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# Photosynthetic Adaptation to Temperature in the Red Algae *Lomentaria baileyana* and *Lomentaria orcadensis*

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Photosynthetic responses to temperature were examined in tetrasporophytes of *Lomentaria baileyana* and *Lomentaria orcadensis* (Rhodophyta). These species have different temperature ranges for growth that reflect seasonal temperature extremes in their natural distributions. *L. baileyana* is a temperate–subtropical species which grows between 15 and 33°C, whereas *L. orcadensis* is a boreal–temperate species which grows between 10 and 20°C. Interspecific differences in the photosynthetic responses to temperature were similar to those for growth, suggesting that photosynthesis may determine the temperature range over which *Lomentaria* tetrasporophytes can grow. Light-saturated rates of photosynthesis were higher in *L. orcadensis* below 15°C, whereas *L. baileyana* could photosynthesize at temperatures above 30°C, which inhibited photosynthesis in *L. orcadensis*. These differences were attributable to genetic adaptations of photosynthetic metabolism because both species were grown under identical conditions for several months prior to the experiments. Phycoerythrin fluorescence studies and photosynthesis–irradiance responses determined in red and green light indicated that the high-temperature-induced breakdown of energy transfer from phycoerythrin to the photosynthetic reaction centres occurred at a lower temperature in *L. orcadensis* than in *L. baileyana*. Low-temperature-enhanced photoinhibition may account for the decreased photosynthetic performance of *L. baileyana* at temperatures below 15°C.

Temperature is a major factor controlling growth and distribution of seaweeds (Lüning, 1984; van den Hoek, 1984). The range of temperature which a species can tolerate is determined by (1) genetic adaptation and (2) the ability to acclimate to changes in temperature. Genetic differences in temperature tolerance and optimum growth temperatures have been reported in many closely related species (Yarish, Breeman & van den Hoek, 1984, 1986; Novaczek, Bird & Maclachlan, 1987; Bolton & Anderson, 1987; Bolton & Stegenga, 1987) and also between populations (ecotypes) of the same species (Bolton, 1983; Gerard & Dubois, 1988). Such adaptations are important because they expand the geographical range available to individual species (in the case of temperature ecotypes) or to larger taxonomic groupings. Temperature acclimation (phenotypic changes) of photosynthesis and respiration have been observed in several marine algae (Rietema & van den Hoek, 1984; Davison, 1987; Davison & Davison, 1987). There are also numerous reports of seasonal changes in photosynthetic and respiratory metabolism (Niemeck & Mathieson, 1978; Newell & Pye, 1968; Yamada, Ikawa & Nisizawa, 1979; Kuppers & Weidner, 1980) which are consistent with temperature acclimation, and suggest that acclimation is a widespread phenomenon in nature. Acclimation is important because it allows seaweeds to optimize photosynthesis, and hence growth, in response to seasonal changes in water temperature (Davison, 1987; Davison & Davison, 1987; Egan, Vlasto & Yarish, 1989).

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A fundamental question in seaweed biology concerns the nature of the physiological mechanisms which confer temperature acclimation and adaptation. The physiological basis of temperature acclimation has been studied in the brown alga *Laminaria saccharina*, in which high rates of photosynthesis are maintained over a wide range of growth temperatures by changes in cellular activities of photosynthetic enzymes (Davison, 1987). Acclimation of the upper thermal tolerance of *L. saccharina* appears to involve changes in the stability of the plasmalemma and, possibly, the thylakoid membranes (Davison, 1987). In contrast, little is known about the physiology of temperature adaptation in seaweeds.

In this study, we have utilized two species of the genus *Lomentaria*, *L. baileyana* (Harvey) Farlow and *L. orcadensis* (Harvey) Collins ex Taylor to study the genetic component of temperature control of photosynthesis. These species have been previously shown to have different growth responses to temperature that reflect seasonal extremes in their geographic ranges. *L. baileyana* grows between 15 and 33°C, allowing it to range from temperate to subtropical seas, and *L. orcadensis* grows between 10 and 20°C, corresponding to a boreal to temperate distribution (Yarish, Breeman & van den Hoek, 1984, 1986). By comparing two species which are ecologically and phylogenetically similar, but divergent with respect to their growth responses to temperature, we address the question of which physiological characteristics in the two species show differences in the range of temperatures to which they are adapted and are related to the growth temperature response. Respiration and photosynthesis were chosen for study because they are important aspects of metabolism, closely related to growth, and because they have been previously implicated in determining the upper thermal tolerance of growth in marine algae (Gerard & Dubois, 1988). Because the objective was to study genetic differences between the two species of *Lomentaria*, plants were grown at a single temperature (20°C) which supports good growth rates of both species (Yarish, Breeman & van den Hoek, 1986).

