Ecological Growth Strategies in the Seaweeds *Gracilaria foliifera* (Rhodophyceae) and *Ulva* sp. (Chlorophyceae): Photosynthesis and Antenna Composition

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ABSTRACT: Observations have been made on photosynthesis (oxygen evolution) and seasonal fluctuations in antenna pigments in 2 seaweeds which co-occur in the vicinity of Beaufort, North Carolina, USA. *Gracilaria foliifera* (Rhodophyceae) and *Ulva* sp. (Chlorophyceae) were grown in outdoor continuous-flow cultures at ambient incident light (I₀) and 1/3I₀. Pigment contents and accessory pigment: chlorophyll a ratios were higher at 1/3I₀ than at I₀. Total pigment levels were correlated with soluble N in seaweed tissue. During the spring/summer growing season, pigment levels were low and peaks in pigment content followed nutrient pulses in the ambient seawater. Pigment contents in both species were higher in winter. In *G. foliifera*, the R-phycoerythrin: chl a ratio was highest in fall-winter and lowest in summer. The higher growth rates achieved by *Ulva* sp. reflected the higher rates of photosynthesis measured in this species. Photosynthesis-light curves showed that *Ulva* sp. had a higher photosynthetic capacity (Pmax = 430 µmol O₂ evolved g dry wt⁻¹ h⁻¹) and initial slope (in shade-acclimated plants) than *G. foliifera* (Pmax = 160 µmol O₂ evolved g dry wt⁻¹ h⁻¹). Increased pigment contents in shade plants of both species resulted in enhanced photosynthetic performance at sub-saturating light intensities. It appears that the effect of transient pigment increases in the summer was to increase Pmax temporarily while, in winter, the effect was to limit the decrease in integrated net photosynthesis in the face of decreased light and temperature.

INTRODUCTION

Accommodation of the seaweed photosynthetic apparatus to variations in light, nutrients, or temperature in the environment may involve changes in both the concentration and ratios of antenna pigments within the thallus. Ramus et al. (1976a, b; 1977) have studied accommodation to photon flux density in several species representing the 3 taxonomic classes of seaweeds. All of the seaweeds tested increased antenna pigment content with decreasing incident light and, in most species, this was accompanied by an increase in the accessory pigment: chlorophyll a ratio. These changes were reversible and did not require cell division. There is comparatively less information available regarding seasonal variations in pigment concentration and ratios.

According to Platt et al. (1977), most of the variance in primary production is accounted for by fluctuations in light. Thus, the scope for growth in a particular habitat should reflect the form of the photosynthesis-light (P vs. I) curve. The characteristics of this curve are, in turn, affected by physiological manipulation of the photosynthetic antenna. Inasmuch as the photosynthetic antenna accounts for much of the protein in plant tissue (Ramus, in press), photosynthesis may also be regulated by N-nutrient availability (LaPointe and Ryther, 1979).

The red seaweed *Gracilaria foliifera* and the green seaweed *Ulva* sp. co-occur in the vicinity of Beaufort, North Carolina. When the 2 species were grown together in an outdoor continuous-flow system, *Ulva* sp. had a higher growth rate than *G. foliifera* (Rosen-
berg, 1981). The difference between the growth rates of the 2 species was greater at ambient incident light (I₀) than at .13I₀. The aims of this study were (1) to determine how the growth rates of these species were related to photosynthetic performance (oxygen evolution) and (2) to determine the seasonal fluctuations in antenna pigment content in response to photon flux density and nutrient availability.

MATERIALS AND METHODS

Gracilaria foliifera (Forsskål) Børgesen and Ulva sp. were collected at monthly intervals from November, 1978, to February, 1980 (total of 14 collections). G. foliifera was always obtained from Fort Macon jetty (34°42’N, 76°41’W) near Beaufort, North Carolina. In November and December, 1978, only, Ulva sp. was also obtained from the jetty. Beginning in January, 1979, the monthly collections of Ulva sp. were made at a nearby site, Bird Shoal, in order to avoid causing excessive damage to the population on the jetty.

