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PHOTOSYNTHETIC TEMPERATURE ACCLIMATION IN TWO COEXISTING SEAGRASSES, *ZOSTERA MARINA* L. AND *RUPPIA MARITIMA* L.

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ABSTRACT

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The physiological responses to temperature were investigated in two coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. sensu lato from the lower Chesapeake Bay, Virginia. Seven plant collections were made from March to July, 1983 at ambient temperatures of 8—30°C. Both species maintained relatively constant fresh:dry weight ratios and chlorophyll *a*:*b* ratios over the five-month period. Total chlorophyll content remained constant in *Z. marina* while that of *R. maritima* doubled from March to July. P_{max} values for both species increased with increasing temperature and declined at temperatures above 19 and 23°C (*Z. marina* and *R. maritima*, respectively). P_{max} values were significantly higher for *R. maritima* compared to *Z. marina* at temperatures above 19°C. Both short-term (laboratory) and long-term (in situ) responses to temperature regimes affected estimates of the photosynthetic capacity of both species. Thus, temperature histories of experimental material should be carefully considered when interpreting temperature effects on photosynthesis. This study provides support of the hypothesis that seasonal community dynamics of *Z. marina* and *R. maritima* in Chesapeake Bay are regulated in part by different responses to light and temperature.

INTRODUCTION

Total insolation and the daily period of photosynthetically saturating intensity (Clough and Attiwill, 1980; Zieman and Wetzel, 1980; Dennison and Alberte, 1982) are principal factors regulating the spatial distribution of temperate seagrasses. Temporal distribution and growth activity may be regulated by these and other factors. Seasonal production variations may be explained by seasonal changes in irradiance for habitats with relatively stable nutrient environments and narrow temperature ranges (Sand-

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Jensen and Borum, 1983). In other regions, seasonal sediment nutrient dynamics are correlated with growth patterns (Bulthuis and Woelkerling, 1981). Wide seasonal temperature fluctuations may also regulate temporal variability in certain environments, due to thermal tolerance ranges of species and populations (Biebl and McRoy, 1971; Penhale, 1977; Drew, 1978, 1979; Bulthuis, 1983; Wetzel and Penhale, 1983).

The seagrasses *Zostera marina* L. and *Ruppia maritima* L. sensu lato coexist in areas of the Chesapeake Bay, where they generally grow as patchy monospecific stands that are spatially defined by water depth. Depth distributions appear to be controlled by species light requirements (Wetzel and Penhale, 1983). The temporal distributions of *Z. marina* and *R. maritima* are quite distinct (Orth and Moore, 1982). Above-ground biomass of *Z. marina* is maximal in late-spring or early-summer, declines in mid- to late-summer, and increases again in the autumn. In contrast, *R. maritima* shows only a single annual above-ground peak in mid-summer.

Temporal separation of growth by coexisting terrestrial species is common in temperate terrestrial regions (Berry and Raison, 1981), and often appears to be regulated by the responses of photosynthesis to temperature (Williams, 1974; Monson and Williams, 1982; Monson et al., 1983). Species differences in the potential for temperature acclimation may lead to seasonal differences in photosynthetic capacity, resulting in temporally offset patterns of resource utilization and growth.

The purpose of this study was to examine the photosynthetic responses related to temperature and light of *Z. marina* and *R. maritima*. A comparison of these responses may suggest photosynthetic temperature adaptation as a basis for temporal separation of each species' growth activity.

MATERIALS AND METHODS

Collection site

The seagrasses, *Z. marina* and *R. maritima*, were collected from March to July, 1983 in an extensive meadow located along the northern shore of the York River mouth (37°16′N, 76°21′W) in the lower Chesapeake Bay, Virginia (Fig. 1). A collection station was established in a mixed bed of *Z. marina* and *R. maritima* approximately 100 m from the shore at approximately 0.75 m depth.