## MATERIALS AND METHODS

Unialgal cultures of *L. baileyana* and *L. orcadensis* tetrasporophytes were grown from lines previously isolated by Yarish, Breeman & van den Hoek (1984, 1986). Plants were vegetatively propagated by chopping into small fragments (approximately 5 mm) with a sterile razor blade. Both species were grown in unialgal batch culture in plexiglass pots containing 1·5 l of aerated, autoclaved, sea-water (32%) enriched with full-strength von Stosch medium (Ott, 1965). Temperature was maintained at 20°C, with a photon flux density (PFD) of 60–70 μmole photons $m^{-2}s^{-1}$ in a 16:8 L:D cycle. The sea-water medium was changed every 4–5 days.

Rates of photosynthesis and respiration were measured in a Clark-type oxygen electrode (Rank Bros., Botisham, England) as described by Gerard (1988). Entire *Lomentaria* plants were enclosed in nylon mesh bags (1 mm mesh) and placed in the electrode chamber, containing 5 ml of millipore-filtered (0·45 μM) 32% sea-water. The output of the electrode was connected to a Kipp and Zonen model BD 40 chart recorder via a Baily Instruments model RC-1 zero suppressor. This allowed the output of the electrode (approximately 10 mV full-scale) to be measured with the recorder set at 1 mV, thus increasing sensitivity. Oxygen flux measurements were corrected for oxygen consumption by the electrode. Temperature was controlled by a refrigerated circulator connected to the water jacket of the electrode. Illumination was supplied by a tungsten–halide bulb in a Kodak slide projector, and attenuated with Schott neutral density glass filters. Photosynthesis in red and green light was measured by placing coloured filters over the lens of the slide projector. The green filter transmitted light between 500 and 600 nm with a peak transmittance at 540 nm, while the red filter transmitted wavelengths $> 600$ nm with a peak transmittance at 685 nm. Photosynthesis vs. irradiance parameters were calculated from the data using the inverse quadratic transformation of Jassby & Platt (1976) with the aid of the computer program of Ben-Zion & Dubinsky (1988).

Photosynthesis vs. temperature responses were measured at saturating PFD (280 μmole photons $m^{-2}s^{-1}$) with plants being placed in the electrode only long enough to measure rates of respiration and photosynthesis (between 5 and 10 min). For photosynthesis vs. irradiance responses, plants were placed in the electrode chamber and irradiance increased progressively from 1·5 to 280 μmole photons $m^{-2}s^{-1}$; PFD was increased

once a stable rate of photosynthesis had been achieved (normally within 5 min).

Carboxylase activities of ribulose-1,5-bisphosphate carboxylase (RubP-c) were measured as described previously (Davison & Reed, 1985). Approximately 0·5 g of plant tissue was frozen rapidly in liquid nitrogen and ground in a mortar and pestle while still frozen. Soluble protein was extracted from the frozen powder with 5 ml of 4°C, pH 7·6, 0·1 M Tris-Cl buffer containing: 2 mM L-ascorbate, 2 mM dithiothreitol, 2 mM $Na_2EDTA$, 2 mM $MgCl_2$, 20% (v/v) glycerol 1% (v/v) Triton X-100 and 0·5 g of insoluble polyvinylpolypyrolidone. The extract was filtered through a 20 μm nylon mesh and centrifuged for 10 min at 20,000 r.p.m. in a Sorval RC-2B refrigerated centrifuge (c. 40,000 *g*). The crude cell-free supernatant was held on ice until used for determination of RubP-c activity (within 60 min of extraction). RubP-c activity was measured by adding 0·1 ml of extract to pH 8·0 50 mM Tris-Cl buffer containing (in a final volume of 0·5 ml): 10 mM dithiothreitol, 4 mM $MgCl_2$, 2 mM ribulose-1,5-bisphosphate and 20 mM $HCO_3$ (containing 1 μCi $^{14}C$). After a 15 min incubation period the reaction was stopped by the addition of 0·25 ml of 6 M acetic acid. After standing for 24 h in a fume-hood to remove unfixed $^{14}CO_2$, 3·5 ml of optifluor scintillant (Packard) was added and $^{14}C$ fixation determined by liquid scintillation counting after allowing chemoluminescence to subside for 24 h.

Chlorophyll was extracted from intact plants using dimethyl sulphoxide and methanol and quantified according to the method of Duncan & Harrison (1982). Phycobiliproteins were extracted by repeatedly freezing and thawing ground tissue in 0·05 M phosphate buffer (pH 6·7) and concentrations determined according to the method of Rosenberg (1981).