The 2 populations were originally thought to consist of Ulva lactuca Linnaeus. Recently, R. B. Searles (pers. comm.) has suggested that the 2 populations may represent distinct Ulva species. Reexamination of preserved specimens using a revised taxonomic key (R. B. Searles, unpubl.) resulted in tentative identification of the Ulva sp. from Bird Shoal as Ulva curvata (Kützing) De Toni, that from the jetty is tentatively identified as Ulva rigida C. Agardh. In view of the uncertain taxonomical distinctions within the genus (Provasoli and Pintner, 1980; C. Yarish, pers. comm.), reference will be made to Ulva sp.

Following collection, the seaweeds were returned to the laboratory where they were blotted and cut to yield individual plants weighing 0.05 ± 0.05 g fresh weight (ca. 5 cm in length) for Gracilaria foliifera and 0.25 ± 0.025 g fresh weight (ca. 25 cm² surface area) for Ulva sp. Four individuals were then placed in each of a number of small Plexiglas tubes (10 cm long, 5 cm diameter) which were riddled with holes and closed at the ends with wide-mesh (7 mm) plastic screening.

The Plexiglas tubes were then suspended in several outdoor continuous-flow seawater tanks (140 l capacity) at the Duke University Marine Laboratory where they were exposed to ambient environmental conditions. In order to simulate the decreased photon flux density in the low intertidal zone, seaweeds were also grown at 13% of ambient incident light (I₀) measured just above the surface of the water in the tanks) obtained using fiberglass neutral-density filters. Two weeks were more than sufficient for complete physiological acclimation (J. Ramus, unpubl.). Seaweeds grown at I₀ are herein termed ‘sun plants’; seaweeds grown at .13I₀ are ‘shade plants’.

Average daily incident light (I₀) ranged from 31 E m⁻² d⁻¹ in December to 80 E m⁻² d⁻¹ in midsummer. Water temperature ranged from 5 °C in January–February to 30 °C in July–August. N-nutrient levels (mostly as ammonium) in the outdoor tanks were variable. The inorganic nitrogen concentration was usually ≤ 2 µg-at N l⁻¹ (= 10 mg-at N d⁻¹ tank⁻¹). In 1979, nutrient pulses were observed in July (up to 6 µg-at N l⁻¹ = 28 mg-at N d⁻¹ tank⁻¹) and again in September (up to 10 µg-at N l⁻¹ = 46 mg-at N d⁻¹ tank⁻¹). High flow rates at the beginning of the study resulted in a peak of 118 mg-at N d⁻¹ tank⁻¹ in December, 1978.

After 2 wk in the outdoor tanks, the acclimated seaweeds were harvested and reweighed. After reweighing, all of the seaweeds, except for the individuals used for dry weight determination (n = 11), were placed in plastic Whirlpak bags and stored frozen at ~15 °C for subsequent tissue analysis. Dry weights were determined after desiccation for 24 h at 90 °C.

Photosynthetic pigment analyses were carried out using five separate individuals of each species. Plant-to-plant variance within each treatment is reported as the average coefficient of variation [CV = (s/μ) × 100] for each analysis. Chlorophyll a (chl a, CV = 20 %) and accessory chl b (in Ulva sp. only, CV = 26 %) were extracted from thawed samples by breaking the tissue in 90 % acetone (in the presence of MgCO₃) in a chilled, motor-driven Ten Broeck tissue homogenizer. Following centrifugation, the chl a and b concentrations were calculated from the spectrophotometric equations (for Ulva sp.) or extinction coefficients (for Gracilaria foliifera) of Jeffrey and Humphrey (1975). Total carotenoid concentrations (CV = 23 %) were estimated using the equation of Strickland and Parsons (1972). All absorbances were measured on a Beckman Model 25 double-beam grating spectrophotometer.

The accessory phycobiliproteins were extracted from Gracilaria foliifera by breaking the tissue in 0.05 M phosphate buffer, pH 6.7 (Siegelman and Kycia, 1978). The homogenate was allowed to extract at 4 °C for 30 min, with occasional stirring. Repeated extractions yielded little additional pigment. Following centrifugation, the absorbance of the supernatant was read at 565 nm, 615 nm, and 650 nm. The concentrations of R-phycoerythrin (R-PE, λmax = 565 nm, CV = 32 %) and the minor phycobiliproteins, R-phycocyanin (λmax = 615 nm) and alliphycocyanin (λmax = 650 nm), were calculated according to the trichromatic spectrophotometric equations given in Rosenberg (1981).

