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Photosynthetic responses of Florida seaweeds to light and temperature: a physiological survey

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PHOTOSYNTHETIC RESPONSES OF FLORIDA SEAWEEDS TO LIGHT AND TEMPERATURE: A PHYSIOLOGICAL SURVEY

Arthur C. Mathieson and Clinton J. Dawes

ABSTRACT

The photosynthetic responses of 37 tropical seaweeds (14 Chlorophyceae, 5 Phaeophyceae and 18 Rhodophyceae) were measured in a Gilson Warburg Apparatus under a variety of light and temperature regimes. The brown algae *Padina vickersiae* and *Sporochnus pedunculatus* exhibited the lowest saturation light intensity (263 $\mu E/m^2/sec$), while five green algae (*Acetabularia crenulata, Cladophora coelothrix, Dictyosphaeria cavernosa, Monostroma oxyspermum* and *Codium repens*) had the highest light optima (3,843–4,258 $\mu E/m^2/sec$). Overall, the Chlorophyceae exhibited the broadest range of light optima; in contrast, the Phaeophyceae primarily had low light optima, while several Rhodophyceae had higher light optima. The thermal optima for 34 seaweeds ranged from 15–30°C. *Caloglossa leprierii, Botryocladia occidentalis, Codium taylorii, Soliera tenera* and *Codium intertextum* exhibited relatively broad thermal optima, with *C. leprierii* having the most eurythermal response. The Chlorophyceae exhibited thermal optima between 15–30°C, the Phaeophyceae between 15–27°C, and most Rhodophyceae between 18–24°C. Few taxa, except for *Cladophora coelothrix* and *Dictyosphaeria cavernosa,* had broad physiological tolerances to both high temperature and light regimes. Overall, the Phaeophyceae exhibited the most restricted temperature and light optima, while the Chlorophyceae and Rhodophyceae exhibited broader tolerances.

Until recently there have been few comparative physiological investigations of Florida seaweeds. Previous studies of photosynthetic and respiratory responses of Florida seaweeds have been concerned with the estuarine intertidal red alga *Bostrychia binderi* (Dawes et al., 1978; Durako and Dawes, 1980; Hoffman and Dawes, 1980; Davis and Dawes, 1981), the euryhaline subtidal red algae *Gracilaria tikvahiae* (Lapointe et al., 1984) and *Hypnea musciformis* (Dawes et al., 1976; Durako and Dawes, 1980) as well as a few open coastal species, including the brown alga *Sargassum* (Prince, 1980), the green alga *Batophora oerstedii* (Morrison, 1984) and the red alga *Eucheuma* (Mathieson and Dawes, 1974; Moon and Dawes, 1976). Overall, the photosynthetic responses of these seaweeds show a broad tolerance to light and temperature, comparable to northern intertidal and shallow subtidal species (Stocker and Holdheide, 1938; Kanwisher, 1966; Mathieson and Burns, 1971; Mathieson and Norall, 1975a; 1975b; Brinkhuis et al., 1976). Even so the limited number of Florida seaweeds studied and the varied techniques employed make it difficult to generalize. The present study was initiated in order to compare the photosynthetic responses to light and temperature of a number of subtropical and tropical species from Florida. Of particular interest was whether the physiological responses of the plants could be correlated with their known distribution (both horizontal and vertical) and/or seasonal occurrence.

METHODS AND MATERIALS

Most of the samples for this study were collected during a series of autecological and floristic studies of Florida marine algae (Dawes et al., 1974a; 1974b; Mathieson and Dawes, 1974; 1975); the remainder were collected during the same period (1971–1972) on the west coast of Florida (Table 1). After being collected, the plants were maintained in an ice chest and were transported to the laboratory within a 0.5–7.0 h of collection. Standard size sections (i.e., 2.5–3.0 cm) were cut from terminal frond portions

Table 1. Dates and collection sites in Florida

Specimens	Sites*	Dates
Chlorophyceae		
Acetabularia crenulata	Surprise Lake	5 March 1972
Anadyomene stellata	Homasassa River	6 March 1972
Bryopsis plumosa	Anclote Key	18 March 1972
Caulerpa paspaloides	Homasassa River	19 May 1972
Chaetomorpha aerea	Point of Rocks	6 March 1972
Chaetomorpha linum	Tampa	19 January 1971
Cladophora coelothrix	Tampa	2 March 1972
Codium intertextum	Florida Middle Grounds	20 January 1972
Codium repens	Florida Middle Grounds	20 January 1972
Codium taylorii	Anclote Key	13 January 1972
Cymopolia barbata	Surprise Lake	5 March 1972
Dictyosphaeria cavernosa	Molasses Key	20 March 1972
Halimeda incrassata	Homasassa River	31 May 1972
Monostroma oxyspermum	Tampa	2 March, 12 May 1972
Phaeophyceae		
Eudesme virescens	Homasassa River	12 November, 13 January 1972
Padina vickersiae	Homasassa River	22 February 1972
Rosenvingiella intricata	Homasassa River	12 November 1971, 13 January 1972
Sargassum hystrix	Homasassa River	13 January, 2 March 1972
Sporochnus pedunculatus	Homasassa River	12 November 1971, 22 February 1972
Rhodophyceae		
Bostrychia rivularis	Tampa	19 January 1971
Botryocladia occidentalis	Anclote Key	28 April 1972
Bryothamnion seaforthii	Money Key	16 February, 20 March 1972
Bryothamnion triquetrum	Money Key	11 December 1971, 16 February 1972
Caloglossa leprierii	Tampa	19 January, 2 March 1972
Corynomorpha clavata	Money Key	11 December 1971
Eucheuma gelidium	Molasses Key	25 October, 11 December 1971
Eucheuma gelidium-acathocladum type	Anclote Key & Sarasota	31 May 1972, 25 October 1971, 20 April 1972
Eucheuma isiforme var. *denudatum*	Anclote Key	5 November 1971
Eucheuma isiforme var. *isiforme*	Molasses Key	16 October, 12 November 1971
Gracilaria confervoides	Tampa	1 & 19 January, 2 March 1972
Gracilaria debilis	Molasses Key	7 January 1972
Halymenia pseudofloresia	Homasassa River Anclote Key	11 November 1971 13 January 1972
Hypnea musciformis	Molasses Key	7 January 1972
Laurencia intricata	Anclote Key	15 March 1972
Laurencia poitei	Bahia Honda Key	5 February 1972
Scinaia complanta	Anclote Key	28 April 1972
Soliera tenera	Tampa & Homasassa River	13 January 1972 11 November 1972