Environmental parameters in the lower Chesapeake Bay vary considerably over an annual cycle. Monthly averages of total daily insolation range from 15 to 47 E m^{-2} day^{-1} (January and July, respectively). Although the coefficient of submarine light attenuation is highest in summer and lowest in winter, calculated submarine intensities at the top of seagrass canopies increase during winter and spring, reaching the highest values in summer (Van Tine and Wetzel, 1982). Water temperature ranges annually from 1 to 30°C; salinity in this area generally ranges from 15 to 25‰.

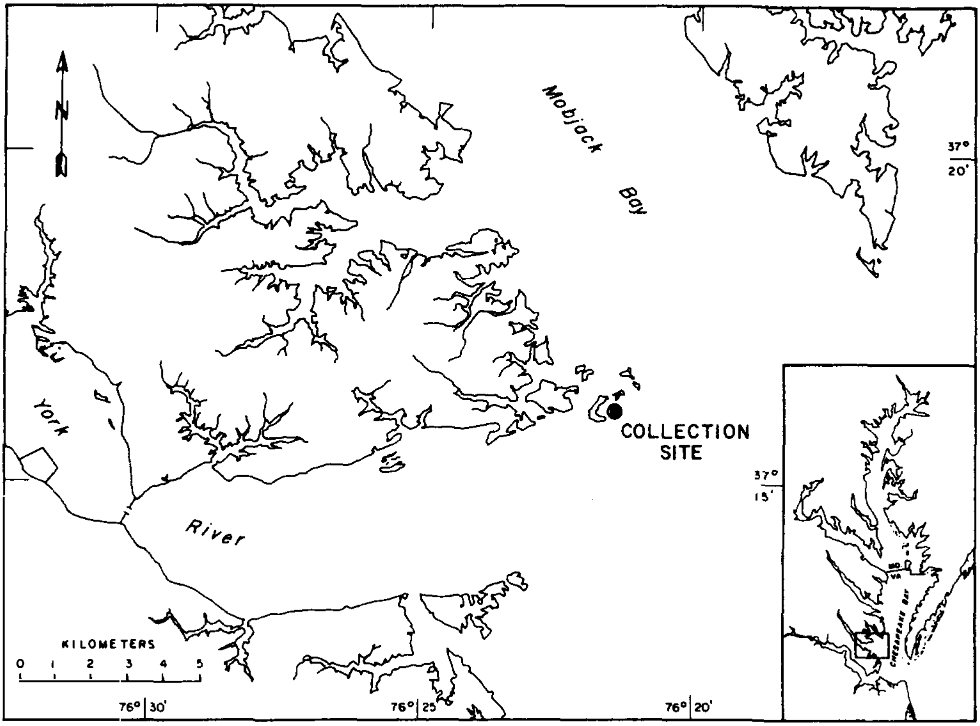

Fig. 1. Map of the collection site.

Plant material

Plants were collected by hand and roots and rhizomes were rinsed free of sediment. Plants were kept in seawater in the dark during transport to the laboratory, where they were held in aquaria in aerated seawater maintained at ± 1°C of the ambient water temperature during collection. Photosynthetically saturating irradiance of 150 μE m^{-2} s^{-1} (400—700 nm), measured with a quantum radiometer (LiCor, U.S.A.) at the water surface, was provided by cool-white fluorescent tubes. Daily light:dark cycles were adjusted to those prevailing at the time of collection. Plants were maintained under these conditions for no longer than 7 days. Photosynthesis was similar on Day 1 and Day 7 in agreement with Bulthuis (1983) who reported that holding periods to 11 days were satisfactory.

Experimental protocol

Seawater from the collection site was filtered (0.45 μm), sparged with N_2 and decanted into 33-ml glass incubation tubes, which were placed in a temperature-controlled (± 1°C) incubator. Light (520 μE m^{-2} s^{-1}) in the incubator was provided by fluorescent Vita-Lite tubes; opaque and neutral density filters were used to provide 100, 50, 20, 2 and 0% of the ambient light. The incubation chamber was placed on a shaker table set at 50 oscillations per min.