Total soluble nitrogen in seaweed tissue (CV = 15 %) was determined by breaking the thawed samples in distilled deionized water. Following centrifug-
gation, the supernatant was analyzed for total persulfate nitrogen (TPN = total Kjeldahl nitrogen + nitrite + nitrate) according to the method of D'Elia et al. (1977) with a nitrate solution as a standard.

Photosynthesis-light (P vs. I) curves were obtained for both freshly collected material and seaweeds acclimated at \( I_0 \) or .13\( I_0 \). Laboratory incubations were carried out by enclosing the seaweeds in a standard biological oxygen demand (BOD) bottle filled with filtered seawater. This bottle was then placed in a Sherer Model 2-113 incubator at ambient water temperature (14 °C). Light was provided by a bank of 12 'cool-white' fluorescent tubes (Sylvania F48T12-CW-VHO) and could be attenuated using neutral-density filters. Photon flux density was measured using a Licor 193S 4\( \pi \) quantum sensor connected to a Licor Model 550 printing integrator. The quantum sensor measured only photosynthetically active radiation (PAR, 400-700 nm, as \( \mu \)E m\(^{-2}\) s\(^{-1}\)). Mixing was provided by a magnetic stir bar. As the photon flux density was increased stepwise, oxygen levels were continuously monitored using a Clark-type polarographic electrode (Yellow Springs Instruments Model 5750) with a YSI Model 57 oxygen meter. The oxygen meter provided input to a Fisher Recordall Series 5000 strip chart recorder. Photosynthetic rate measurements (expressed as \( \mu \)mol O\(_2\) evolved g dry wt\(^{-1}\) min\(^{-1}\)) were based on 10-min exposures at each light intensity.

Incubations were also carried out in situ by enclosing individual seaweeds in BOD bottles which were suspended from a vertically-buoyed polypropylene line at 1-m intervals from the surface to 4 m. Control bottles contained filtered seawater only. Mixing was promoted by placing a glass marble in each bottle. All in situ incubations were carried out around midday and lasted about 2.5 h. Incident light and its attenuation in the water column were measured using either the Licor 4\( \pi \) quantum sensor or a Kettering LDC Model 68 radiometer calibrated to the Licor unit. Rates of photosynthesis (expressed as \( \mu \)mol O\(_2\) evolved g dry wt\(^{-1}\) h\(^{-1}\)) were determined by measuring the change in dissolved oxygen. During oxygen measurements, mixing was provided by a magnetic stir bar. Dark respiration was determined by incubating the seaweeds in BOD bottles wrapped with black electrician's tape.

Seaweeds were also incubated outdoors in a clear Plexiglas tank provided with circulating seawater at the ambient temperature. The seawater surrounding the BOD bottles had the effect of reducing the incident light (\( I_\infty \) measured just above the surface) to 70% of its initial value. For some measurements, the light was further attenuated to .03\( I_\infty \) with fiberglass neutral-density filters wrapped around the BOD bottles. The contents of the bottles were mixed by bars turned by water-driven magnetic stirrers. Net photosynthesis and dark respiration were determined as described for the in situ incubations. Following incubation, in vivo thallus absorbance was determined with an Optronic Laboratories Model 740 autoranging scanning spectroradiometer system. The use of this device is described in Ramus (1978). Absorbance (\( a \)), that fraction of the incident light absorbed, was calculated as 1 - (\( I/I_\infty \)) where \( I_0 \) = incident PAR and \( I \) = transmitted PAR.

**RESULTS**

**Photosynthetic Performance**

The characteristics of the in situ P vs. I curves for freshly collected *Gracilaria foliifera* and *Ulva* sp. are shown in Table 1. *Ulva* sp. showed higher values of \( P_{max} \) (406 vs. 150 \( \mu \)mol O\(_2\) evolved g dry wt\(^{-1}\) h\(^{-1}\)), paired t-test, \( p < .01 \) and \( I_0 \) (465 vs. 200 E m\(^{-2}\) s\(^{-1}\)), paired t-test, \( p < .05 \) than *G. foliifera*. The initial slopes of the in situ curves were similar for the two species (Table 1). These results may be compared with similar curves for *Codium decorticatum* (Woodward) Howe and *Dictyota dichotoma* (Hudson) Lamouroux, 2 other seaweeds from the Beaufort area (Table 1). The \( P_{max} \) values were higher in *Ulva* sp. and *D. dichotoma*, species with high surface area: volume (SA:V) ratios, than in *Gracilaria foliifera* and *C. decorticatum* which had lower SA:V ratios (2-sample t-tests, \( p < .01 \)). A similar pattern was found for dark respiration expressed on a dry weight basis (Table 1; 2-sample t-tests, \( p < .05 \)). Photoinhibition was less pronounced in the optically translucent species (*Ulva* sp. and *D. dichotoma*) than in seaweeds which were optically more opaque (*G. foliifera* and *C. decorticatum*) (Table 1).