* See Dawes (1974), Dawes et al. (1974b) and Mathieson and Dawes (1975) for detailed habitat descriptions of most of the sites.

and immersed in artificial seawater (Chapman, 1962). The sections were held for 24–36 h at 20°C and at 986–1,972 microeinsteins (i.e., $\mu E/m^2/sec$) to minimize wound respiration prior to initiating the experiment. The rates of net photosynthesis were then measured in a Gilson Warburg Apparatus (Model RWBP-3), equipped with a series of 60-watt incandescent light bulbs. The light intensities

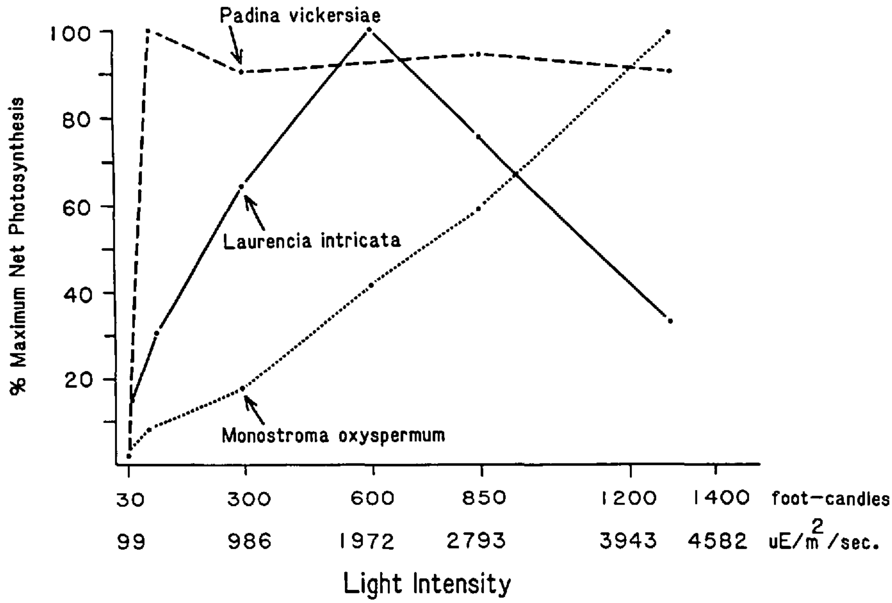

Figure 1. Net photosynthesis (as % of maximum) of *Laurencia intricata, Monostroma oxyspermum* and *Padina vickersiae* at various light intensities and 20°C.

reaching the bottom of the manometric flasks were varied by means of a rheostat. The intensities were measured with both a Lambda Model L.K. 185 Quantum Photometer (microeinsteins) and a General Electric Model 2.3 Photometer (foot-candles). The former instrument records photosynthetically active radiation in the 400–700 nm wave band. As stressed by Bickford and Dunn (1972), temperature affects the spectral emission of lamps; however, the spectral shift over the temperature range in our studies is small.

In all of the photosynthetic studies a single thallus section was placed in a reaction flask containing 10 ml of buffered seawater (Chapman, 1962). The samples were equilibrated for 30–40 min prior to the initiation of each photosynthetic run, in order to keep the temperature of the flasks and water bath identical. Each run was made for 50–60 min, with readings taken at 10- to 20-min intervals. Six replicates were used in each experiment; the mean and standard deviations for each parameter were calculated for subsequent statistical comparisons (Sokal and Rohlf, 1981). All light experiments were run at 20°C, while the subsequent temperature runs were conducted at the individual light optimum determined for each species. All of the photosynthetic data (i.e., net photosynthesis) were calculated as μl oxygen/g dry weight/h. Only a few representative light and temperature photosynthetic response curves (i.e., expressed as percentage of maximum net photosynthesis) are summarized herein, while a detailed compilation of the individual light and temperature optima (i.e., as designated by the P max values) for each species and class of seaweed is given. In the latter summaries, which are expressed as frequency (%) distribution plots, only the initial P max values are employed.