Leaf tips (20—80 mg fresh weight) for photosynthesis measurements were held for 30 min in filtered, sparged seawater to reduce the O_2 content of the tissue. Single *Z. marina* or *R. maritima* leaf tips (free of visible epiphytes, but otherwise selected without an age bias) were then placed in glass incubation tubes in each of the incubator compartments. After approximately 2 h, the tissue was removed and O_2 measurements were made with a Clark-type polarographic electrode (Orbisphere Laboratories Inc., Switzerland). Initial O_2 values were determined from filtered, sparged seawater in control tubes which did not contain plant tissue.

Fresh weights (after blotting) were recorded, and the samples were frozen and lyophilized (—80°C, 200 millitorr) for determination of dry weights. Chlorophylls *a* and *b* were determined on the lyophilized samples after extraction in 90% acetone (Jeffrey and Humphrey, 1975).

Experimental design and statistical treatment

Photosynthesis versus irradiance (P vs. I) relationships were determined for both *Z. marina* and *R. maritima* at temperatures (8, 12, 14, 19, 23, 26 and 30°C) corresponding to ambient water temperatures at the time of collection. In addition, P vs. I curves were generated at temperatures which were 10°C above ambient for all but the two highest collection temperatures. Photosynthetic rates at each light intensity were calculated as the mean ± SE of 7 replicates. Light-saturated rates (P_{max}) for each species were determined as gross photosynthesis for the highest measured rate at each measurement temperature. A linear regression of rates at 0 and 10 or 15 $\mu E\ m^{-2}\ s^{-1}$ was used to calculate the initial slope. Values of I_k were derived from the regression as the intersection of the initial slope with P_{max}. Physiological characteristics such as the fresh:dry weight ratio were calculated as the mean ± SE of 30—70 samples for each species at each collection temperature.

Statistical tests were performed using Subprogram T-Test SPSS, Update 9 (Nie et al., 1975). Tests for significant differences ($P < 0.05$) between species for each collection were conducted for variables P_{max}, fresh:dry weight ratio, chlorophyll *a*:*b* ratio and total chlorophyll per fresh weight. Tests were also performed between P_{max} and temperature treatments for each species.

RESULTS

Physiological characteristics

Physiological characteristics of *Z. marina* and *R. maritima* are summarized in Table I. The ratio of fresh:dry weight was significantly greater ($P < 0.05$)

for *R. maritima* than for *Z. marina* for each collection; however, neither species showed any seasonal trend. Chlorophyll *a*:*b* ratios were significantly greater for *R. maritima* (2.6—3.4) than for *Z. marina* (2.3—2.7) for each collection. The two species also differed in total chlorophyll content over the study period. Values for *R. maritima* doubled with temperature from 0.7 to 1.5 mg chlorophyll g-fresh wt.$^{-1}$ (8°C and 26°C, respectively), while *Z. marina* values ranged between 1.4 and 1.6 mg chlorophyll g-fresh wt.$^{-1}$ (Fig. 2). Except for collections at the highest temperatures (26 and 30°C),

TABLE I

Physiological characteristics of *Zostera marina* and *Ruppia maritima*. Means and standard errors of 65—70 samples for collections on 24 March to 23 May are presented. Sample sizes for the July collections were 30—35

Date	Temperature (°C)	Fresh:Dry weight (ratio)			Chlorophyll *a*:*b* (ratio)		
		Zostera		*Ruppia*	*Zostera*		*Ruppia*
24 Mar.	8	4.79 ± 0.06	*	5.55 ± 0.08	2.41 ± 0.03	*	2.61 ± 0.04
8 Apr.	12	4.58 ± 0.07	*	5.57 ± 0.11	2.67 ± 0.03	*	3.05 ± 0.06
24 Apr.	14	4.38 ± 0.07	*	5.45 ± 0.10	2.62 ± 0.07	*	2.93 ± 0.05
4 May	19	4.51 ± 0.04	*	5.77 ± 0.06	2.56 ± 0.03	*	2.81 ± 0.05
23 May	23	4.84 ± 0.03	*	5.81 ± 0.06	2.62 ± 0.07	*	3.38 ± 0.07
27 Jul.	26	3.88 ± 0.05	*	5.54 ± 0.20	2.28 ± 0.03	*	2.86 ± 0.06
19 Jul.	30	4.07 ± 0.06	*	5.81 ± 0.17	2.27 ± 0.04	*	2.65 ± 0.09

*Significant difference ($P < 0.05$) between the 2 species at a given collection.

