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A Short Day Photoperiodic Response in *Constantinea subulifera*[1]

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SYNOPSIS. *Constantinea subulifera*, a perennial red alga with a bushy type growth, uses a short day (long night) photoperiodic response to initiate a new blade at the tips of several stipes in September to October. These blades complete the lag phase of their growth during the winter via a food transfer from the old blade.

Under a 9L-15D photoperiod it requires 21–28 days to initiate a new blade. The critical photoperiod is 11–12 hr. This is a phytochrome-mediated response which can be negated by a low quantum dose light break of red or blue light in the middle of a 16-hr dark period. Blades will initiate and grow in complete darkness.

The initiation of new blades in the fall and their slow growth throughout the winter (lag phase) gives *Constantinea subulifera* an advantage in capture of habitat space.

INTRODUCTION

In the algae the photoperiodic responses are quite diverse and are in some cases mediated by pigments other than phytochrome. Temperature is very important and can drastically modify the photoperiodic response (Lüning, 1980*a*). A short day photoperiodic response in *Acrochaetium asparagopsis* is responsive to an endogenous circadian rhythm which further complicates the elucidation of the photoperiod under experimental conditions (Hafez *et al.*, 1982).

It is the length of the dark period that determines the photoperiodic response. Short day (SD) plants respond if the period of uninterrupted darkness in a light-dark cycle of 24 hr exceeds some critical length; long day (LD) plants respond if the period of uninterrupted darkness in a light-dark cycle of 24 hr is less than some critical length.

I have categorized the photoperiodic responses in the algae under three general headings: those in which the growth is effected, those in which there is a change in vegetative morphology and those which initiate a development in the reproductive process. These changes are important in the life history and ecology of the individual organism.

Algae in which growth is effected are *Acetabularia crenulata*, where SD increase growth and chlorophyll content. In long day conditions under high light intensity they have an increased rate of cap formations (Terborgh and Thimann, 1964, 1965). *Pediastrum duplex* has increased growth and development under LD (Ermolaeva, 1960). Growth in the Mediterranean form of *Ulva lactuca* is inhibited in LD (Føyn, 1955). The diatoms *Fragilaria striatula* and *Synedra tabulata* have increased growth under LD whereas *Biddulphia aurita* and *Melosira moniliformis* show inhibition of growth under LD and high light conditions (Castenholz, 1964). One red alga *Porphyra tenera* has inhibited thallus growth under LD (Iwasaki, 1961).

Two genera of red algae that are under photoperiodic control show vegetative morphological changes. *Dumontia contorta* switches from microthalli formation under LD to macrothalli formation under SD (Rietema, 1982). The three species of *Constantinea* all initiate new blades under SD: *C. subulifera* (Powell, 1964), *C. rosa marina* (Lindstrom, 1980) and *C. simplex* (Powell, 1978, unpublished data).

In the brown algae, *Scytosiphon lomentaria* (Dring and Lüning, 1975), *Petalonia fascia* (Roelewald *et al.*, 1974) and *P. zosterifolia* (Lüning, 1980*a*), erect thalli arise from a prostrate crust under SD and within certain temperature ranges. In *Laminaria hyperborea* SD conditions induce new blade formation (Lobban *et al.*, 1981).

The remaining photoperiodic responses all involve reproduction in some way. In

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the green algae, *Chara fragilis* is vegetative in SD but undergoes sexual reproduction under LD (Karling, 1924); *Klebsormiduim flaccidum* produces zoospores under SD (Cain *et al.*, 1974); *Stigeoclonium amoenum* forms zygotes under LD (Abbas and Godward, 1963); *Ulothrix flacca* produces gametes under LD but the zygotes are dormant in LD germinating only under SD (Føyn, 1955); three *Monostroma* species (Tatewaki, 1972) and the *Monostroma grevellei* (Lüning, 1980*b*) produce zoospores in SD.

In the diatoms auxospore formation occurs in *Coscinodiscus concinnus* in SD (Holmes, 1966) and in *Melosira mummuloides* under intermediate days (Bruckmayer-Berkenbusch, 1955). In *Stephanopyxis palmeriana* resting spores are formed under SD and sexual reproduction occurs under LD (Steele, 1965).