Phycoerythrin (PE) fluorescence was measured essentially as described by Dudgeon, Davison & Vadas (1989). Whole *Lomentaria* plants were held flat in nylon mesh bags (1 mm mesh) placed diagonally in plastic fluorescence cuvettes containing 3 ml of millipore-filtered (0·45 μm) 32% sea-water. This procedure flattened the thallus and held it at 45° to both the excitation irradiance and fluorescence monitor of a Perkin-Elmer model 650-10S spectrofluorometer. PE fluorescence was produced by excitation at 380 nm at a PFD of approximately 20 μmole photons $m^{-2}s^{-1}$ and measured at 580 nm. Slit width for both emission and excitation was 10 nm. The temperature-controlled cuvette holder of the spectrofluorometer could be rapidly connected to either of two temperature-controlled circulators set at 20 and 50°C. Cuvettes containing plants were held in the dark at 5°C for 1 h before measuring initial rates of fluorescence at 20°C. The cuvette holder was then connected to the 50°C circulator, causing the temperature to increase at approximately $1°C\,min^{-1}$ Temperature was monitored continuously within the spectrophotometer cuvette using a YSI model 44TD thermocouple thermometer. The output of the thermocouple and of the spectrofluorometer were recorded on a Soltec VP-67235 two-channel chart recorder, allowing simultaneous measurement of temperature and fluorescence.

Comparisons between the two species were made using the Mann–Whitney test at a significance level of 0·05. In experiments involving comparisons over a range of experimental temperatures the Kruskal–Wallis test statistic was used with multiple comparisons where appropriate.

## RESULTS

### Photosynthesis and respiration

The pattern of net photosynthetic response to temperature [Fig. 1(a)] was similar to that of gross photosynthetic response to temperature [Fig. 1(b)] for both *L. baileyana* and *L. orcadensis*. Net photosynthetic rates in both species increased

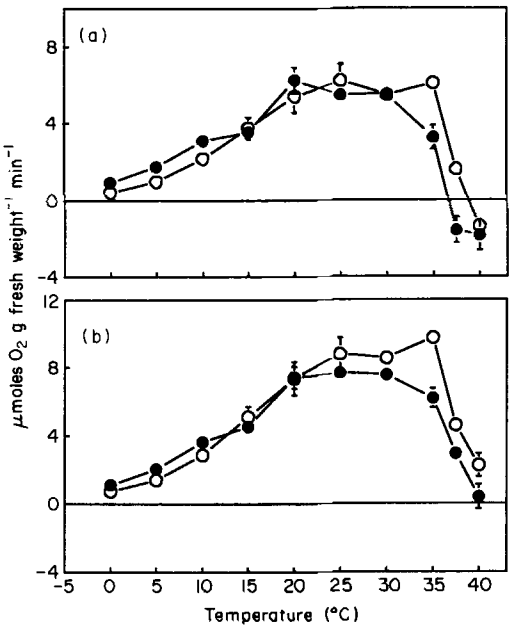


FIG. 1. Rates of (a) net and (b) gross photosynthesis measured over a range of temperatures for *L. baileyana* (○) and *L. orcadensis* (●). Error bars denote one standard error except where the size of symbols exceeds this value. ($N > 9$.)

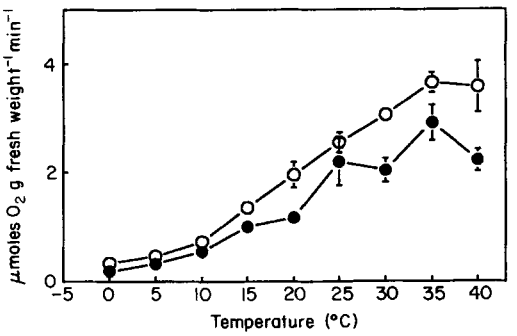


FIG. 2. Respiration rates of *L. baileyana* (○) and *L. orcadensis* (●). Error bars denote one standard error except where the size of symbols exceeds this value. ($N > 9$.)

gradually from 0 to 20°C, remained constant between 20 and 30°C (35°C for *L. baileyana*) and declined rapidly at higher temperatures. *L. orcadensis* had higher photosynthetic rates than *L. baileyana* at temperatures below 15°C (e.g. 3·08 cf. 2·15 μmoles $O_2$ g fresh weight$^{-1}$ min$^{-1}$ at 10°C). Photosynthetic rates were not significantly different between *L. orcadensis* and *L. baileyana*, (c. 5·8 μmoles $O_2$ g$^{-1}$ min$^{-1}$) at optimal temperatures. Net photosynthesis in *L. orcadensis* declined rapidly at temperatures above 30°C and no net photosynthesis was measured above 35°C. *L. baileyana* achieved net photosynthesis up to 37·5°C. Neither species could photosynthesize at 40°C.