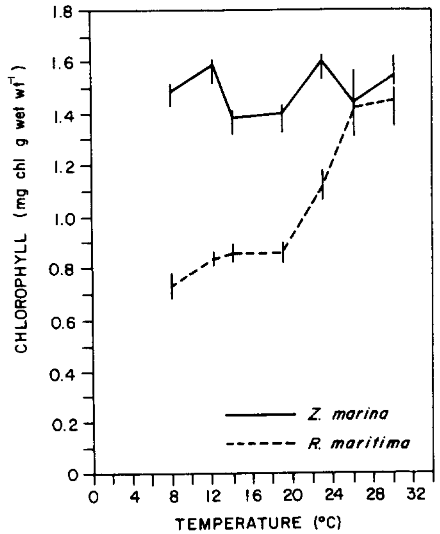

Fig. 2. The temperature dependence of chlorophyll content g fresh weight^{-1} for *Zostera* and *Ruppia*. The vertical bars represent ± SE.

Z. marina leaves had a significantly higher total chlorophyll content than *R. maritima* leaves.

Photosynthetic responses to ambient temperature

Photosynthetic capacities, or P_{max} values, for *Z. marina* and *R. maritima* are shown in Table II. Both species exhibited their lowest P_{max} values at 8°C with the highest values occurring at 19 and 23°C for *Z. marina* and *R. maritima*, respectively. Except for one case, significant differences between species were not seen in P_{max} values from 8 to 19°C; at the three higher temperatures, *R. maritima* exhibited significantly higher P_{max} values. For comparison to Q_{10} values (see below), a similar calculation was performed on seasonal P_{max} data using linear regressions of log transformed data (Berry and Raison, 1981). For *R. maritima*, a break in the temperature response curve was observed at 23°C with temperature coefficients (a seasonal Q_{10} equivalence) of 1.26 and —1.35 calculated below and above this temperature, respectively. For *Z. marina*, the break occurred at 19°C with the temperature coefficients being 1.34 and —1.26 below and above 19°C, respectively.

TABLE II

Photosynthetic capacities of *Zostera marina* and *Ruppia maritima*. Plants were collected and measured at the temperatures indicated. Means and standard errors of 7 replicates are presented

Date	Temperature (°C)	Photosynthetic capacity (μmol O_2 mg chlorophyll^{-1} min^{-1})		
		Zostera		*Ruppia*
24 Mar.	8	0.36 ± 0.02		0.39 ± 0.02
8 Apr.	12	0.38 ± 0.02	*	0.48 ± 0.02
24 Apr.	14	0.40 ± 0.02		0.42 ± 0.03
4 May	19	0.50 ± 0.04		0.58 ± 0.02
23 May	23	0.44 ± 0.04	*	0.67 ± 0.06
27 Jul.	26	0.41 ± 0.02	*	0.64 ± 0.05
17 Jul.	30	0.39 ± 0.04	*	0.55 ± 0.03

*Statistically significant difference ($P < 0.05$) between the two species at a given temperature.

The relationship between α, P_{max} and I_k is usually described as $\alpha = P_{max}/I_k$; it is thus apparent that if P_{max} changes with season, as indicated above, then either α and/or I_k must do likewise. The ranges and means of α values, often related to photosynthetic efficiencies, were similar for the two species, with *Z. marina* exhibiting a slightly higher α than *R. maritima* (Table III). Both species exhibited a positive trend in α values within the experimental temperature range. The photosynthetic light saturation intensity, I_k, was negatively related to temperature for both species, the values being about one-third lower and less variable for *Z. marina*. I_k ranged from 28 to 46 $\mu E\ m^{-2}\ s^{-1}$ for *Z. marina* and from 39 to 72 $\mu E\ m^{-2}\ s^{-1}$ for *R. maritima*. The α and I_k data sets for both species are less variable when values obtained at 26°C are discarded. This collection date followed the temperature peak a week earlier and, based on P_{max} trends, the plants were already showing stress.