In the Xanthophytes *Vaucheria sessilis* gametangia formation occurs under LD (League and Greulach, 1955).

In the brown alga *Ectocarpus siliculosus* the ratio of unilocular to plurilocular sporangia increases under LD (Müller, 1962); *Scytosiphon lomentaria* forms unilocular sporangia under SD (Tatewaki, 1966) and in *Laminaria saccharina* (Lüning and Dring, 1975) gametogenesis is triggered by SD.

Seven species of red algae form tetraspores under short days. These are *Acrochaetium pectinatum* (West, 1968), *A. asparagopsis* (Abdel-Rahman, 1982*a* and *b*), *Rhodochorton purpureum* (West, 1968, 1969; Dring and West, 1983) and *R. tenue* (West, 1968, 1969) and *Halymenia latifolia* (Maggs and Guiry, 1982), the *Hymenoclonium* stage of *Calosiphonia vermicularis* (Mayhoub, 1976) and the *Trailliella* stage of *Bonnemaisonia hamifera* (Lüning, 1980*b*).

Spyridia sp. germinates tetraspores in LD, conchosporangia are formed under SD in *Bangia fuscopurpurea* (Richardson and Dixon, 1968), *Porphyra tenera* (Kurogi, 1959), *P.* sp. (Kurogi and Sata, 1967), *P. abbotae* and *P. perforata* (Waaland and Dickson, 1983), whereas in *P. umbilicalis* (Kurogi and Sato, 1967) they are formed in LD. In *P. tenera* LD triggers carpospore formation and inhibits thallus growth. Two other observations made during cultivation experiments were "spore" formation under SD in *Goniotrichium elegans* and *Acrochaetium* sp. (Fries, 1963).

Most of these reactions involve the reproduction of the organism in some way and usually initiate a new phase in the life history of the plant. The initiation of a new phase is also the result of vegetative changes. Both the reproductive changes and the vegetative changes are timed by day length to take advantage of the changing environmental conditions with the habitat of the plant.

MATERIALS AND METHODS

I observed *Constantinea subulifera* in the natural habitat by SCUBA diving on marked transects for 14 months, on an outplanting device in the sea for one year (Neushul and Powell, 1964) and in the laboratory during three different periods (1963–1964, 1967–1968 and 1978–1979).

I collected the plants in the summer and held them in the laboratory in running sea water under continuous cool white fluorescent light until they were used for experiments. All the plants used in photoperiod experiments were collected from a rocky sublittoral reef adjacent to Friday Island (Brown Island on older maps) which is located in Friday Harbor, San Juan Island, Washington. *C. subulifera* is a perennial reaching ages of 14–15 yr. These older plants will have numerous apices. It is these apices that were used in the photoperiod experiments. I removed these from the plant by cutting the stipe 2–3 cm below the new blade, then trimmed the new blade to an approximate 5-cm circle surrounding the stipe. These were mounted in photoperiod boxes in sponge rubber holders. I fed sea water in one side and out the other by black rubber tubing inserted in a hole in the sides with the outlet tube adjusted to maintain a water depth which submerged the apices approximately 10 cm below the water surface. I used fluorescent fixtures mounted on the lids with a light-tight seal. These lights were controlled by interval timers and light break experiments were conducted with

incandescent and monochromatic light. The monochromatic light was provided by passing incandescent light through plexiglass filters and an aqueous solution of copper sulphate (Zalik and Miller, 1960). The transmission spectra at 50% transmission, the peak transmission and the quantum energies are shown in Table 1.

The quantum energy is that which reaches the water surface. The light breaks were 15 min for the red and far-red light and one hour for the blue because of the high quantum requirement and the transmission characteristics of the filter.

The response of apices to the photoperiod was measured weekly by removing the plant, cleaning off the epiphytes, observing the tip under a dissecting scope and measuring the length of the stipe from blade to stipe tip (Table 1, Fig. 5). Medial cross-sections of stipes were made on a freezing microtome, stained with aniline blue and mounted in Karo syrup mounting media for viewing microscopic characteristics.