Results

Light Intensity.—Figure 1 illustrates the net photosynthesis (as percentage of maximum) of three representative green, brown and red algae at various light intensities. The light response of the red alga *Laurencia intricata,* which was typical of the majority of seaweeds tested, showed increased photosynthesis with increasing light intensity up to 1,972 $\mu E/m^2/sec$, beyond which it declined. Thus, light intensities above 1,972 $\mu E/m^2/sec$ were saturating, while lower intensities were limiting. Among the other plants studied, similar low to intermediate light optima were observed for *Codium taylorii, Sargassum hystrix, Sporochnus pedunculatus, Caloglossa leprierii* and *Halymenia pseudofloresia* (Fig. 2). The light response of

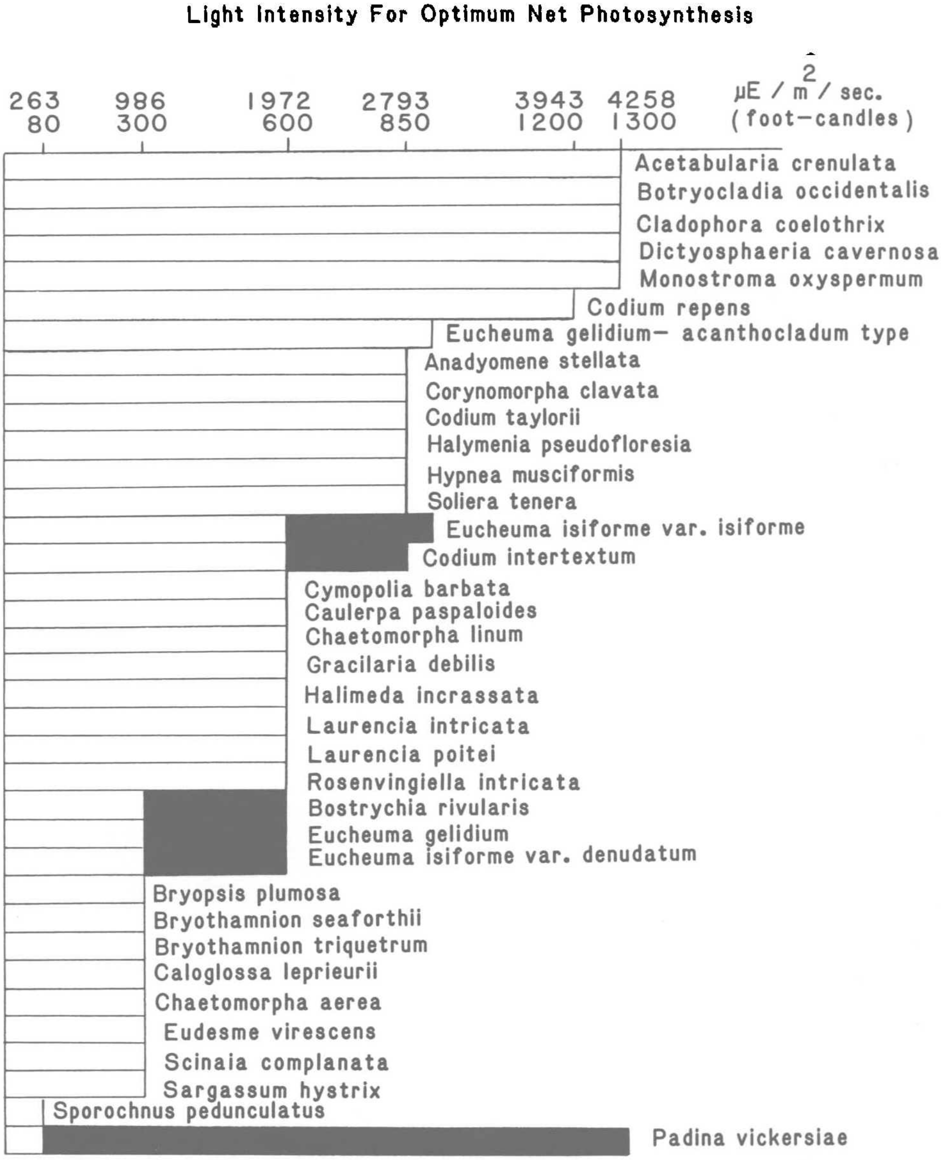

Figure 2. Summary of optimal light intensities (based upon P max values) for 36 species of Florida seaweeds at 20°C. The statistically equivalent photosynthetic responses at higher intensities are designated in black.

the lightly calcified brown alga *Padina vickersiae* was the most extreme (Fig. 1), having a low saturation intensity (263 $\mu E/m^2/sec$) with a broad optimum/tolerance to high light intensities—i.e., up to 4,258 $\mu E/m^2/sec$. The photosynthetic response of the green alga *Monostroma oxyspermum* increased correspondingly between 99 and 4,258 $\mu E/m^2/sec$, with no light saturation being evident.