A comparison was made of P-I curves generated in the laboratory and in situ. The results showed that, in spite of differences in the incubation time (10 min vs. 2.5 h) and light regime (constant vs. fluctuating), there was good agreement between the 2 methods for freshly collected *Gracilaria foliifera* and *Ulva* sp. Laboratory P-I curves for *G. foliifera* and *Ulva* sp. acclimated for 2 wk at \( I_0 \) or .13\( I_0 \) are shown in Fig. 1. *Ulva* sp. showed higher values of \( P_{max} \) and initial slope (in shade plants) than *G. foliifera*. In both species, shade plants (with higher pigment contents) showed enhanced photosynthetic performance at all light intensities tested when compared to sun plants. However, acclimation to low light intensities also resulted in a decrease in the threshold intensity for photoinhibition (Fig. 1). At light intensities below about 50 \( \mu \)E m\(^{-2}\) s\(^{-1}\), there was no significant difference in photosynthetic performances of the two species for plants acclimated to \( I_0 \).

Comparison of the in situ P-I curves for freshly col-
Table 1. Summary of the characteristics of in situ P vs. I curves for 4 species of seaweeds collected in late summer to early fall (1979) near Beaufort, North Carolina (USA). Pmax: photosynthetic capacity; Ic: saturation light intensity (sensu Talling, 1957). Mean values ± 1/2 x range ([n = 3]. Incubations were carried out on 5 successive days.

<table>
<thead>
<tr>
<th>Item measured</th>
<th>Ulva curvata</th>
<th>Dictyota dichotoma</th>
<th>Gracilaria foliifera</th>
<th>Codium decorticatum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thallus form</td>
<td>Flat sheet</td>
<td>Flat sheet</td>
<td>Suberete axis</td>
<td>Cylindrical axis</td>
</tr>
<tr>
<td>Surface area: volumea</td>
<td>165</td>
<td>Approx. 165</td>
<td>30</td>
<td>9</td>
</tr>
<tr>
<td>Thallus anatomy</td>
<td>Bilayer</td>
<td>3 cells thick; cortex + medulla</td>
<td>Cortex + medulla</td>
<td>Coenocytic; cortex + medulla</td>
</tr>
<tr>
<td>Chloroplasts</td>
<td>One per cell; thylakoids stacked</td>
<td>Many per cell; thylakoids stacked</td>
<td>Several per cell; thylakoids single</td>
<td>Numerous; thylakoids stacked</td>
</tr>
<tr>
<td>Antenna composition</td>
<td>chl a + b</td>
<td>chl a + c, fucoxanthin</td>
<td>chl a, phycobilins</td>
<td>chl a + b</td>
</tr>
<tr>
<td>Absorptanceb</td>
<td>0.43</td>
<td>0.72</td>
<td>0.84</td>
<td>0.98</td>
</tr>
<tr>
<td>Pmax, µmol O2 evolved g dry wt−1 h−1</td>
<td>406 ± 34</td>
<td>435 ± 84</td>
<td>150 ± 13</td>
<td>116 ± 23</td>
</tr>
<tr>
<td>Ic, µE m−2 s−1</td>
<td>485 ± 200</td>
<td>275 ± 85</td>
<td>200 ± 75</td>
<td>378 ± 173</td>
</tr>
<tr>
<td>Initial slope</td>
<td>250 ± 54</td>
<td>536 ± 214</td>
<td>254 ± 104</td>
<td>111 ± 54</td>
</tr>
<tr>
<td>Dark respirationf</td>
<td>31 ± 6</td>
<td>82 ± 29</td>
<td>11 ± 2</td>
<td>14 ± 2</td>
</tr>
<tr>
<td>Photoinhibitionb</td>
<td>Weak</td>
<td>Weak</td>
<td>Strong</td>
<td>Moderate</td>
</tr>
</tbody>
</table>

a cm²: cm³  b cm²: cm³  c µmol O₂ evolved g dry wt−1 h−1  d µE m−2 s−1  e µmol O₂ evolved g dry wt−1 (E m−2)−1  f µmol O₂ g dry wt−1 h−1