TABLE 1. *Transmission data for light breaks in experiment 78-3, Table 2.*

Light quality	Peak transmission	Band width at 50% transmission	Quantum energy μmoles sec^{-1} cm^2
Blue	475	440–515	1.88 × 10
Red	630	585–660	1.70 × 10
Far-red	725	700–740	1.62 × 10

RESULTS

Constantinea subulifera has an erect thallus with a terete stipe arising from a disc-shaped holdfast. This stipe may reach a diameter of 5 mm and in older plants may dichotomize with each stipe branch terminated in a perfoliate, horizontal circular blade which is at first entire then splitting into pie-shaped segments. Internodes between blades average 8–10 mm with the lower portions of the stipe bearing "annual scars" which are the nodes where the previous year's blades were located. Counting these scars gives the age of the plant.

C. subulifera from the Friday Island population has an average age of 6.85 years. They initiate a new blade at the tip of the terete stipe in September to October. At this time, stipe elongation ceases and the new blade grows at a slow steady rate throughout the winter. In March a new stipe emerges on the upper surface of the new blade directly above the existing stipe and grows at a steady rate until initiation of a new blade in September to October (Fig. 5). At the same time the new stipe emerges, there is an approximately 1 mm elongation of the internode length caused by elongation of cortical cells directly beneath the new blade that was laid down at the time of blade initiation (Fig. 2). Initiation of the new blade in *C. subulifera* is first macroscopically observed as a roughening of the stipe tip followed by a flattening of the tip. A normal stipe before initiation is rounded and has a cortical area of 8–12 cells thick surrounding medullary tissue of elongated cells (see tip of stipe in Fig. 2). At the onset of blade initiation the medullary cells cease to elongate. This results in a buildup of cortical cells at the stipe tip which continues until there is a zone of cortical cells 50–60 cells thick. At this time a band of cortical cells 8–10 cells thick on the periphery of the stipe begins to cut off cells obliquely which results in the initiation of a cup-shaped blade (Figs. 3 and 4). In a population survey involving 88 mature plants with 711 apices there were 25 apices which initiated two blades in one year. These were all on two of the 88 plants. When this happens the first blade is initiated very soon after the onset of new stipe growth in March. This new blade initiates a new stipe which then in turn initiates a new blade, giving these plants shortened internode lengths (Powell, 1964).

The initiation of the blade in *C. subulifera* is an SD photoperiodic response with a critical day length of approximately 11–12 hr. On a 9L-15D regime it requires somewhere between 21 and 28 days of critical day lengths to insure initiation of a blade (Table 2, Exp. 9). On day lengths longer than the critical day length the number of critical day lengths needed for initiation increases.

Newly initiated stipes less than 1 mm in length will respond to SD by initiating new blades. A portion of the old blade is necessary for a healthy response. If it is all

TABLE 2. *Record of photoperiodic experiments.**

Exp. no.	Light intensity at water surface in foot candles	Light regime	No. of light treatments	Days until harvest	Average elongation in mm per 30 days	No. of apices	No. initiating new blade
9	100	9L-15D	7	175	1.16	9	0
		9L-15D	14	175	0.81	9	0
		9L-15D	21	175	0.86	9	0
		9L-15D	28	175	0.49	9	9
78-1	100	24L-0D	132	132	1.00	10	0
		10L-14D	50	132	0.44	10	10
		11L-13D	50	132	0.51	10	10
		12L-12D	50	132	0.67	10	5
		13L-11D	50	132	0.98	10	0
		14L-10D	50	132	1.07	10	0
		0L-24D	169	169	0.45	10	10
38	240	11L-13D	45	95	0.72	20	20
	240	12L-12D	45	95	0.79	20	15
	240	13L-11D	45	95	1.07	20	0
	45	12L-12D	45	95	0.78	20	7
	10	12L-12D	45	95	0.71	20	1
78-3	100	8L-8D-0.25L-7.75D	28 Blue	102	0.77	10	0
See Table 1		8L-8D-0.25L-7.75D	28 Red	102	0.75	10	0
		8L-8D-0.25L-7.75D	28 FR	102	0.64	10	10
		8L-8D-0.5L-7.5D	28 Red-FR	102	0.66	10	1
		8L-8D-0.5L-7.5D	28 FR-Red	102	0.69	10	0
		8L-16D	28	102	0.42	10	10
78-5	100	8L-8D-15 sec L-8D	28	94	0.87	10	0
		8L-8D-5 sec L-8D	28	94	0.66	10	3