A summary of the optimum light intensity for 36 seaweeds is outlined in Figure 2, the data being derived from photosynthetic responses as described above (Fig. 1). If the photosynthetic responses of an individual species were statistically equiv-

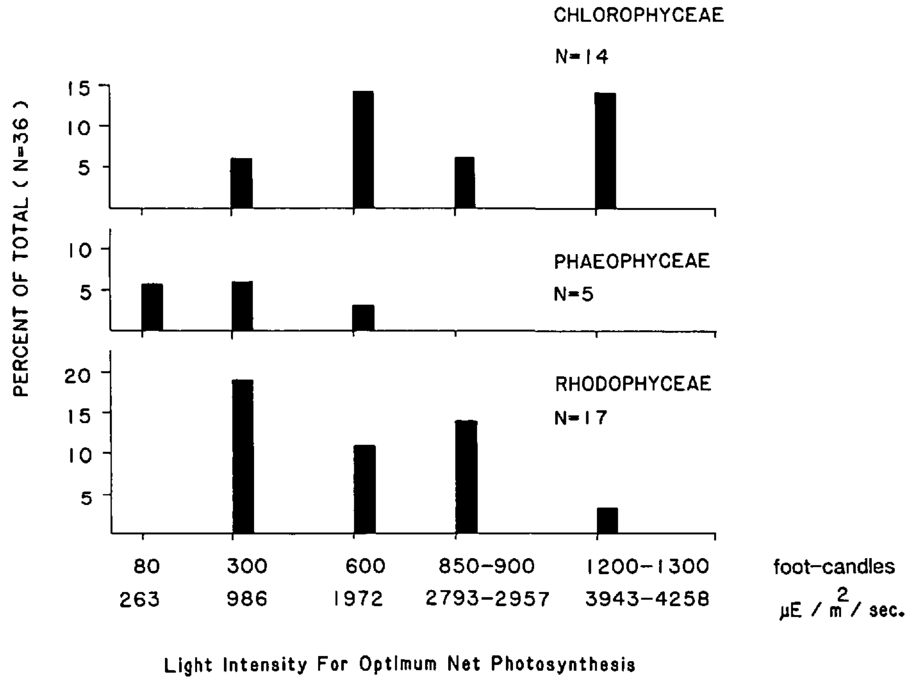

Figure 3. Frequency (%) distribution patterns of optimal light intensities for 36 species of Florida Chlorophyceae, Phaeophyceae and Rhodophyceae at 20°C.

alent for a series of higher light intensities (i.e., above the P max value) then these values were designated graphically in black. For example, *Padina vickersiae* exhibited a "plateau" of statistically equivalent values between 263–4,258 $\mu E/m^2/sec$, and this was demonstrated in Figure 2 by a long black line. On the other hand, a second brown alga, *Sporochnus pedunculatus,* which also had a low light saturation level of 263 $\mu E/m^2/sec$, exhibited a restricted light optimum, with its photosynthetic response dropping off after P max was attained. Most of the other 34 taxa evaluated had higher light optima, ranging from 986–4,258 $\mu E/m^2/sec$. Eleven seaweeds exhibited maximum photosynthesis at 986 $\mu E/m^2/sec$, 10 at 1,972, 6 at 2,793, 1 at 2,947, and 6 between 3,943–4,258 $\mu E/m^2/sec$. Five of the six taxa with the highest light optima (i.e., 3,843–4,258 $\mu E/m^2/sec$) were green algae: *Acetabularia crenulata, Cladophora coelothrix, Dictyosphaeria cavernosa, Monostroma oxyspermum* and *Codium repens.* In addition, *Eucheuma isiforme* var. *isiforme, Codium intertextum, Bostrychia rivularis, E. gelidium* and *E. isiforme* var. *denudatum* all exhibited relatively broad light optima, although not of the same magnitude as *P. vickersiae* (Fig. 2). In comparing the light optima for the different *Eucheuma* taxa (sensu Cheney, 1975) substantial differences were evident.

Figure 3 gives a further evaluation of the photosynthetic responses to light up to P max for the 36 seaweeds, expressed as a frequency (%) distribution plot. Overall, the Phaeophyceae and Rhodophyceae exhibited a pattern of decreasing frequency from low to high light intensities. Even so, the Phaeophyceae primarily had low light optima, while several Rhodophyceae had higher light optima. Of the three major groups of seaweeds, the Chlorophyceae had the broadest range of light optima (Fig. 2).

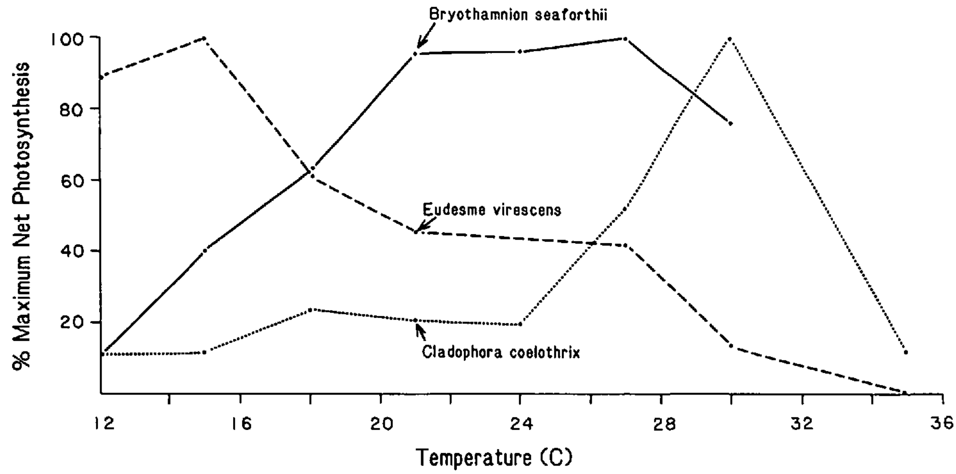

Figure 4. Net photosynthesis (as % of maximum) of *Bryothamnion seaforthii, Cladophora coelothrix,* and *Eudesme virescens* at various temperatures and at their individual light optima (cf. Fig. 2).