Fig. 1 Gracilaria foliifera and Ulva sp. Laboratory photosynthesis-light curves for November (1979) seaweeds acclimated for 2 wk in outdoor continuous-flow seawater tanks at Ic and .13Ic. Each point represents the combined photosynthetic performance of 3 individuals. Curves were fitted by eye.

The seasonal fluctuations in the photosynthetic antenna pigments are shown in Fig. 2 (Gracilaria foliifera) and Fig. 3 (Ulva sp.). Seaweeds grown at .13Ic had higher antenna pigment concentrations than seaweeds grown at Ic. Accessory pigment: chl a ratios (Fig. 4, a Plexiglas tank at .70Ic and .03Ic. The experimental light intensities (.70Ic and .03Ic, measured underwater) approximated the light intensities to which the seaweeds had been acclimated (Ic and .13Ic, measured in air). Net photosynthesis of Ulva sp. exceeded that of Gracilaria foliifera at both .70Ic and .03Ic. This applied to both sun and shade plants and was reflected in the higher growth rates (at Ic and .13Ic) observed in Ulva sp. over the preceding two weeks (Table 2). Sun plants of both species showed a higher rate of photosynthesis at .70Ic than at .03Ic. On the other hand, shade plants showed a higher rate of photosynthesis at .03Ic than at .70Ic. This effect was particularly noticeable in shade plants of G. foliifera and was presumably due to increased sensitivity to photoinhibition in shade-acclimated plants (Fig. 1). The effect of shade acclimation was to enhance the photosynthetic performance of both species at .03Ic and of Ulva sp. at .70Ic.

For Gracilaria foliifera, the in vivo absorptance of shade plants was 2.6 times that of sun plants while Ulva sp. shade plants had an absorptance which was twice as high as in sun plants (Table 2). The difference spectrum for G. foliifera clearly showed that most of this increase was due to higher concentrations of R-phycoerythrin.

**Antenna Pigments**

The seasonal fluctuations in the photosynthetic antenna pigments are shown in Fig. 2 (Gracilaria foliifera) and Fig. 3 (Ulva sp.). Seaweeds grown at .13Ic had higher antenna pigment concentrations than seaweeds grown at Ic. Accessory pigment: chl a ratios (Fig. 4,
Table 2. Gracilaria foliifera and Ulva sp. Photosynthetic performance of sun and shade plants measured outdoors in mid-October (1979) at .70 I, and .03 I, a in vivo absorptance; μ specific growth rate (from Rosenberg, 1981); R dark respiration; P, net photosynthesis. μ: Mean values ± s (n = 32); R, P, Net mean values ± ½ × range (n = 2)

<table>
<thead>
<tr>
<th>Species</th>
<th>αa</th>
<th>μb</th>
<th>Rc</th>
<th>( P_n ) at 0.70 I₀</th>
<th>( P_n ) at 0.03 I₀</th>
<th>( P_n ) at 0.03 I₀</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gracilaria foliifera</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sun</td>
<td>0.30</td>
<td>37 ± 7</td>
<td>93</td>
<td>50 ± 6</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>Shade</td>
<td>0.78</td>
<td>33 ± 3</td>
<td>71 ± 17</td>
<td>164 ± 20</td>
<td>2.32</td>
<td></td>
</tr>
<tr>
<td>Ulva curvata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sun</td>
<td>0.10</td>
<td>40 ± 3</td>
<td>126 ± 22</td>
<td>89 ± 21</td>
<td>0.70</td>
<td></td>
</tr>
<tr>
<td>Shade</td>
<td>0.20</td>
<td>32 ± 2</td>
<td>206 ± 10</td>
<td>311 ± 13</td>
<td>1.51</td>
<td></td>
</tr>
</tbody>
</table>