The respiratory response to temperature (Fig. 2) differed from that of photosynthesis. Respiration rates increased with increasing temperature to 35°C with *L. baileyana* respiring 0·33 μmoles $O_2$ fresh weight$^{-1}$ min$^{-1}$ at 0°C and 3·65 μmoles $O_2$ fresh weight$^{-1}$ min$^{-1}$ at 35°C and *L. orcadensis* respiring 0·19 and 2·91 μmoles $O_2$ g fresh weight$^{-1}$ min$^{-1}$ at 0 and 35°C respectively. *L. baileyana* had significantly higher respiration rates than *L. orcadensis* at temperatures of 30°C or above.

## Light-harvesting characteristics

The inverse quadratic curve fitting (Ben-Zion & Dubinsky, 1988; Jassby & Platt, 1976) was successful in describing the photosynthesis vs. irradiance responses for the two *Lomentaria* species; $r^2$ values averaged 0·986 (S.D. = 0·016) and were never less than 0·945.

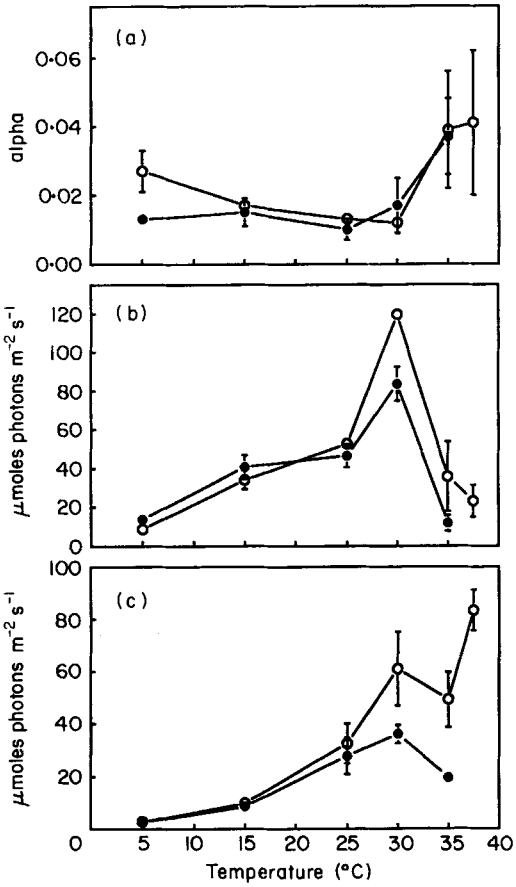


FIG. 3. (a) Alpha [(μmoles $O_2$ fresh weight$^{-1}$ min$^{-1}$)/(μmoles photons m$^{-2}$s$^{-1}$)], (b) $I_k$ and (c) $I_c$ calculated from an inverse quadratic transformation of P vs. I curves measured over a range of six temperatures for *L. baileyana* (○) and *L. orcadensis* (●). Error bars denote one standard error except where the size of symbols exceeds this value. ($N = 6$.)

The light-harvesting efficiency, alpha, [Fig. 3(a)] was constant over the range 5–30°C and was not significantly different between the two species (0·015 μmoles $O_2$ g fresh weight$^{-1}$ min$^{-1}$/μmoles photons m$^{-2}$s$^{-1}$), except for *L. baileyana* at 5°C which was 0·027 μmoles $O_2$ g fresh weight$^{-1}$ min$^{-1}$/μmoles photons m$^{-2}$s$^{-1}$. Above 30°C, alpha appeared to increase, but variability

also increased and there was no significant difference between these values and those at lower temperatures.

Saturation irradiance ($I_k$) [Fig. 3(b)] increased with increasing temperature from approximately 10 μmoles photons $m^{-2}s^{-1}$ at 5°C to approximately 75 μmoles photons $m^{-2}s^{-1}$ (*L. orcadensis*) and 120 μmoles photons $m^{-2}s^{-1}$ (*L. baileyana*) at 30°C. $I_k$ declined above 30°C in both species. $I_k$ was significantly higher for *L. baileyana* than for *L. orcadensis* at 30 and 35°C.

Compensation irradiance ($I_c$) [Fig. 3(c)] also increased with increasing temperature from c. 2·6 μmoles photons $m^{-2}s^{-1}$ for both species at 5°C to maxima of 36·0 μmoles photons $m^{-2}s^{-1}$ for *L. orcadensis* at 30°C and 78·0 μmoles photons $m^{-2}s^{-1}$ for *L. baileyana* at 37·5°C. Above 30°C compensation irradiance declined in *L. orcadensis*, but not in *L. baileyana*, and $I_c$ was significantly higher for *L. baileyana* at 30 and 35°C.