Temperature.—Figure 4 illustrates the net photosynthesis (as percentage of maximum) of three representative green, brown and red algae at various temperatures between 12–34°C. The thermal optima of these plants were extremely variable, being 15–29°C. Typically, net photosynthesis increased with increasing temperature up to a maximum (i.e., the thermal optimum or P max), beyond which it decreased either gradually or precipitously.

A summary of the temperature optima (P max) for all 34 seaweeds studied is given in Figure 5. The statistically equivalent photosynthetic values beyond the thermal optima are designated in black. Overall, the thermal optima ranged from 15–30°C, with 5 seaweeds having their maximum net photosynthesis at 15° C, 4 at 18°C, 2 at 20°C, 6 at 23°C, 7 at 27°C and 4 at 30°C. *Caloglossa leprierii, Botryocladia occidentalis, Codium taylorii, Soliera tenera,* and *Codium intertextum* exhibited relatively broad thermal optima, with the first taxa being the most tolerant. A frequency distribution plot of the temperature of initial maximum photosynthesis (P max) is given for all 34 seaweeds (Fig. 6). The Chlorophyceae exhibited a pattern of broad tolerance, with the frequency of thermal optima increasing between 15–21°C and being approximately the same at 30°C. The Phaeophyceae showed a contrasting pattern with decreasing frequencies between 15–27°C. The Rhodophyceae exhibited an intermediate pattern with their highest frequencies between 18–24°C.

Temperature and Light.—A summary of the corresponding temperature and light optima of 34 seaweeds is given in Figure 5. Relatively few taxa had broad tolerances to both parameters, while most were more tolerant to one parameter than the other. For example, *Cladophora coelothrix* and *Dictyosphaeria cavernosa* had high temperature and light optima (i.e., 30°C and 4,258 μE/m^2/sec). In contrast, *Botryocladia occidentalis* and *Acetabularia crenulatus* exhibited high light but reduced thermal optima (i.e., 4,258 μE/m^2/sec and 20°C). The broad tolerance to light (i.e., 263–4,258 μE/m^2/sec) but reduced thermal optima (20°C) of *Padina vickersiae* should also be noted. In contrast, species found within shallow subtidal communities such as *Bostrychia rivularis, Bryopsis plumosa, Bryothemnion seaforthii, B. triquetrum* and *Sargassum hystrix* had low light optima (986 μE/m^2/sec) but high temperature optima (27–30°C). *Eudesme virescens, Scinaia com-*

