. *Can. J. Bot.* 64: 2538-47
 39. Giles, K. L. 1970. The phytochrome system, phenolic compounds, and aplanospore formation in a lichenized strain of *Trebouxia*. *Can. J. Bot.* 48:1343-46
 40. Gostan, J., Lcchuga-Deveze, C. 1986. Does blue light affect the growth of *Chaetoceros protuberans* (Bacillariophyceae)? *J. Phycol.* 22:63-71
 41. Guiry, M. D., Cunningham, E. M. 1984. Photoperiodic and temperature responses in the reproduction of north eastern Atlantic *Gigartina acicularis* (Rhodophyta: Gigartinales). *Phycologia* 23:357-67
 42. Häder, D.-P. 1987. Photomovement. See Ref. 23, 1:101-30
 43. Haupt, W. 1959. Die Chloroplastendrehung bei *Mougeotia*. I. Über den quantitativen und qualitativen Lichtbedarf der Schwachlichtbewegung. *Planta* 53:484-501
 44. Haupt, W., Thiele, R. 1961. Chloroplastenbewegung bei *Mesotaenium*. *Planta* 56:388-401
 45. Haupt, W. 1982. Light-mediated movement of chloroplasts. *Ann. Rev. Plant Physiol.* 33:205-33
 46. Haury, J. F., Bogorad, L. 1977. Action spectra for phycobiliprotein synthesis in a chromatically adapting cyanophyte, *Fremyella diplosiphon*. *Plant Physiol.* 60:835-39
 47. Hillman, W. S. 1979. *Photoperiodism in Plants and Animals* (Carolina Biology Reader 107). Burlington, NC: Carolina Biological Supply Co. 16 pp.
 48. Howland, G. P., Edwards, E. E. 1979. Photomorphogenesis of fern gametophytes. In *The Experimental Biology of Ferns*, ed. A. F. Dyer, pp. 393-434. London: Academic
 49. Humbeck, K., Schumann, R., Senger, H. 1984. The influence of blue light on the formation of chlorophyll-protein complexes in *Scenedesmus*. See Ref. 22, pp. 359-65
 50. Humphrey, G. H. 1983. The effect of the spectral composition of light on the growth, pigments and photosynthetic rate of unicellular marine algae. *J. Exp. Mar. Biol. Ecol.* 66:49-67
 51. Huth, K. 1979. Einfluss von Tageslänge und Beleuchtungsstärke auf den Generationswechsel bei *Batrachospermum monoliforme*. *Ber. Dtsch. Bot. Ges.* 92: 467-72
 52. Jaffe, L. 1954. Stimulation of the discharge of gametangia from a brown alga by a change from light to darkness. *Nature* 174:743
 53. Kamiya, A., Miyachi, S. 1984. Blue-green and green light adaptations on photosynthetic activity in some algae collected from subsurface chlorophyll layer in the western Pacific Ocean. See Ref. 22, pp. 517-28
 54. Kataoka, H. 1987. The light-growth response of *Vaucheria*. A *conditio sine qua non* of the phototropic response? *Plant Cell Physiol.* 28:61-71
 55. Kaufman, L. S., Lyman, H. 1982. A 600 nm receptor in *Euglena gracilis*: its role in chlorophyll accumulation. *Plant Sci. Lett.* 26:293-99
 56. Kirk, M. M., Kirk, D. L. 1985. Translational regulation of protein synthesis, in response to light, at a critical stage of *Volvox* development. *Cell* 41:419-28
 57. Kowallik, W., Schürmann, R. 1984. Chlorophyll a/chlorophyll b ratios of *Chlorella vulgaris* in blue or red light. See Ref. 22, pp. 353-58
 58. Kume, J. 1973. Beiträge zur Periozität der Oogon-Entleerung bei *Dicthyota dichotoma* (Phaeophyta). *Z. Pflanzenphysiol.* 70:191-210
 59. Lang, A. 1965. Physiology of growth and development in algae. A synopsis. In *Encyclopedia of Plant Physiology*, Vol. 15/1, ed. W. Ruhland, pp. 680-715. Berlin: Springer-Verlag
 60. Lazaroff, N., Vishniac, W. 1961. The effect of light on the development cycle of *Nostoc muscorum*, a filamentous blue-green alga. *J. Gen. Microbiol.* 25: 365-74
 61. Lipps, M. J. 1973. The determination of the far-red effect in marine phytoplankton. *J. Phycol.* 9:237-42
 62. Lobban, C. S., Weidner, M., Lüning, K. 1981. Photoperiod affects enzyme activities in the kelp, *Laminaria hyperborea*. *Z. Pflanzenphysiol.* 105:81-83
 63. Lockhart, J. C. 1982. Influence of light, temperature and nitrogen on morphogenesis of *Desmotrichum undulatum* (J. Agardh) Reinke (Phaeophyta, Punctariaceae). *Phycologia* 21:264-72
 64. Lüning, K. 1980. Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* species. *J. Phycol.* 16:1-15

65. Lüning, K. 1981. Photomorphogenesis of reproduction in marine macroalgae. *Ber. Dtsch. Bot. Ges.* 94:401-17
66. Lüning, K. 1981. Egg release in gametophytes of *Laminaria saccharina*: induction by darkness and inhibition by blue light and U.V. *Br. Phycol. J.* 16:379-93
67. Lüning, K. 1984. Growth and lack of chlorophyll *a* in a dark-cultivated *Delesseria sanguinea*. *Br. Phycol. J.* 19: 196-97
68. Lüning, K. 1986. New frond formation in *Laminaria hyperborea* (Phaeophyta): a photoperiodic response. *Br. Phycol. J.* 21:269-73
69. Lüning, K., Dring, M. J. 1973. The influence of light quality on the development of the brown algae *Petalonia* and *Scytosiphon*. *Br. Phycol. J.* 8:333-38
70. Lüning, K., Dring, M. J. 1975. Reproduction, growth and photosynthesis of gametophytes of *Laminaria saccharina* grown in blue and red light. *Mar. Biol.* 29:195-200
71. Lüning, K., Neushul, M. 1978. Light and temperature demands for growth and reproduction of laminarian gametophytes in Southern and Central California. *Mar. Biol.* 45:297-309