* See "Materials and Methods" for conditions of light breaks in Exp. 78-3. In experiment 78-5 light breaks were incandescent light of 15 seconds and 5 seconds. After all light treatments plants were held in continuous cool white fluorescent light until time of harvest.

trimmed away the stipe will respond to a critical photoperiod but it will also shrivel. The new blade will be poorly developed, and will not grow.

Continuous light at a quantum flux of 1×10^5 μmoles sec^{-1} cm^2 at the water surface will keep the plant from initiating new blades. Under continuous light or photoperiods longer than 13 hr the stipe continues to elongate. Plants held under continuous light for over a year have stipes 22 mm long (Fig. 1) which are still responsive to a critical photoperiod. Light breaks in the middle of the dark period in an 8L-16D regime of 15 sec at a quantum flux of 1.0×10^5 μmoles sec^{-1} cm^2 of incandescent light will inhibit blade initiation. A light break of five seconds partially blocks the response (Table 2, Exp. 78-5). Light breaks with monochromatic light prove the response is mediated by phytochrome (Table 2, Exp. 78-3). Blue and red lights break the response, far-red does not break the response (Fig. 5). Red, far-red reversal and far-red, red reversal show some plants under both treatments with a partial response (Exp. 78-3). This is a low energy response and seems to be more sensitive than the response in *Porphyra tenera* (Dring, 1967*a*, 1970; Rentschler, 1967). Dring obtained 50% inhibition of sporangia production with red light at the same total energy as those used with *Constantinea subulifera*. In *C. subulifera* there is a total supression of blade initiation with both the red and the blue light breaks. Experiment 78-5 also indicates that the photoreceptive pigment saturates very quickly, requiring somewhere between 5 to 15 sec at 1.0×10^5 μmoles sec^{-1} cm^2.

When a plant is subjected to a critical photoperiod it is approximately two weeks before I can detect any microscopic change in the stipe tip and there is no appreciable difference in stipe elongation between those under a critical photoperiod and those which are not until about five weeks after the treatment begins. It is six to seven weeks

before the cortical cells achieve their maximum thickness and begin to initiate the new blade. The process becomes irreversible under a 9L-15D photoperiod between 21 and 28 days (Exp. 9). Between 7 and 14 days it has committed itself morphologically to the laying down of cortical cells in preparation for new blade formation. If removed from the critical photoperiod at this time and placed under a noninductive period, stipe elongation resumes, but at a slower rate and with a restricted diameter (Figs. 2, 3).

New blades can be initiated in complete darkness and will grow blades up to 13 mm in diameter. This is possible because there is a transfer of energy from the old blade to the new blade.

DISCUSSION

Photoperiodic responses are used by organisms to enhance their fitness in some way. In *C. subulifera,* a perennial plant, the lag phase of its annual vegetative growth is completed during the winter months, giving it a distinct advantage over other perennials which cannot do this or annuals that start from a spore at the beginning of the growing season. The short day response which initiates new blade growth in the autumn is enhanced by a food storage facility which allows the lag phase of the blade to grow during the adverse winter season. In certain habitats this growth pattern, triggered by the photoperiodic response, in conjunction with the perennial habit and bushy, expanding growth habit, allow *C. subulifera* to become the dominant alga.

One additional factor which aids optimum growth of *C. subulifera* in the late spring and summer is the presence of two snail genera (*Margarites* and *Lacuna*) which live on the surface of the *C. subulifera* blades in large numbers. My experiments in the laboratory and the inspection of plants in the field show that the snails do not eat the *Constantinea* but rather remove the epiphytes. Plants we maintained on an outplanting device (Neushul and Powell, 1964) without a snail population were covered with epiphytes which had to be removed by hand at the monthly measuring time.