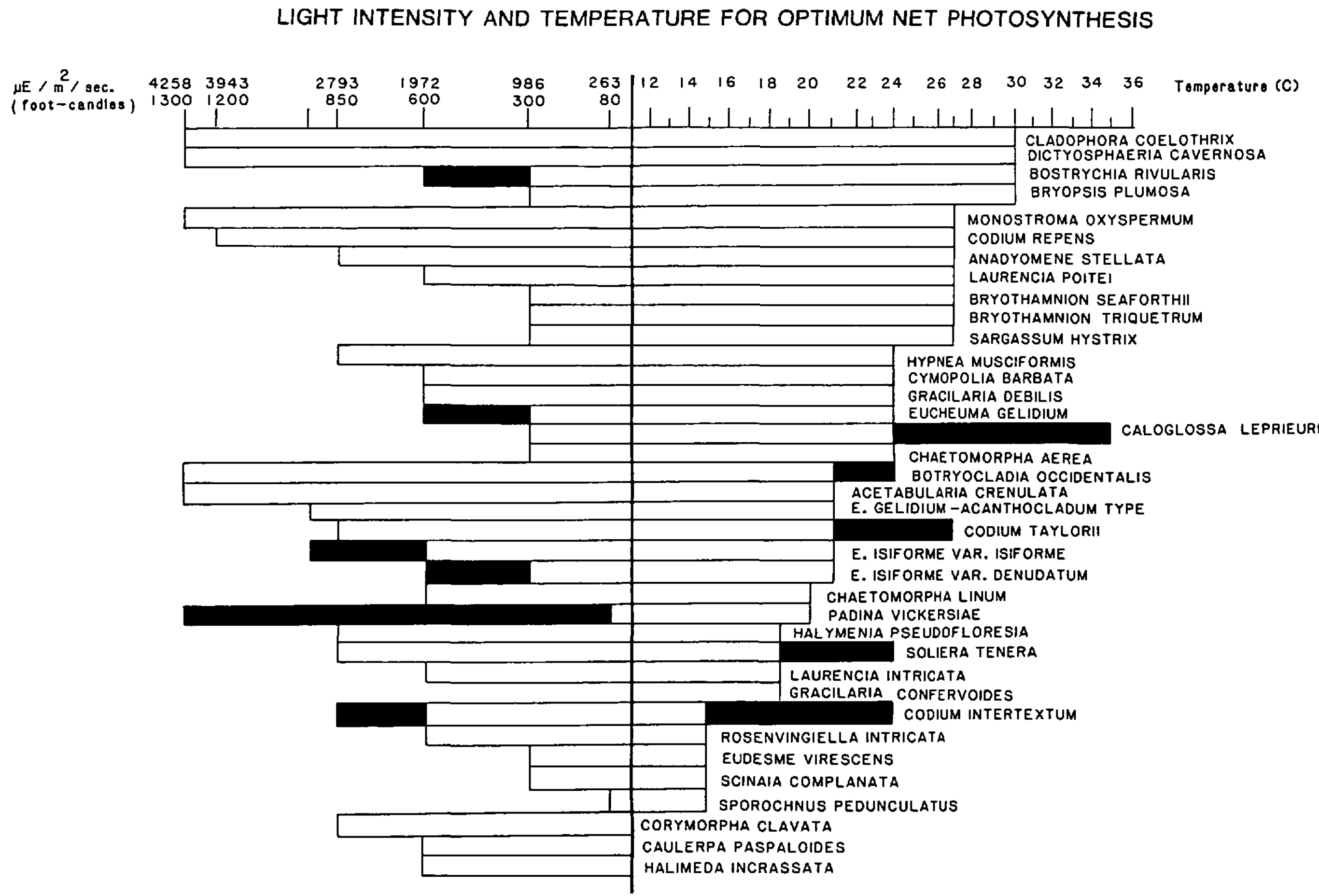

Figure 5. Summary of corresponding temperature and light optima of 37 species of Florida seaweeds; the light optima of *Corymorpha clavata*, *Caulerpa paspaloides* and *Halimeda incrassata* were not determined. The statistically equivalent photosynthetic responses above the respective optima are designated in black.

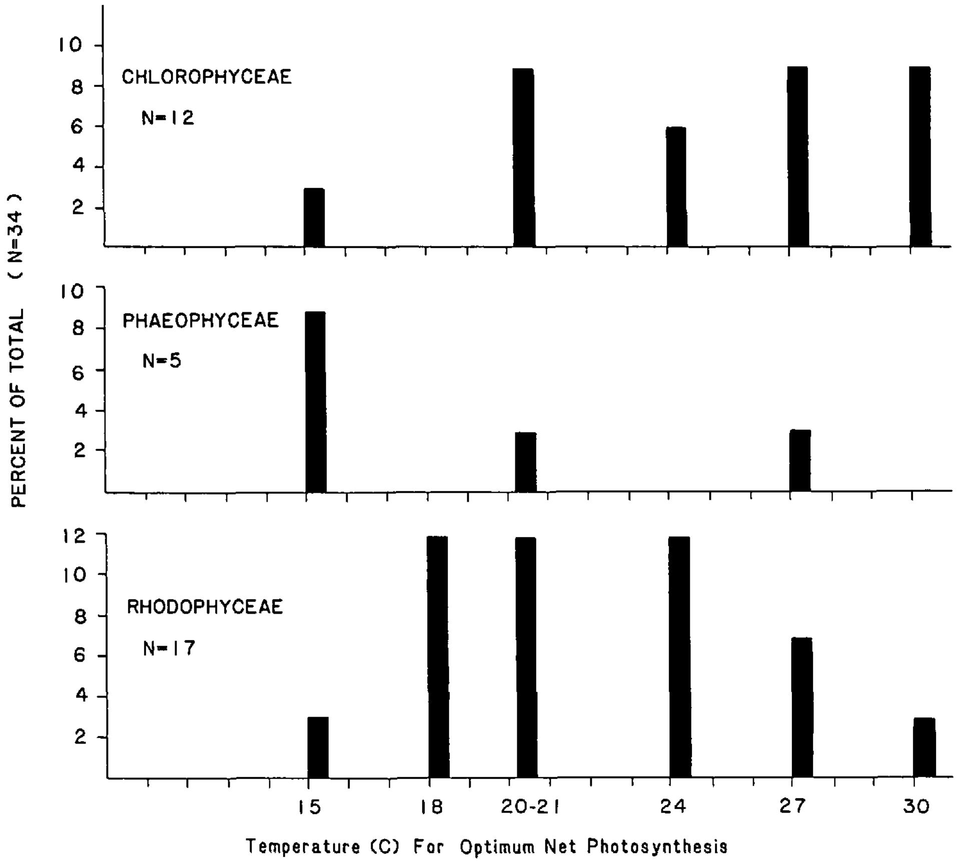

Figure 6. Frequency (%) distribution pattern of optimal temperature for 34 species of Florida Chlorophyceae, Phaeophyceae and Rhodophyceae.

planata and *Sporochnus pedunculatus* had low light and temperature optima. Overall, there was little statistical correlation (i.e., $R = -0.38$) between the corresponding temperature and light optima of each taxa.

A summary of the light and temperature optima for all three classes of seaweeds is given in Figure 7, with the physiological optima being circumscribed as polygons. The Phaeophyceae exhibited the most restricted temperature and light optima, while the Chlorophyceae and Rhodophyceae exhibited broader tolerances. Even so, a comparison of Figures 3 and 6 suggests that the Chlorophyceae have a broader tolerance than the Rhodophyceae to both parameters.