TABLE III

Photosynthetic characteristics of *Zostera marina* and *Ruppia maritima*. Plants were collected and measured at the temperatures indicated. Values of α were calculated from a linear regression of mean photosynthetic rates at the lowest light intensities. Values of I_k were calculated from the regression as the intersection of P_{max} and α

Date	Temperature (°C)	α (μmol O_2 mg chlorophyll^{-1} min^{-1} μE^{-1} m^2 s^{-1})		I_k ($\mu E\ m^{-1}\ s^{-1}$)	
		Zostera	*Ruppia*	*Zostera*	*Ruppia*
24 Mar.	8	0.0087	0.0087	41	45
8 Apr.	12	0.0100	0.0067	38	72
24 Apr.	14	0.0100	0.0070	40	60
4 May	19	0.0140	0.0110	36	53
23 May	23	0.0140	0.0120	31	56
27 Jul.	26	0.0090	0.0090	46	71
17 Jul.	30	0.0140	0.0140	28	39
	$\bar{x}$	0.0114	0.0098	37	57
	SE	0.0009	0.0010	2	5

Photosynthetic responses to temperatures above ambient

A comparison of P_{max} values at ambient and 10°C above ambient temperatures revealed differences for both species (Table IV). With the exception of the *R. maritima* 23/33°C pair, P_{max} values were significantly higher at the increased measurement temperature. Q_{10} values, defined as the ratio of photosynthetic rate at one temperature to the rate at 10°C lower, were similar for both species.

DISCUSSION

Ecological observations of *Z. marina* and *R. maritima* in Chesapeake Bay prompted the present study of the photosynthetic physiology of the two species. This research was aimed at determining the underlying mechanisms responsible for the spatial and temporal distribution of the two species. *Z. marina* grows to greater depth in the subtidal than *R. maritima*, which is found in higher light environments of the intertidal and shallow

TABLE IV

Photosynthetic capacities of *Zostera marina* and *Ruppia maritima*. Plants were collected at the ambient temperatures indicated, and measurements were made both at ambient temperatures and at 10°C above ambient. Means and standard errors of 7 replicates are presented

Date	Temperature (°)	Photosynthetic capacity (μmol O_2 mg chlorophyll^{-1} min^{-1})			
		Ambient		Ambient +10°C	Q_{10}[1]
Zostera marina					
24 Mar.	8	0.36 ± 0.02	*	0.62 ± 0.02	1.7
8 Apr.	12	0.38 ± 0.02	*	0.60 ± 0.04	1.6
24 Apr.	14	0.40 ± 0.02	*	0.59 ± 0.03	1.5
4 May	19	0.50 ± 0.04	*	0.68 ± 0.02	1.4
23 May	23	0.44 ± 0.04	*	0.61 ± 0.01	1.4
Ruppia maritima					
24 Mar.	8	0.39 ± 0.02	*	0.63 ± 0.04	1.6
8 Apr.	12	0.47 ± 0.02	*	0.82 ± 0.04	1.7
24 Apr.	14	0.42 ± 0.03	*	0.70 ± 0.04	1.7
4 May	19	0.58 ± 0.02	*	1.01 ± 0.04	1.7
23 May	23	0.67 ± 0.06		0.84 ± 0.05	1.3

[1] Q_{10} is the ratio of the photosynthetic rate at one temperature and the rate at a temperature 10°C lower.