Photoperiodic responses in the algae do not all fit into the pattern found in flowering plants where phytochrome is the chief photomorphogenic light receptor. Phytochrome has been isolated from the algae by Van der Velde and Hemrika-Wagner (1978). *Porphyra tenera* (Dring, 1967*b*; Rentschler, 1967), *Bangia fuscopurpurea* (Richardson and Dixon, 1968; Richardson, 1970), the *Hymenclonium* stage of *Calosiphonia vermicolaris* (Mayhoub, 1976) are all SD plants which respond to low intensity light breaks in the red, far-red area of the spectrum when given in the middle of a critical dark period. Lipps (1973) has found four species of marine phytoplankton, a diatom, a coccolithophorid, a green flagellate and a dinoflagellate, which have a decrease in division rate if given far-red light just before the dark period. This effect is reversed by giving a red treatment after the far-red. Stipe elongation in *Nereocystis luetkeana* is increased by far-red and inhibited by red (Duncan and Foreman, 1980). This research provides evidence that phytochrome-like responses occur in all the major groups of marine algae except the Cyanobacteria.

There are several other reported responses which accomplish the same results but seem to be mediated by pigments other than phytochrome and do not respond to a light break in the dark period. West (1968) reported a SD response in *Acrochaetium pectinatum* which did not respond to a light break. Several of the photoperiodic responses I have cited in this paper have similar responses. A very interesting SD response in a brown alga, *Scytosiphon lomentaria* (Dring and Lüning, 1975), is responsive to a low intensity blue light break which was not reversed by other wavelengths. Neither was the plant responsive to red or far-red light breaks. Dring and West (1983) show an even more complex reaction in *Rhodochorton purpureum,* a SD response which can be inhibited by both red and blue light breaks. The red break could not be reversed by far-red light. This is very similar to the response in *C. subulifera* in which only partial reversal can be achieved with red, far-red reversal (Table 2, Exp. 78-3). In our search for phytochrome-like responses and photoperiods we sometimes forget the separation of the initial light reception from the measured