\( a \): In vivo absorptance = 1 - (I/I₀), where I₀ = incident PAR, I = transmitted PAR
\( b \): Specific growth rate as the percentage increase in fresh weight per week
\( c \): Dark respiration (μmol O₂ g dry wt⁻¹ h⁻¹)
\( d \): Net photosynthesis (μmol O₂ evolved g dry wt⁻¹ h⁻¹)

Table 3) were usually higher at .13I₀ than at I₀ (paired t-test, p < .01 for G. foliifera, p < .05 for Ulva sp.). In G. foliifera, most of the variation in total pigment content was due to fluctuation in the levels of R-PE. Thus, at I₀, chl a only ranged from 0.28 to 1.33 mg g dry wt⁻¹ while R-PE ranged from 1.34 to 11.19 mg g dry wt⁻¹. Corresponding figures at .13I₀ were 0.43 to 1.25 mg g dry wt⁻¹ for chl a and 4.56 to 15.22 mg g dry wt⁻¹ for R-PE. These figures for G. foliifera are in agreement with those of LaPointe and Ryther (1979). In Ulva sp., the chlorophyll a concentration was more variable. At I₀, chl a ranged from 0.14 to 2.64 mg g dry wt⁻¹ while chl b ranged from 0.08 to 1.45 mg g dry wt⁻¹. At .13I₀, the ranges for chl a and b were 0.29 to 3.50 mg g dry wt⁻¹ and 0.07 to 2.10 mg g dry wt⁻¹, respectively.

At both I₀ and .13I₀, antenna pigment concentrations were correlated with the levels of soluble tissue N (Figs. 2 and 3; r = .90, p < .001 for R-PE in Gracilaria foliifera; r = .56, p < .01 for chl a in Ulva sp.). In particular, during the April-to-September growing season, N-nutrient pulses in the ambient seawater resulted in peaks in both soluble tissue N and antenna pigments in July (G. foliifera) and September (both species). Low growth rates in the fall and winter coincided with the accumulation of soluble N within the thallus and correspondingly high antenna pigment concentrations. In G. foliifera, R-PE alone accounted for about one third of the total protein (Rosenberg, 1981).

Nevertheless, there was some evidence that the pigment ratios responded to changes in light intensity to different extents and, occasionally, in different directions (e.g. in April–May; Table 3) at different times of year. This may partly depend on the state of the pigments and the nutrient status in the freshly collected plants prior to acclimation.

The total carotenoid concentrations were higher in Ulva sp. than in Gracilaria foliifera at both I₀ and .13I₀ (Figs. 2 and 3). In G. foliifera, the total carotenoid concentrations at I₀ and .13I₀ were not significantly different (paired t-test, p = .06). On the other hand, Ulva sp. grown at .13I₀ had higher total carotenoid concentrations than plants grown at I₀ (paired t-test, p < .001). The ratio of total carotenoids to total chl a was similar in both species and did not vary seasonally (Table 4). This ratio was usually higher at I₀ than at .13I₀ (paired t-test, p < .001 for G. foliifera). However, in Ulva sp., this difference was not significant (paired t-test, p = .12, df = 13) unless the April–May data are not included (p < .001, df = 11).

**DISCUSSION**

The higher growth rates achieved by Ulva sp. in comparison with Gracilaria foliifera reflected the photosynthesis-light curves for the 2 species. At a time (October, 1979) when the ratio of the in situ Pmax values for freshly collected plants was 2.7:1 (Ulva sp.: G. foliifera; Table 1), the ratio of the specific growth rates for 2-wk acclimated plants was 4.0:1 at I₀ and 2.1:1 at .13I₀ (Table 2). The higher Pmax value for Ulva sp. was characteristic despite the variability (including seasonal and nutrient-related effects) to which such P vs. I curves are known to be subject (Ramus and Rosenberg, 1980).

Together with the data for Dictyota dichotoma and
Codium decorticatum, these results showed higher productivity in the thin, sheet-like species with high surface area: volume ratios than in the thicker species with low SA:V ratios. In general, this ratio seems to be a better predictor of $P_{\text{max}}$ (but not necessarily initial slope; cf. Ramus, 1978) than the identity of the antenna pigments, the in vivo absorptance, or the internal thallus and chloroplast anatomy (Table 1; Littler and Murray, 1974; Littler, 1980). Nutrient uptake rates have also been found to be correlated with the SA:V ratio (Rosenberg, 1981).