*Statistically significant ($P < 0.05$) difference between rate measurements at the 2 temperatures.

subtidal regions of the Bay. The biomass of *Z. marina* exhibits two seasonal peaks, one in late-spring to early-summer and the other in the autumn. A depressed biomass accompanied by leaf sloughing occurs in the warmest summer months. In contrast, *R. maritima* exhibits its single biomass peak in mid-summer (Orth and Moore, 1982). A temperature preference is also seen in the arctic and temperate distribution of *Z. marina* which reaches its southernmost limit on the east coast at Cape Fear, North Carolina (Thayer et al., 1975). In general, *R. maritima* appears tolerant of higher temperatures based on seasonal studies and its biogeography (Richardson, 1980).

Gross photosynthesis rates reported here are within the range reported by other workers. In the present study, ambient rates ranged from 0.36 to 0.50 μmol O_2 mg chlorophyll^{-1} min^{-1} for *Z. marina* and from 0.39 to 0.57 μmol O_2 mg chlorophyll^{-1} min^{-1} for *R. maritima*. Dennison and Alberte (1982) reported rates ranging from 0.40 to 0.60 μmol O_2 mg chlorophyll^{-1} min^{-1} for *Z. marina* from Massachusetts. Rates of 0.40 to 1.04 μmol O_2 mg chlorophyll^{-1} min^{-1} were measured for the Australian seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog (Bulthuis, 1983).

The values for α and for I_k were higher and lower, respectively, in the present study than other values reported for seagrasses (Penhale, 1977; Drew, 1978, 1979; Bulthuis, 1983). For another Chesapeake Bay site, Wetzel and Penhale (1983) reported different α and I_k values, based on ^{14}C methodology, for *Z. marina* and *R. maritima*; however, the relationships for these values between the two species were similar in both of these Chesapeake Bay studies: *Z. marina* had lower I_k and similar α values compared to *R. maritima*. Thus, at lower light environments, *Z. marina* should be more successful.

The changes in photosynthetic capacities of the two species over the study period suggest that *R. maritima* has the competitive advantage over *Z. marina* at higher temperatures (Fig. 3). A similar conclusion was reached by Wetzel and Penhale (1983). For *Z. marina*, P_{max} increased from 1 to 28°C, but decreased from 28 to 30°C. *Ruppia maritima* from the same location generally showed higher P_{max} values at the upper end of the temperature range. A *Z. marina* population in North Carolina showed an increase in P_{max} from 15 to 22°C, but at 29°C, P_{max} was lower than at 15°C (Penhale, 1977). All of these studies suggest that the photosynthetic optimum for *Z. marina* is below 30°C. Furthermore, if photosynthetic capacity and biomass are assumed to respond similarly to temperature, the leaf sloughing of *Z. marina* in the grassbed at that time supports the concept of long-term high-temperature stress in this species. Annual mortality of *Z. marina* has been associated with high summertime temperatures at several locations (Marsh, 1970; Thayer et al., 1975; Orth and Moore, 1982).

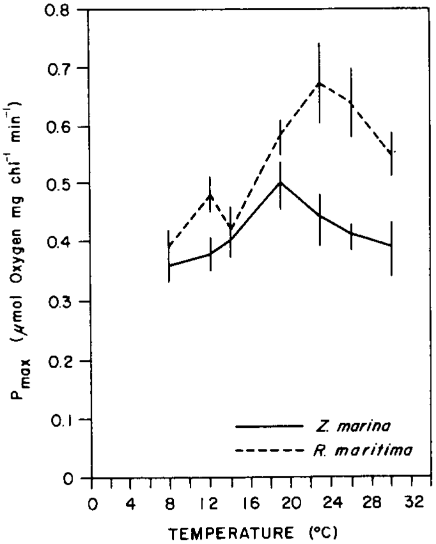

Fig. 3. The temperature dependence of gross P_{max} in *Zostera* and *Ruppia*. Plants were collected and measured at the temperatures indicated. Plotted values represent the mean of 7 replicates. The vertical bars represent ± SE.