*L. baileyana* had a significantly higher concentration of chlorophyll *a* than *L. orcadensis* (0·46 vs. 0·38 μmoles chl *a* g fresh weight$^{-1}$). However, there was no difference between the phycobilin concentrations (7·6 μmoles total phycobiliproteins g fresh weight$^{-1}$) of the two species.

## Photosynthetic responses to red and green light

Alpha, measured in green light in *L. orcadensis*, declined from 15 to 30°C [Fig. 4(a)]. However, there was no significant difference in alpha measured in red light in *L. orcadensis* at these two temperatures [Fig. 4(b)]. In *L. baileyana* alpha measured

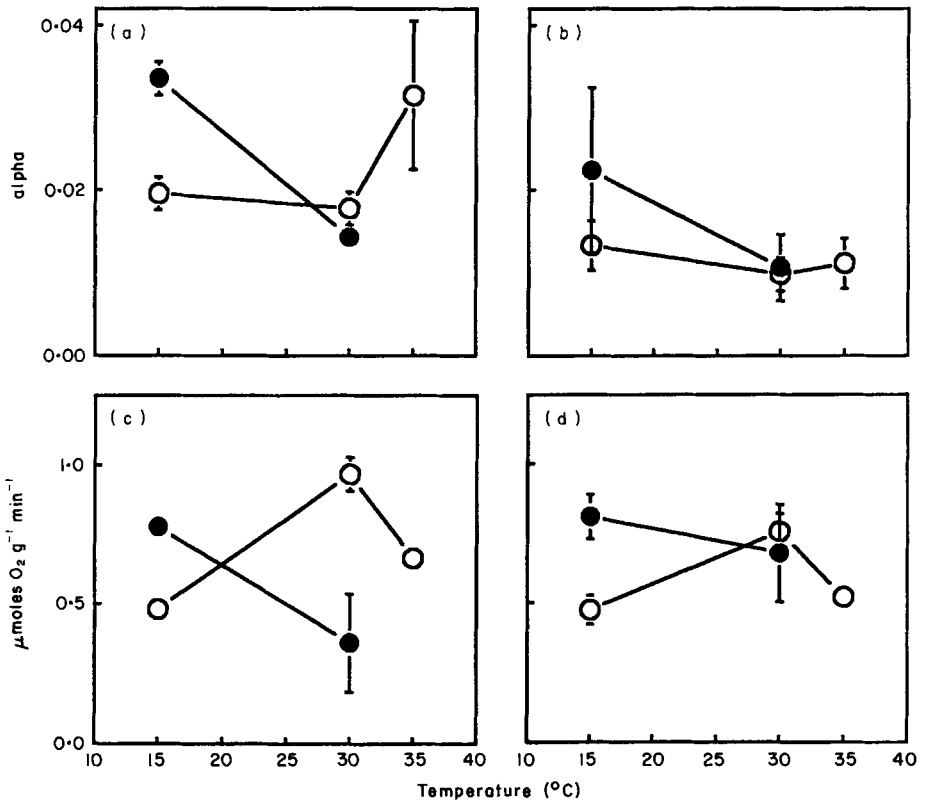


FIG. 4. Alpha values measured in (a) green light and (b) red light and $P_{max}$ measured in (c) green light and (d) red light for *L. baileyana* (○) and *L. orcadensis* (●). Error bars equal one standard error except where the size of symbols exceeds this value. ($N = 5$.) *L. orcadensis* had no net photosynthesis at 35°C.

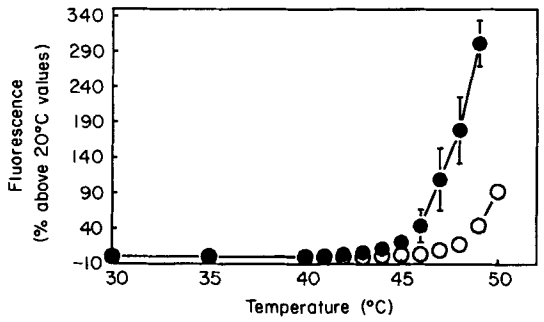


FIG. 5. Per cent increase in phycoerythrin fluorescence above that recorded at 20°C for *L. baileyana* (○) and *L. orcadensis* (●). Error bars equal one standard error except where the size of symbols exceeds this value. ($N = 5$.)