Although the photosynthetic performance and growth rates of Ulva sp. exceeded those of Gracilaria foliifera at both $I_o$ and $1.3I_o$, there are indications that this relationship may be reversed at very low light intensities. Using deep shade acclimated plants sampled from natural populations, Ramus and Rosenberg (1980) found that the integrated diurnal net photosynthesis of G. foliifera at $0.03I_o$ not only exceeded that of Ulva sp., but was higher than its own diurnal net photosynthesis at $0.70I_o$. This would not be predictable from the P-I curves of Fig. 1 and emphasizes the desire-
Table 3. Ulva sp. Chlorophyll b: chlorophyll a ratios (molar basis) for seaweeds grown in outdoor continuous-flow cultures at $I_o$ and $1.3I_o$. Dates refer to last day of 2-wk acclimation periods. Mean values ± σ (n = 5)

<table>
<thead>
<tr>
<th>Date</th>
<th>Chlorophyll b: a (moles)</th>
<th>0.13 $I_o$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dec 11, 1978</td>
<td>60 ± 0.01</td>
<td>0.64 ± 0.01</td>
</tr>
<tr>
<td>Dec 28</td>
<td>67 ± 0.03</td>
<td>0.64 ± 0.02</td>
</tr>
<tr>
<td>Feb 5, 1979</td>
<td>60 ± 0.03</td>
<td>0.56 ± 0.04</td>
</tr>
<tr>
<td>Mar 5</td>
<td>57 ± 0.09</td>
<td>0.73 ± 0.11</td>
</tr>
<tr>
<td>Apr 2</td>
<td>72 ± 0.05</td>
<td>0.53 ± 0.07</td>
</tr>
<tr>
<td>May 22</td>
<td>33 ± 0.10</td>
<td>0.22 ± 0.04</td>
</tr>
<tr>
<td>Jun 19</td>
<td>62 ± 0.05</td>
<td>0.67 ± 0.03</td>
</tr>
<tr>
<td>Jul 17</td>
<td>29 ± 0.14</td>
<td>0.67 ± 0.07</td>
</tr>
<tr>
<td>Aug 13</td>
<td>67 ± 0.05</td>
<td>0.55 ± 0.05</td>
</tr>
<tr>
<td>Sep 18</td>
<td>54 ± 0.01</td>
<td>0.65 ± 0.03</td>
</tr>
<tr>
<td>Oct 22</td>
<td>57 ± 0.08</td>
<td>0.71 ± 0.02</td>
</tr>
<tr>
<td>Nov 21</td>
<td>48 ± 0.05</td>
<td>0.59 ± 0.05</td>
</tr>
<tr>
<td>Dec 20</td>
<td>38 ± 0.02</td>
<td>0.56 ± 0.02</td>
</tr>
<tr>
<td>Jan 17, 1980</td>
<td>51 ± 0.03</td>
<td>0.73 ± 0.10</td>
</tr>
<tr>
<td>Mean</td>
<td>54 ± 0.13</td>
<td>0.62 ± 0.13</td>
</tr>
</tbody>
</table>

Table 4. Gracilaria foliifera and Ulva sp. Ratio of total carotenoids: total chlorophyll (molar basis, assuming an average carotenoid molecular weight = 600) for seaweeds grown in outdoor continuous-flow cultures at $I_o$ and $1.3I_o$. Dates refer to last day of 2-wk acclimation periods. Mean values ± σ (n = 5)