Discussion

The light response of the shallow-water, perennial brown alga *Padina vickersiae* was one of the most unique as it exhibited a low light optimum and a broad tolerance to high light intensities. Several investigators (Kanwisher, 1966; Brinkhuis et al., 1976; Niemeck and Mathieson, 1978; Chock and Mathieson, 1979; Lüning, 1981) have recorded similar photosynthetic responses for intertidal fucoid brown algae and emphasized that it allows such plants to maximize their photosynthesis throughout the day, independent of seasonal and diurnal light variations. In contrast, most of the other tropical seaweeds evaluated (986–4,258 μE/

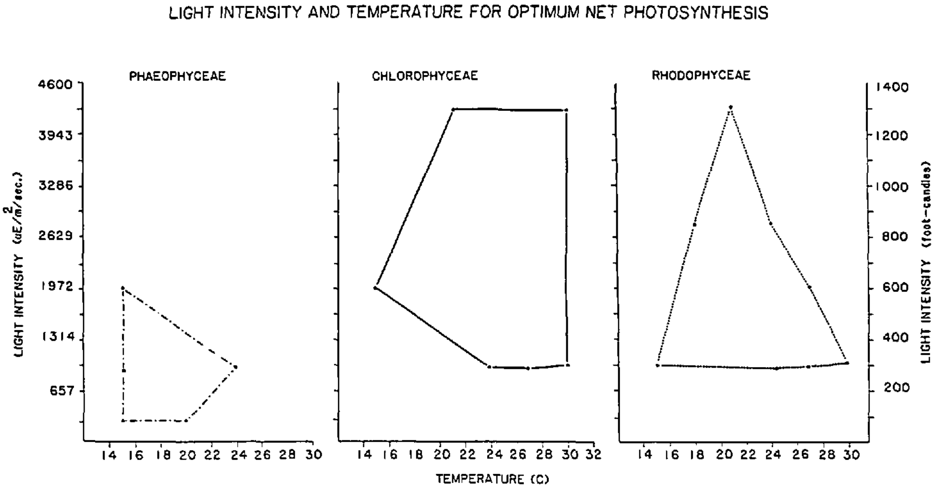

Figure 7. Summary of the corresponding temperature and light optima for the various Chlorophyceae, Phaeophyceae and Rhodophyceae, with the physiological optima being circumscribed as polygons.

m²/sec) either exhibited intermediate or high light optima. Thus, the intertidal green alga *Monostroma oxyspermum* was not saturated at the highest intensity tested (4,258 μE/m²/sec), while the optimal light intensity for the shallow subtidal red alga *Laurencia intricata* was 1,972 μE/m²/sec. The photosynthetic response of *L. intricata* was representative of the largest number of seaweeds, particularly subtidal taxa. Similar tolerances to high light (i.e., without photosynthetic inhibition) have been shown for *Hypnea musciformis* (Dawes et al., 1976; Durako and Dawes, 1980) and *Gracilaria verrucosa* (Dawes et al., 1978). Comparable light optima have been recorded for several temperate subtidal seaweeds like *Chondrus crispus* (Mathieson and Burns, 1971), *Macrocystis pyrifera* (Clendenning and Sargent, 1957), and *Egregia laevigata* (Chapman, 1962); also see Lüning (1981) for a further summary.

Many of the photosynthetic-light experiments described above are supportive of other field and culture observations (Dawes et al., 1974b; Mathieson and Dawes, 1975). For example, all four of the subtidal *Eucheuma* taxa evaluated had relatively low light optima (Fig. 2), and they were extremely sensitive to high light intensities. Thus, when they were transplanted from the deep to the shallow subtidal zone, they became bleached or greenish-brown in color; this bleaching could be reversed if the plants were cultured under reduced illumination (i.e., <986 μE/m²/sec, Dawes et al., 1974a). As suggested previously, there is a general correlation between the vertical distribution of seaweeds and their photosynthetic light responses (Stocker and Holdheide, 1938; Rabinowitch, 1956; Mathieson and Burns, 1971; Mathieson and Norall, 1975a; 1975b; Lüning, 1981). Thus, subtidal seaweeds tend to have lower light optima (i.e., <3,259 μE/m²/sec) and are sensitive to high light intensities. Similarly, the Chlorophyceae, which often dominate in shallow waters (Dawes, 1974; Mathieson and Dawes, 1975), exhibit a broad tolerance to high light intensities (Figs. 1 and 2). In contrast, the Phaeophyceae and Rhodophyceae, which exhibit a pattern of greater sensitivity to high light intensities (Figs. 1 and 2), are typically found within deeper waters (Mathieson and Dawes, 1975; Lüning, 1981). However, as with most generalizations, there are obvious exceptions, including the high light optima of the deep-growing green alga *Codium repens* (Fig. 2 and Cheney and Dyer, 1974), as well as the opposite response for the intertidal red alga *Bostrichia rivularis.* In the latter case the adaptation to low light does reflect the habitat in which *B. rivularis* grows, namely on shaded mangrove prop roots. Ramus (1978) and Littler and Littler (1980) also emphasize that few phylogenetic generalizations can be made regarding light saturation levels for photosynthesis, as well as the magnitude of the corresponding net productivity. Rather there is a closer relationship between thallus form and light-saturated photosynthesis—e.g., amount of pigment/cell or ratio of pigmented/non-pigmented cells.