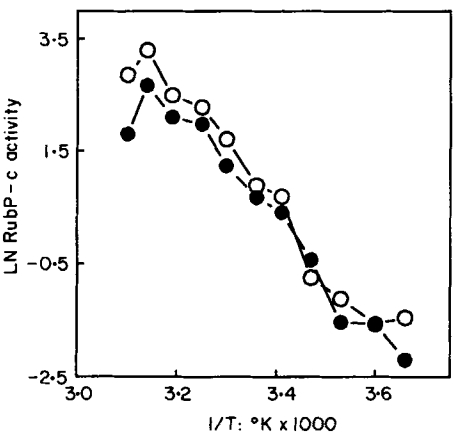


FIG. 6. Arrhenius plot of RubP-case activity measured at a range of temperatures for *L. baileyana* (○) and *L. orcadensis* (●). ($N > 5$.)

in green or red light [Fig. 4(a), (b)] did not change with temperature over the range 15–35°C, as occurred in white light [Fig. 4(a), (b) cf. Fig. 3(a)]. Gross $P_{max}$ in *L. orcadensis* was significantly lower at 30 than 15°C when measured in green light [Fig. 4(c)] but not when measured in red light [Fig. 4(d)]. $P_{max}$ for *L. baileyana* increased from 15 to 30°C in both green and red light.

### Phycoerythrin fluorescence

The relative intensity of phycoerythrin fluorescence (Fig. 5) sharply increased at high temperatures in both species. The temperature at which fluorescence increased by 100% above the initial value was significantly higher for *L. baileyana* (49°C) than for *L. orcadensis* (46°C).

### RubP-c activity

RubP-c activity (Fig. 6) increased for both species with increasing temperature. There was no difference in activity between the two species below 318°K (45°C). At 318 and 323°K (45 and 50°C) *L. baileyana* had significantly greater RubP-c activity than *L. orcadensis*. There were no evident breaks in the Arrhenius plots of activity in either species and the activation energy for the two species was not significantly different ($E_a = -95{\cdot}2$ kJ mole$^{-1}$).

## DISCUSSION

The *Lomentaria* plants used in these experiments were grown at a constant temperature (20°C) for at least 4 months. The differences in the response of photosynthesis to temperature observed between the two species can, therefore, be attributed to genetic adaptation, rather than phenotypic acclimation. Our data indicate that two major differences exist between the thermal responses of light-saturated net photosynthesis in the two species of *Lomentaria* [Fig. 1(a)]. First, high-temperature inhibition of photosynthesis occurred at a lower temperature in *L. orcadensis* ( > 30°C) than in *L. baileyana* ( > 35°C), and second, below 15°C photosynthetic rates were higher in *L. orcadensis* than in *L. baileyana*. There were no significant differences in rates of light-saturated net photosynthesis between the two species over the range 15–30°C. The patterns of photosynthetic response to temperature and photosynthetic rates at optimal temperatures were similar to those reported for other red algae (Lapointe, Tenore & Dawes, 1984; Mathieson & Burns, 1971; Smith & Berry, 1986). Similar results were obtained with gross light-saturated photosynthesis [i.e. net photosynthesis plus respiration; Fig. 1(b)]. The differences in the temperature response of light-saturated

photosynthesis between *L. baileyana* and *L. orcadensis* (Fig. 1) were similar to the differences in the growth vs. temperature response (Yarish, Breeman & van den Hoek, 1984, 1986). For example, photosynthetic rates of *L. orcadensis* were significantly greater than those of *L. baileyana* below 15°C [Fig. 1(a), (b)], consistent with the fact that *L. orcadensis*, but not *L. baileyana*, achieved high growth rates between 10 and 15°C (Yarish, Breeman & van den Hoek, 1984, 1986). Similarly, high-temperature inhibition of both growth and photosynthesis occurred at lower temperatures in *L. orcadensis* than in *L. baileyana*. Overall, our data are consistent with those of other workers (e.g. Bolton, 1983; Gerard & Dubois, 1988) and support the hypothesis that temperature adaptation of photosynthesis is important in controlling seaweed growth. Thus, both adaptation and acclimation of photosynthesis appear to play an important role in the temperature responses of marine macroalgae (Rietema & van den Hoek, 1984; Davison, 1987; Davison & Davison, 1987; Gerard & Dubois, 1988).

In both species of *Lomentaria* thermal inhibition of growth occurred at a lower temperature than inhibition of photosynthesis (30 and 35°C, respectively for *L. baileyana* and 20 and 30°C, respectively for *L. orcadensis*) (Yarish, Breeman & van den Hoek, 1984, 1986, cf. Fig. 1). Similar differences in the upper temperature tolerance of photosynthesis and growth have been reported previously in macroalgae (e.g. Davison, 1987) and are typical of higher plants (Berry & Raison, 1981). This indicates that, although instantaneous measurements of photosynthesis vs. temperature are useful for comparing the relative thermal tolerances of different species, they are of limited value in predicting precise upper and lower limits for long-term growth and survival. There are several possible explanations for the lack of correspondence between temperatures required to inhibit photosynthesis and growth. The first possibility is that short-term photosynthetic measurements overestimate the upper thermal tolerance of long-term growth and survival. The second possibility is that respiratory consumption of carbon, which continued to increase up to the highest temperature tested (40°C; Fig. 2), would reduce the maximum temperature at which the plants could achieve a positive daily carbon balance (Gerard & Dubois, 1988). The third possibility is growth limitation by some other aspect of metabolism (e.g. nitrogen uptake and assimilation), which has a lower thermal stability than photosynthesis. Currently, it is not known which of the three possible mechanisms is the most important.