<table>
<thead>
<tr>
<th>Date</th>
<th>Gracilaria</th>
<th>Ulva</th>
</tr>
</thead>
<tbody>
<tr>
<td>$I_o$</td>
<td>$0.13 I_o$</td>
<td>$0.13 I_o$</td>
</tr>
<tr>
<td>Dec 11, 1978</td>
<td>14 ± 0.01</td>
<td>17 ± 0.02</td>
</tr>
<tr>
<td>Dec 28</td>
<td>18 ± 0.04</td>
<td>11 ± 0.03</td>
</tr>
<tr>
<td>Feb 5, 1979</td>
<td>12 ± 0.01</td>
<td>14 ± 0.05</td>
</tr>
<tr>
<td>Mar 5</td>
<td>22 ± 0.10</td>
<td>20 ± 0.05</td>
</tr>
<tr>
<td>Apr 2</td>
<td>19 ± 0.03</td>
<td>23 ± 0.09</td>
</tr>
<tr>
<td>May 22</td>
<td>27 ± 0.03</td>
<td>19 ± 0.03</td>
</tr>
<tr>
<td>Jun 19</td>
<td>24 ± 0.07</td>
<td>17 ± 0.03</td>
</tr>
<tr>
<td>Jul 17</td>
<td>22 ± 0.04</td>
<td>15 ± 0.01</td>
</tr>
<tr>
<td>Aug 13</td>
<td>25 ± 0.03</td>
<td>16 ± 0.01</td>
</tr>
<tr>
<td>Sep 18</td>
<td>21 ± 0.03</td>
<td>19 ± 0.02</td>
</tr>
<tr>
<td>Oct 22</td>
<td>21 ± 0.01</td>
<td>14 ± 0.02</td>
</tr>
<tr>
<td>Nov 21</td>
<td>26 ± 0.06</td>
<td>13 ± 0.01</td>
</tr>
<tr>
<td>Dec 20</td>
<td>25 ± 0.03</td>
<td>15 ± 0.02</td>
</tr>
<tr>
<td>Jan 17, 1980</td>
<td>19 ± 0.01</td>
<td>14 ± 0.01</td>
</tr>
<tr>
<td>Mean</td>
<td>21 ± 0.04</td>
<td>16 ± 0.03</td>
</tr>
</tbody>
</table>

Shade acclimation is only one factor promoting increased antenna pigment levels in seaweeds. At a particular light intensity, peaks in pigment content of Gracilaria foliifera and Ulva sp. tended to follow peaks in ambient N-nutrient availability. Increased pigment content in response to nitrogen enrichment has also been observed in the red seaweeds Neogardhiella bayleri (DeBoer and Ryther, 1978) and Gracilaria foliifera from Florida (LaPointe and Ryther, 1979).

Photosynthetic pigment content and, in Gracilaria foliifera, the R-PE: chl a ratio, were also higher during winter, at a time of low growth rates, than in summer. Similar seasonal patterns for total pigment content have been reported for the red seaweeds Chondrus crispus (Rhee and Briggs, 1977), Eucheuma isiforme (Moon and Dawes, 1976), and Hypnea musiformis (Durako and Dawes, 1980), as well as for several brown fucoids (Jensen, 1966; Zavodnik, 1973; Brinkhuis, 1977). In Hypnea musiformis and Fucus viride (Zavodnik, 1973), pigment content was correlated with protein levels in the thallus. This is not surprising inasmuch as it is likely that a considerable fraction of this protein was directly associated with the photosynthetic antenna (Ramus, in press). Although part of the seasonal variability was undoubtedly due to nutrient availability, none of these studies reported fluctuations in inorganic nitrogen levels in the ambient seawater. The increase in the ratio of total carotenoids to total chlorophyll at high photon flux density and its apparent seasonal constancy in G. foliifera and Ulva sp. is consistent with the proposed role of carotenoids in protecting against photo-oxidation and stabilizing the chlorophyll-protein complex (Krinsky, 1968).

In general, the main effect of increased antenna pigment content is to increase the photosynthetic performance expressed on a biomass basis (Fig. 1) and, thus, the carbon capital available for growth. This has been observed in seaweeds sampled from natural populations (Zavodnik, 1973; Mishkind et al., 1979), in seaweeds which were shade-acclimated in situ (Ramus et al., 1976b, 1977), in seaweeds which have been N-enriched (Chapman et al., 1978; LaPointe and Ryther, 1979), and within individual plants (Wheeler, 1980). Shade acclimation per se may (Fig. 1; Table 2) or may not (Ramus et al., 1976b, 1977) result in a greater sensitivity to photoinhibition. It is worthwhile to note that this condition did not occur in Laminaria sac-
changes in pigment content with photosynthetic capacity


Further work needs to be done in order to test this hypothesis. In particular, it is necessary to determine how growth under different N-nutrient loading regimes affects the P-I curve and how this compares to curves representing acclimation to shade and low temperature. It is likely that the responses to nitrogen enrichment involve metabolic processes beyond the realm of the photosynthetic antenna, including RuBPCase activity and electron transport. Only when this information becomes available will it become possible to understand seasonal variations in pigment content in the context of seaweed growth strategies.

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LITERATURE CITED


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