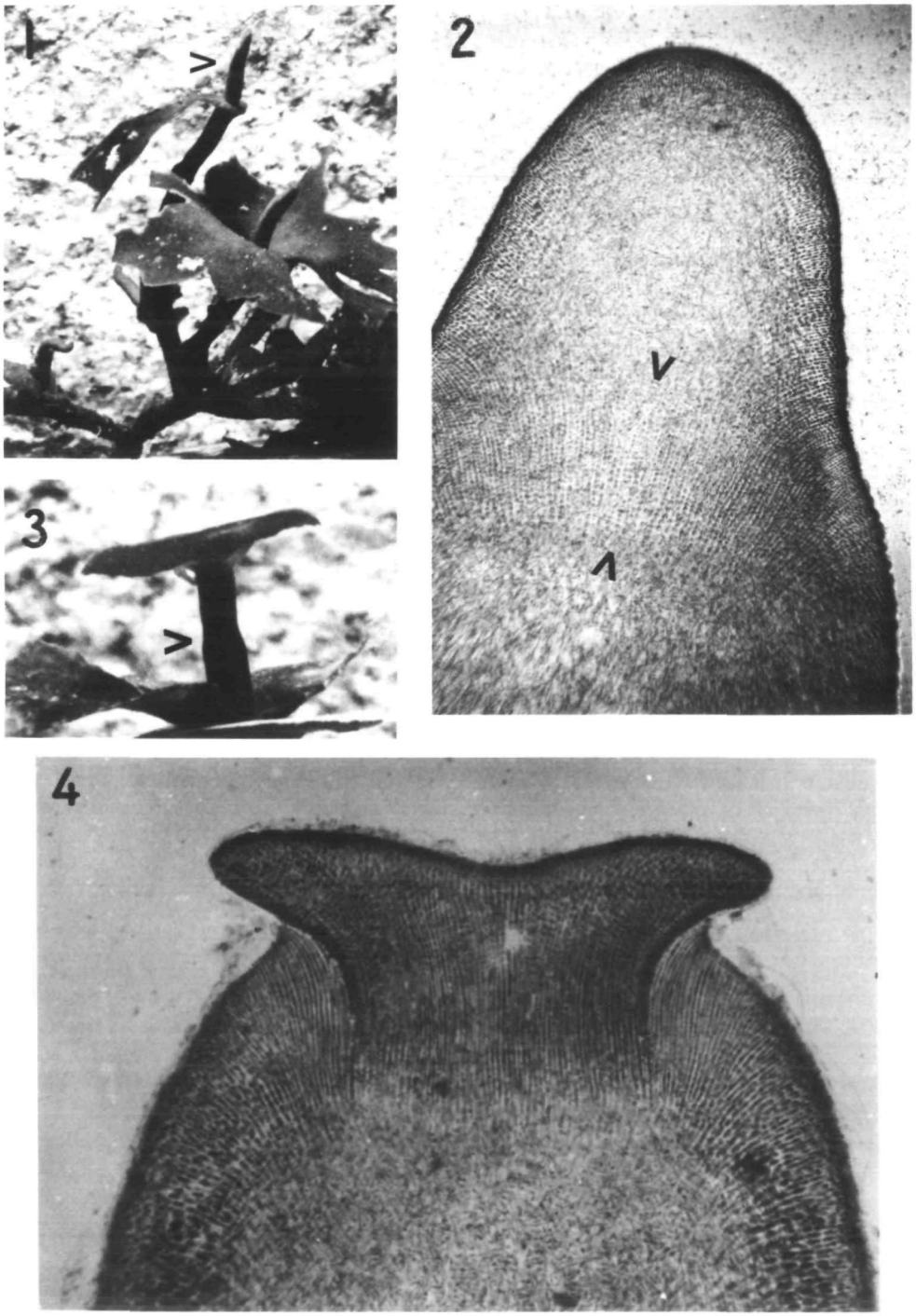

FIG. 1. Portion of a plant held under continuous light for 14 mo. Stipe above blade is approximately twice the normal length.

FIG. 2. Medial longitudinal section of apical tip. Collected on 26 August, it had already started to initiate a new blade. This section shows the stipe after three months of continuous light which caused it to resume apical growth. Area between arrows is where cortical cells are laid down in response to SD. Note the restriction