One major difference between the species was observed in total chlorophyll content. While the amount of chlorophyll present remained relatively constant for *Z. marina* over the 5-month sampling period, the chlorophyll content more than doubled for *R. maritima*. Variations in chlorophyll content may be affected by a number of external factors as well as genotype. Growth temperature influences leaf chlorophyll content (Patterson, 1980). For example, Barko and Filbin (1983) observed an increased chlorophyll content with increased temperature in 2 out of 3 freshwater angiosperms investigated. Rice et al. (1983) measured chlorophyll content in 3 seagrasses. They observed summer periods of maximal chlorophyll content for *Halodule wrightii* Aschers. and *Halophila engelmanni* Aschers. and a relatively constant chlorophyll content for *Syringodium filiforme* Kütz. throughout the year. Differences in total chlorophyll content have also been observed in different populations of the same submerged angiosperm species (Spence and Chrystal, 1970; McMillan and Phillips, 1979). In addition, many submerged angiosperms have been shown to increase pigment content in response to decreasing light (Dennison, 1979; McMillan and Phillips, 1979; Wiginton and McMillan, 1979; Barko and Filbin, 1983).

Pigment ratios may also vary with temperature and light. A decrease in chlorophyll *a*:*b* ratio with increasing temperature was reported for *Potamogeton nodosus* Poiret, but not for two other freshwater angiosperms (Barko and Filbin, 1983). Some submerged species (Wiginton and McMillan, 1979; Marcus, 1980; Barko and Filbin, 1983), including *Z. marina* (Dennison, 1979), exhibited decreased chlorophyll *a*:*b* ratios in response to decreased light. However, other species show no significant change in pigment composition with respect to light intensity (Van et al., 1977; Wiginton and McMillan, 1979). In the present study, no changes were observed in chlorophyll *a*:*b* ratios for *Z. marina* or *R. maritima* over the 5-month period. The significantly lower chlorophyll *a*:*b* ratio of *Z. marina* compared to *R. maritima* suggests one mechanism to account for the spatial distribution of the two species. With a larger proportion of accessory pigments, *Z. marina* should be more successful at greater depths where light is limiting.

Temperature histories of field-collected plants may affect photosynthesis estimates, particularly if the experimentation involves short-term acclimation to non-ambient temperatures. The present data confirm that both growth and measurement temperature influence photosynthetic capacity in *Z. marina* and *R. maritima*. For example, in *Z. marina*, the P_{max} measured after short-term acclimation at 18°C on material collected at 8°C was significantly different from P_{max} values of material both growing and measured at 19°C. The former value overestimated the latter by nearly 25%. In contrast, a comparison of the same measurements on *R. maritima* yielded rates which were not significantly different. Thus, depending on the species, the response to a short-term increase in temperature could be misleading when the aim is to understand the dynamics of an in situ population. Other seagrass populations have been shown to exhibit different responses at different times of the year (Drew, 1978). Although *Cymodocea nodosa* (Ucria) Aschers. exhibited similar photosynthetic rates in spring and summer, the optimal temperature was higher in summer than in spring. *Posidonia oceanica* (L.) Delile had a similar temperature optimum in both seasons, but P_{max} in summer was twice that in spring.

The Q_{10} values obtained in the present study are between 1 and 2 for both species, which suggests that the combination of both light harvesting and enzymatic reactions limit the maximum rate of photosynthesis in this study. The present values are comparable to the Q_{10} of 1.5 for *Z. marina* based on P_{max} measurements made after short-term exposures to temperatures of 0—35°C (Marsh et al., 1983). Both species showed an ability to respond positively to short-term temperature increases within the range of 8—23°C as shown by significantly higher P_{max} values at ambient +10°C temperatures compared to ambient temperatures. However, over the long term, both species responded negatively as summer temperatures increased above 19°C.

The present research provides additional data to support the hypothesis presented earlier (Wetzel and Penhale, 1983) that seasonal community dynamics of *Z. marina* and *R. maritima* in the lower Chesapeake Bay are regulated in part by the differing responses to light and temperature. The precise role of these variables in controlling primary production is unclear, due to the unknown involvement of other environmental as well as genetic influences.

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