Temperature also had an effect on photosynthesis at subsaturating PFD. In both species of *Lomentaria* compensation irradiance ($I_c$) and saturation irradiance ($I_k$) increased with temperature up to the point at which photosynthesis was inhibited [Fig. 3(b), (c)]. There was no significant difference between the $I_c$ and $I_k$ values of the two species, except above 25°C, where the $I_c$ of *L. baileyana* exceeded that of *L. orcadensis*. The responses of $I_c$ and $I_k$ to temperature were similar to those observed previously in higher plants (Berry & Bjorkman, 1980) and unicellular algae (Kirk, 1983). Because alpha was largely independent of temperature over the range 0–30°C [Fig. 3(a)], increases in $I_c$ were presumably due primarily to increased respiration (Fig. 2). At incubation temperatures above 30°C the variability of alpha values increased [Fig. 3(a)].

Rates of light-saturated photosynthesis are controlled by activities of Calvin-cycle enzymes, rates of inorganic carbon uptake and rates of electron transport. Thus, increased rates of RubP-c activity and electron transport at high temperatures (Mitchell & Barber, 1986; Davison, 1987; Fig. 6) presumably allow *Lomentaria* sp. to utilize more light in photosynthesis. This is indicated by the increase in $I_k$ with increasing temperature [Fig. 3(b)]. This observation is supported by the growth data of Yarish, Breeman & van den Hoek (1984) which indicate that *L. orcadensis* can grow faster at 40 than 10 μmole photons $m^{-2}s^{-1}$ at the

upper end of its temperature range, whereas no effect of PFD on growth rate at 5–10°C was observed.

One important difference between *L. baileyana* and *L. orcadensis* is in their ability to achieve photosynthesis at high temperatures [Fig. 1(a)]. Two key questions are therefore: (1) what factor(s) control the upper thermal tolerance of photosynthesis in *Lomentaria* sp., and, (2) what factor(s) account for the differences in high-temperature tolerance between *L. baileyana* and *L. orcadensis*? Our data on *in vivo* PE fluorescence suggest that differences in the thermal stability of the light-harvesting apparatus may control the upper thermal tolerance of photosynthesis. *In vivo* PE fluorescence increased to twice the initial values at high temperatures (Fig. 5), presumably due either to a disruption in energy transfer somewhere in the sequence PE–phycocyanin – allophycocyanin – PSII (Gantt, 1981) or to an inhibition of photosynthetic electron transport. Phycoerythrin fluorescence increased at significantly higher temperatures in *L. baileyana* than in *L. orcadensis* (49 and 46°C, respectively; Fig. 5), indicating that energy transfer is more susceptible to thermal disruption in *L. orcadensis* than in *L. baileyana*.

Despite the correlation between thermal stability of energy transfer (as measured by PE fluorescence) and whole plant photosynthesis, the temperature at which fluorescence increased was higher than that required to inhibit photosynthesis [Fig. 1(a), cf. Fig. 5]. It is possible that these differences may be due to differences in the duration of temperature exposure between the different experiments. Fluorescence measurements were made under a regime of rapid temperature increases (approximately 2°C $min^{-1}$), whereas determinations of photosynthetic rate required a longer period of exposure to a single temperature (approximately 5 min). However, when the fluorescence measurements were repeated with temperature changing in 5°C steps, fluorescence jumps occurred at the same temperatures as when temperature was allowed to increase rapidly (data not presented). The thermal shock incurred in measuring photosynthesis where plants were transferred directly from 20°C to the measuring temperature may have been greater than that in the fluorescence jump experiments when plants were exposed to a progressive increase in temperature. Alternatively, the lower irradiance used in the fluorescence measurements (20 vs. 280 μmoles photons $m^{-2}s^{-1}$ for $P_{max}$) may have resulted in the apparently higher thermal tolerance.