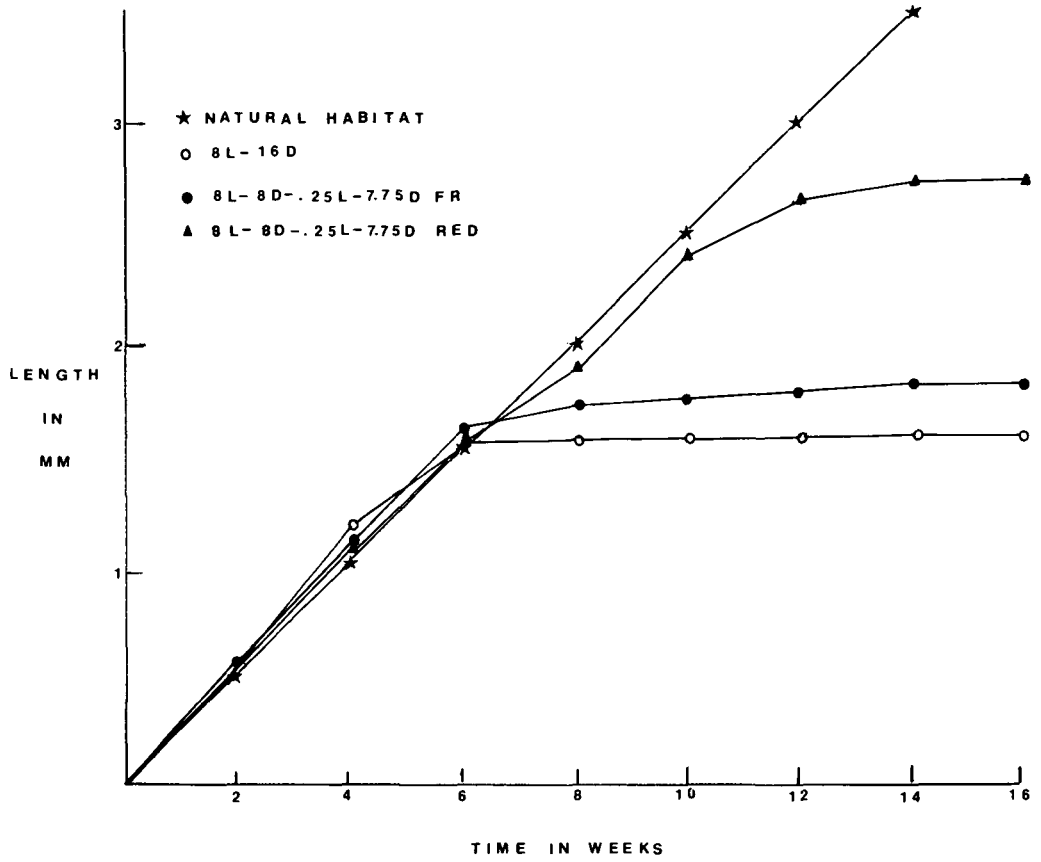

FIG. 5. Stipe elongation in the natural habitat proceeds at the rate of approximately 1 mm per month. Plants on long days or under continuous light in the laboratory grow at this same rate (see Table 1). This graph compares stipe elongation with time in the natural habitat to those plants used in experiment 78-3. The curves for the two reversal treatments (Red-FR and FR-Red) were left out. They were approximately the same and would fall between Red treatment and the FR treatment.

response (generally a gross response in growth or reproduction) which in most cases is separated by a long chain or web of intermediate reactions, some of which are dependent on light, temperature and other growth factors. For example, Lobban *et al.* (1981) have shown enzyme activity changes in the SD response of *Laminaria hypoborea* where light breaks effect the activity level of four enzymes. It matters little what type of molecule the initial light receptor is as long as it can trigger the physiological response necessary to initiate the eventual measured response. Nor does it matter to the plant whether the response is negated or enhanced by a light break. The importance to the plant is the measurement of seasons so that it might take advantage of an ecological situation in order to establish its position in the habitat. The important test is whether the response can continue in a viable way into either lengthening or shortening days depending on whether it is a SD or a LD response.

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of the stipe on resumption of apical growth and the return to medullary-type cells in the central portion of the stipe.

FIG. 3. New blade on a stipe like the one in Figure 2. Note constriction where stipe resumed apical growth (arrow).

FIG. 4. Medial longitudinal section of a newly intitiated blade.

Any molecule that can absorb photons and initiate a change in the physiology of the organism is capable of initiating a photoperiodic response and in a sense is a photoreceptor just as are more discrete photoreceptors in the animals. All photoperiodic responses are initiated by the absorption of photons occurring at a discrete wavelength. This makes it important that researchers pay close attention to light quality.

An additional factor that further complicates photoperiodic experiments is the existence of endogenous rhythms which make the pigments (or physiological reactions downstream from light absorption) more reactive at certain times than at others. It is becoming increasingly apparent that all organisms probably have endogenous rhythms. Whether these enter into all photoperiodic responses can only be shown by the proper experiments, such as those by Hafez and Abdel-Rahman (1982) in *Acrochaetium asparagopsis.*

I believe future investigations will reveal a lot more vegetative responses in the benthic algae which are sensitive to day length for the initiation of their vegetative thallus. In many respects the initiation of the vegetative thallus, given proper growing conditions, is really the advent of the development of reproductive structures which need no further clues and thus this vegetative initiation is the beginning of "flowering." In *C. subulifera* the basic response is one which stops apical growth and initiates lateral growth. This is analogous to the initiation of lateral flower buds in flowering plants. Thus, in a sense, the initiation of the new blade in *C. subulifera* is not only the initiation of new vegetative growth but also the production of gametes and tetraspores.

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