72. Mohr, H. 1972. *Lectures on Photomorphogenesis*. Heidelberg: Springer-Verlag. 237 pp.
73. Müller, S., Clauss, H. 1976. Aspects of photomorphogenesis in the brown alga *Dictyota dichotoma*. *Z. Pflanzenphysiol.* 78:461-65
74. Nagata, Y. 1973. Rhizoid differentiation in *Spirogyra*. II. Photoreversibility of rhizoid induction by red and far-red light. *Plant Cell Physiol.* 14:543-54
75. Nultsch, W. 1980. Effects of blue light on movement of microorganisms. In *The Blue Light Syndrome*, ed. H. Senger, pp. 38-49. Berlin: Springer-Verlag
76. Ohad, I., Schneider, H.-J. A. W., Gendel, S., Bogorad, L. 1980. Light-induced changes in allophycocyanin. *Plant Physiol.* 65:6-12
77. Ohki, K., Fujita, Y. 1979. In vitro transformation of phycobiliproteins during photobleaching of *Tolypothrix tenuis* to forms active in photoreversible absorption changes. *Plant Cell Physiol.* 20:1341-47
78. O'Kelley, J. C., Hardman, J. K. 1977. A blue light reaction involving flavin nucleotides and plastocyanin from *Protothrix botryoides*. *Photochem. Photobiol.* 25:559-64
79. Powell, J. 1986. A short-day photoperiodic response in *Constantinea subulifera*. *Am. Zool.* 26:479-87
80. Reddy, P. M., Talpasyi, E. R. S. 1981. Some observations related to red-far red antagonism in germination of spores of the cyanobacterium *Anabaena fertilissima*. *Biochem. Physiol. Pflanzen* 176: 105-7
81. Rentschler, H.-G. 1967. Photoperiodische Induktion der Monosporenbildung bei *Porphyra tenera* Kjellm. (Rhodophyta-Bangiophyceae). *Planta* 76:65-74
82. Rethy, R. 1968. Red (R), far-red (FR) photoreversible effects on the growth of *Chara* sporelings. *Z. Pflanzenphysiol.* 59:100-2
83. Richardson, N. 1970. Studies on the photobiology of *Bangia fuscopurpurea*. *J. Phycol.* 6:215-19
84. Rietema, H. 1973. The influence of day-length on the morphology of the *Halicystis parvula* phase of *Derbesia tenuissima* (De Not.) Crn. (Chlorophyceae, Caulerpales). *Phycologia* 12:11-16
85. Rietema, H., Breeman, A. M. 1982. The regulation of the life history of *Dumontia contorta* in comparison to that of several other Dumontiaceae (Rhodophyta). *Bot. Mar.* 25:569-76
86. Robinson, B. L., Miller, J. H. 1970. Photomorphogenesis in the blue-green alga *Nostoc commune* 584. *Physiol. Plant.* 23:461-72
87. Roscher, E., Zetsche, K. 1986. The effects of light quality and intensity on the synthesis of ribulose-1,5-bisphosphate carboxylase and its mRNAs in the green alga *Chlorogonium elongatum*. *Planta* 167:582-86
88. Ruyters, G. 1984. Effects of blue light on enzymes. See Ref. 22, pp. 283-301
89. Ruyters, G. 1987. Control of enzyme capacity and enzyme activity. See Ref. 23, 2:71-88
90. Ruyters, G., Hirose, T., Miyachi, S. 1984. Blue light effects on carbon metabolism in *Dunaliella*. See Ref. 22, pp. 317-22
91. Scheibe, J. 1972. Photoreversible pigment: occurrence in a blue-green alga. *Science* 176:1037-39
92. Schiff, J. A. 1980. Blue light and the photocontrol of chloroplast development in *Euglena*. See Ref. 22, pp. 495-511
93. Schmid, R. 1984. Blue light effects on morphogenesis and metabolism in *Acetabularia*. See Ref. 22, pp. 419-32
94. Schmid, R., Idziak, E.-M., Tünnermann, M. 1987. Action spectrum for the blue-light-dependent morphogenesis of hair whorls in *Acetabularia mediterranea*. *Planta* 171:96-103
95. Senger, H. 1987. Blue light control of

- pigment biosynthesis—chlorophyll biosynthesis. See Ref. 23, 1:75–85