The conclusion that the disruption of photosynthetic energy transfer or electron transport is important in setting the upper temperature limits of photosynthesis is supported by our data on the effect of temperature on photosynthesis in red and green light. These data suggest that disruption of energy transfer between PE and chlorophyll occurs at 30°C in *L. orcadensis* but not in *L. baileyana* (Fig. 5). At 30°C both alpha and $P_{max}$ measured in green light harvested by phycobilins (Kursur & Alberte, 1983; Gantt, 1981) were higher in *L. baileyana* than in *L. orcadensis*. In contrast, these parameters did not differ between species when chlorophyll was excited directly by red light at the same temperature. These results suggest that the thermal inactivation of photosynthesis is due to the breakdown of energy transfer between phycoerythrin and chlorophyll rather than inhibition of electron transport. Thermal instability of thylakoid membrane has been associated with inhibition of photosynthesis in higher plants (Berry & Raison, 1981) but has not previously been studied in red algae where the light-harvesting complexes (phycobilisomes) are arranged on the surface of the thylakoid membrane rather than embedded within it (Gantt, 1981). There is evidence that energy is preferentially transferred from the phycobilisomes to PSII (Kursur & Alberte, 1983). Thus, the situation in *Lomentaria* is analogous to that in higher plants where PSII is more susceptible to high-temperature breakdown than PSI and produces an increase in *in vivo* chlorophyll fluorescence (Berry & Bjorkman, 1980; Berry & Raison, 1981).

The Calvin-cycle enzyme RubP-c

extracted from *L. baileyana* was significantly more stable at 45–50°C than the enzyme from *L. orcadensis* (Fig. 6). However, the temperatures required to inhibit RubP-c are well above those which inhibit photosynthesis (Fig. 1, cf. Fig. 6). The direct comparison between photosynthesis and RubP-c activity is justified because incubation times for enzyme assays, and hence exposure to high temperature, exceeded those for photosynthesis (15 min and 5 min, respectively). On this basis, it appears improbable that thermal denaturation of RubP-c is responsible for the high-temperature inhibition of photosynthesis in either species of *Lomentaria*.

Another important question about the photosynthesis–temperature responses of *Lomentaria* sp. concerns the higher photosynthetic rates achieved by *L. orcadensis* over the range 0–15°C (Fig. 1). Increases in Calvin-cycle enzymes play an important role in the maintenance of high photosynthetic rates in seaweeds acclimated to low temperature (Kuppers & Weidner, 1980; Davison & Davison, 1987; Davison, 1987). This does not appear to be an important factor in the temperature adaptation in *Lomentaria* because neither activities nor activation energy of RubP-c were significantly different in the two species over the range 0–40°C (Fig. 3). Rates of whole-chain photosynthetic electron transport have been shown to control differences in light-saturated photosynthesis between peas grown at different temperatures (Mitchell & Barber, 1986). A similar mechanism, based on genetic differences in rates of electron transport could explain the differences in $P_{max}$ between the *Lomentaria* sp.

Photoinhibition is a reversible reduction in quantum yield of photosynthesis, related to the absorption of light energy in excess of that which can be used in photosynthesis, and which ultimately produces chlorophyll bleaching (Osmond, 1981). Any environmental factor which reduces photosynthesis may result in damage to the photosynthetic apparatus when exposed to irradiances which would not otherwise be inhibitory (Powles, 1984; Greer, Berry & Bjorkman, 1986). Both low- and high-temperature-enhanced photoinhibition have been observed in unicellular algae and higher plants (Sadakane *et al.*, 1981; Ludlow, 1987; Oquist, Greer & Ogren, 1987), and recent work with *Porphyra* sp. (Bose, Herbert & Fork, 1988; Herbert & Waaland, 1988) indicates that the mechanism of photoinhibition in macroalgae is the same as that in higher plants. *L. baileyana* plants transferred from 20 to 5°C bleach rapidly and die within 1–2 days at 100 μmole photons $m^{-2}s^{-1}$ but survive several days at 40 μmole photons $m^{-2}s^{-1}$. In contrast, *L. orcadensis* survives and/or grows at 5°C at 40, 70 and 100 μmole photons $m^{-2}s^{-1}$ (data not shown). Taken together, the above lines of evidence suggest that low-temperature-induced photoinhibition may be responsible for the reduced photosynthetic performance of *L. baileyana* relative to *L. orcadensis*.

Overall, the results of this study indicate that genetic adaptation in *L. orcadensis* and *L. baileyana* produces photosynthesis vs. temperature responses which are similar to, and potentially determine, growth responses to temperature. Differences in photosynthetic performance of the two species occurred at both high and low temperatures. The temperature responses of phycoerythrin fluorescence indicated a difference in the high-temperature stability of electron transport or energy transfer in the two species. This breakdown in energy transfer appears to occur between phycoerythrin and chlorophyll *a*. Differences between the two species' photosynthetic rates at low temperature may have been due to differences in their susceptibility to low-temperature-enhanced photoinhibition. The temperature responses of aspects of the dark reactions of photosynthesis, including RubP-case activity and photorespiration, as well as that of dark respiration, were similar for the two species.

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