Several generalizations regarding the marine flora of Florida may be helpful in interpreting the thermal characteristics of the seaweeds evaluated. Foremost, the flora consists of diverse geographical components, and exhibits pronounced seasonal and spatial fluctuations (Humm and Taylor, 1961; Dawes, 1974; Mathieson and Dawes, 1975; Cheney and Dyer, 1974). Much of this phenological variation is primarily due to temperature variation (Setchell, 1915), which, as noted by Earle (1972), is spatially and temporally variable in the Gulf of Mexico. For example, the offshore summer temperatures in the southern Gulf are tropical (i.e., 25–30°C), while the average temperatures for inshore waters in the northern Gulf are approximately the same as those in New England during the summer. Earle (1972) further states that 50 species with New England affinities thrive during the winter in the northern Gulf, but they do not occur in the southern Gulf. Many of the latter species (e.g., *Eudesme virescens*) are summer annuals at Cape Cod, Massachusetts (Coleman and Mathieson, 1975).

Considering the above information, it is not surprising that the thermal optima of the 34 species evaluated were so variable (i.e., 15–30°C), as they were collected seasonally at a variety of sites (Table 1). Even so, several generalizations can be made regarding the thermal ecology of these species. Foremost, the Phaeophyceae exhibited the most restricted tolerance to high temperatures; by contrast, the Chlorophyceae showed the opposite pattern, while the Rhodophyceae had an intermediate trend. It should be recalled that the Phaeophyceae are often used as biological indicators of cold water floristic affinities (Druehl, 1981), while subtropical to tropical floras as found in Florida have high ratios of Rhodophyceae/Phaeophyceae or Rhodophyceae + Chlorophyceae/Phaeophyceae (Feldmann, 1937; Mathieson and Dawes, 1975; Cheney, 1977). With this in mind, it is not surprising that three of the four plants with the lowest thermal optima (15°C) were ephemeral brown algae–i.e., *Rosenvingiella intricata, Eudesme virescens,* and *Sporochnus pedunculatus.* Each of these plants is found in Florida during the winter/spring period (Mathieson and Dawes, 1975) versus the summer occurrence of *E. virescens* in New England (Coleman and Mathieson, 1975; Mathieson and Hehre, 1982). In contrast to the above-described ephemeral brown algae, three green algae (i.e., *Cladophora coelothrix, Dictyosphaeria cavernosa* and *Bryopsis plumosa*) and one red alga (*Bostrychia rivularis*) exhibited the highest thermal optima (30°C) recorded; each of these plants is particularly common in shallow water habitats. The annual green algae *B. plumosa* and *Monostroma oxyspermum,* which have thermal optima of 27–30°C (Fig. 5), also grow abundantly during the summer in shallow New England estuarine habitats (Mathieson and Hehre, 1983) where the temperatures often reach 25–27°C (Norall et al., 1982).

The thermal optima of several perennial green and red algae (e.g., *Chaetomorpha aerea, C. linum, Eucheuma* ssp., *Gracilaria* spp. and *Laurencia intricata*) were intermediate to those described above. In addition, they were relatively low (i.e., 20–24°C) when compared to the seasonal temperature regimes prevalent where they grow (i.e., 15–33°C, Dawes et al., 1974b; 1978). The two *Chaetomorpha* species grow abundantly in the North Atlantic (Blair, 1983; Taylor, 1962), and they may have cold water affinities. On the other hand, the period of maximum growth for some of the other tropical perennial species (e.g., *Eucheuma* ssp.) is primarily during the adverse summer period of high temperatures and low nutrients, and they became reproductive in the fall (Dawes et al., 1974b). An evaluation of the temperature optima for several perennial New England species, such as *Chondrus crispus* and *Gigartina stellata* (Mathieson and Burns, 1971; Mathieson and Norall, 1975b), *Phyllophora truncata* (Mathieson and Norall, 1975a), *Polysiphonia elongata* and *P. lanosa* (Fralick and Mathieson, 1975), and *Ascophyllum nodosum* and *Fucus* spp. (Niemeck and Mathieson, 1978; Chock and Mathieson, 1979), shows that they are comparable to these tropical, perennial species (i.e., 21–24°C). Even so, their growth occurs primarily during the late spring and summer. Thus, the seasonal growth patterns of several northern and southern perennial species are different, although their optimal temperatures for photosynthesis may be approximately the same. Differential tolerances to low and high temperatures can obviously restrict tropical and temperate plants, respectively, to distinct geographical areas.

As noted by Fralick and Mathieson (1975), cosmopolitan species of the genus *Polysiphonia* tolerate a variety of environmental factors, such as temperature, light and salinity. In contrast to this pattern, relatively few tropical taxa exhibited broad tolerances to both temperature and light (Fig. 5); rather, they seemed to exhibit a strategy of being more tolerant to one parameter than the other. The broad cosmopolitan distribution of *Monostroma oxyspermum* was previously noted; it extends from the tropical Atlantic to Newfoundland (Taylor, 1962; South and Hooper, 1980). Thus, it was one of the few cosmopolitan species that conformed to the above generalization, having broad physiological tolerances to both light and temperature. *Bostrychia rivularis* was representative of the majority of species examined, as it exhibited a very high thermal optimum (30°C) but a moderately low light optimum (986–1,972 $\mu E/m^2/sec$). As is well known, *B. rivularis* grows abundantly in shaded and turbid intertidal habitats, especially on mangrove roots (Dawes, 1974). In such habitats, the above described physiological traits may be of adaptive significance, as suggested by Littler and Littler (1980).

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