96. Senger, H. 1987. Sun and shade effects of blue light on plants. See Ref. 23, 2:141–49
 97. Senger, H., Schoser, G. 1966. Die spektralabhängige Teilungsinduktion in mixotrophen Synchronkulturen von *Chlorella*. *Z. Pflanzenphysiol.* 54:308–20
 98. Shevlin, D. E., West, J. A. 1977. Gamete discharge in *Bryopsis hypnoides*: a blue light phenomenon. *J. Phycol.* 13(Suppl.):62
 99. Shihara, I. 1958. The effect of light on gamete liberation in *Monostroma*. *Bot. Mag. (Tokyo)* 71:378–85
 100. Sokol, R. C., Stross, R. G. 1986. Annual germination window in oospores of *Nitella furcata* (Charophyceae). *J. Phycol.* 22:403–6
 101. Stabenau, H. 1972. Aktivitätsänderungen von Enzymen bei *Chlorogonium elongatum* unter dem Einfluss von rotem und blauem Licht. *Z. Pflanzenphysiol.* 67:105–12
 102. Steinmüller, K., Zetsche, K. 1984. Photo- and metabolite regulation of the synthesis of ribulose biphosphate carboxylase/oxygenase and the phycobiliproteins in the alga *Cyanidium caldarium*. *Plant Physiol.* 76:935–39
 103. Takatori, S., Imahori, K. 1971. Light reactions in the control of oospore germination of *Chara delicatula*. *Phycologia* 10:221–28
 104. Taylor, A. O., Bonner, B. A. 1967. Isolation of phytochrome from the alga *Mesotaenium* and liverwort *Sphaerocarpaceus*. *Plant Physiol.* 42:762–66
 105. ten Hoopen, A., Bos, S., Breeman, A. M. 1983. Photoperiodic response in the formation of gametangia of the long-day plant *Sphacelaria rigidula* (Phaeophyceae). *Mar. Ecol. Prog. Ser.* 13:285–89
 106. Terborgh, J. 1965. Effects of red and blue light on the growth and morphogenesis of *Acetabularia crenulata*. *Nature* 207:1360–63
 107. Terry, L. A., Moss, B. L. 1980. The effect of photoperiod on receptacle initiation in *Ascophyllum nodosum* (L.) Le Jol. *Br. Phycol. J.* 15:291–301
 108. Thomas, J. P., O'Kelley, J. C., Hardman, J. K., Aldridge, E. F. 1975. Flavin as an active component of the photoreversible pigment system of the green alga *Protosiphon botryoides* Klebs. *Photochem. Photobiol.* 22:135–38
 109. Thompson, R. J., Davies, J. P., Mosig, G. 1985. "Dark lethality" of certain *Chlamydomonas reinhardtii* strains is prevented by dim blue light. *Plant Physiol.* 79:903–7
 110. van der Velde, H. H., Guiking, P., van der Wulp, D. 1975. Glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase in *Acrochaetium daviesii* cultured under red, white and blue light. *Z. Pflanzenphysiol.* 76:95–108
 111. van der Velde, H. H., Hemrika-Wagner, A. M. 1978. The detection of phytochrome in the red alga *Acrochaetium daviesii*. *Plant Sci. Lett.* 11:145–49
 112. Vince-Prue, D. 1975. *Photoperiodism in Plants*. London: McGraw-Hill. 444 pp.
 113. Vince-Prue, D. 1976. Phytochrome and photoperiodism. In *Light and Plant Development*, ed. H. Smith, pp. 347–69. London: Butterworths
 114. Vince-Prue, D. 1983. Phytochrome and photoperiodic physiology in plants. See Ref. 26, pp. 457–90
 115. Virgin, H. I. 1978. Inhibition of etiolation in *Spirogyra* by phytochrome. *Physiol. Plant.* 44:241–45
 116. Vogelmann, T. C., Scheibe, J. 1978. Action spectra for chromatic adaptation in the blue-green alga *Fremyella diplosiphon*. *Planta* 143:233–39
 117. Wallen, D. G., Green, G. H. 1971. Light quality in relation to growth, photosynthetic rates and carbon metabolism in two species of marine plankton algae. *Mar. Biol.* 10:34–43