

Light harvesting and the package effect in the seagrasses *Thalassia testudinum* Banks ex König and *Zostera marina* L.: optical constraints on photoacclimation

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Received 24 April 2002; received in revised form 6 September 2002; accepted 4 November 2002

Abstract

Although seagrasses possess numerous adaptations for life underwater, they lack the specialized accessory pigments for the efficient harvesting of green light that dominates many aquatic environments. Without these specialized pigments, photoacclimation by seagrasses is likely to result in a severe package effect, i.e. the loss of linearity between light harvesting efficiency and pigment loading. Here, we investigated the optical constraints imposed by the package effect on photoacclimation in seagrass leaves. Pigment concentrations and optical properties (absorptances, absorption coefficients and optical cross-sections) of turtlegrass (*Thalassia testudinum*) leaves from Lee Stocking Island (LSI; Bahamas) and eelgrass (*Zostera marina*) leaves from Monterey Bay, CL, USA were measured at different times of the year. Chlorophyll concentrations and optical cross-sections differed by a factor of five across sampling dates and populations. Increases in leaf-specific absorption among seagrass leaves were greatest in the green (500–600 nm), while the package effect, as measured by a decrease in leaf optical cross-section, was most severe in the blue (400–500 nm) and red (600–700 nm). Consequently, the five-fold range in pigment concentration resulted in similar photosynthetic light harvest efficiencies ($\phi_L \approx 50\%$ of incident PAR) for intact seagrass leaves in their native light environments. Although the package effect has significant impacts on the optical properties of seagrass leaves, chlorophyll use efficiency does not appear to play a strong role in the ecology or evolution of seagrasses.

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Keywords: Seagrass; Photoacclimation; Package effect; Chlorophyll; Light harvesting

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1. Introduction

Seagrasses possess numerous adaptations that promote the growth and survival of these fully submerged aquatic plants in permanently flooded sediments. Adaptive morphological features include arenchyma that transport photosynthetically-generated oxygen from the shoot to below-ground tissues (Smith et al., 1984), flowers specifically adapted for underwater pollination (Ackerman, 1986), leaves that lack stomata and are covered by a thin, porous cuticle that permits gas and solute transfer, an epidermis rich in chloroplasts and a largely unpigmented mesophyll (Hemminga and Duarte, 2000). The leaves also possess longitudinal fibers that facilitate the maintenance of structural integrity in a fluid medium. Biochemical adaptations include a reverse Pasteur effect in response to tissue anoxia, a prolonged tolerance of low adenylate energy charge that conserve carbon reserves (Smith et al., 1988) and the capacity for photoacclimation to different light environments (Dennison and Alberte, 1982; Abal et al., 1994; Alcoverro et al., 2001).

Photoacclimation can result in a number of changes in leaf properties including total pigment content, relative abundance of accessory pigments and leaf thickness (Lambers et al., 1998). Acclimation to high-light environments usually involves the maximization of photosynthetic capacity per unit leaf area. Acclimation to low light compensates for light limitation by increasing photon capture efficiency, but often at the expense of photosynthetic capacity. Simple adjustment of pigment content in response to different light environments, however, represents an imperfect adaptive mechanism because changes in cellular chlorophyll content do not generate proportional changes in the capacity for light absorption (Dubinsky et al., 1986). Consequently, the change in leaf pigment content is associated with a reciprocal change in the optical absorption cross-section normalized to chlorophyll, primarily because of chromophore self-shading between layers of the thylakoid membranes in the chloroplast. This phenomenon, referred to as the “package” (or sometimes “sieve”) effect, limits the utility of simple changes in pigment content as a strategy for photoacclimation (Duysens, 1956; Morel and Bricaud, 1981; Falkowski et al., 1985; Dubinsky et al., 1986; Berner et al., 1989).

Seagrass leaves lack accessory pigments that permit efficient harvesting of green light. Chloroplasts are limited to the epidermal cell layer of the leaf. Consequently, increases in leaf pigment content should result in a profound package effect, potentially limiting the capacity for photoacclimation. Chlorophyll content of seagrass leaves, however, varies among species and habitats by at least a factor of five, and shows plastic responses to seasonal variations in light availability as well as direct experimental manipulation (Dennison and Alberte, 1982; Herzka and Dunton, 1997; Alcoverro et al., 2001). Light-saturated rates of photosynthesis have also been linearly related to leaf chlorophyll content in *Phyllospadix torreyi* and *Posidonia oceanica* (Drew, 1979). Although the reported variations in leaf chlorophyll content are consistent with photoacclimation theory, the impact of leaf chlorophyll content on light harvesting efficiency has not been investigated in seagrasses.

The purpose of this study was to compare the effects of pigment content on photosynthetic light absorption of seagrass leaves collected from a high-light tropical environment and a relatively low-light temperate environment. Our second objective was to examine the cost to light harvesting efficiency imposed by the resulting package effect in seagrass leaves. This study provides a better understanding of the environmental and physiological constraints

on seagrass performance in nature by quantifying the optical limits of photoacclimation for submerged aquatic vegetation pigmented by chlorophylls (Chls) *a* and *b*.

2. Methods

2.1. Leaf optical properties

Ninety-four *Thalassia testudinum* Banks ex König (turtlegrass) shoots (2 to 3 leaves per shoot) were collected using SCUBA from subtidal meadows (5 to 10 m deep) near Lee Stocking Island (LSI), Bahamas in May 1998 and May 1999. Forty turtlegrass shoots were collected from the same meadows in January 1999. Five *Zostera marina* L. (eelgrass) shoots (5 to 7 leaves per shoot) were collected using SCUBA in Monterey Bay from 5 to 10 m deep meadows in October 1998. Nine eelgrass shoots were collected from these same meadows in April 1999. Epiphytes were removed by gently scraping both sides of all leaves with a razor blade. Leaf reflectance [$R(\lambda)$] and raw absorbance [$D(\lambda)$] spectra were measured from 350 to 750 nm using a Shimadzu UV 2101PC scanning spectrophotometer fitted with an integrating sphere attachment that corrects for light scattering by turbid samples (e.g. leaf tissue). In total, 188 turtlegrass leaves were measured in May 1998 and 1999, 107 leaves were measured in January 1999. Twenty eelgrass leaves were measured in October 1998, and 45 leaves were measured in April 1999.

Photosynthetic leaf absorptances [$A_L(\lambda)$] were calculated by converting raw values of $D(\lambda)$ to absorbance according to Kirk (1994), followed by correction for leaf reflectance [$R_L(\lambda)$] and non-photosynthetic absorbance at 750 nm [$A(750)$]:

$$A(750) = [1 - 10^{-D(750)}] - R_L(750)$$

$$A_L(\lambda) = [1 - 10^{-D(\lambda)}] - R_L(\lambda) - A(750)$$

Leaf-specific photosynthetic absorption coefficients [$a_L(\lambda)$] were then calculated as:

$$a_L(\lambda) = -\ln[1 - A_L(\lambda)]$$

Pigments were extracted by grinding weighed leaf samples in ice cold 80% acetone using a ground glass tissue homogenizer. Concentrations of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and total carotenoids were determined spectrophotometrically using the equations and extinction coefficients of Jeffrey and Humphrey (1975). The optical cross-section of each leaf, $a_L^*(\lambda)$, was calculated by normalizing $a_L(\lambda)$ to the area-specific Chl *a* concentration of each leaf:

$$a_L^*(\lambda) = \frac{a_L(\lambda)}{[\text{Chl } a]}$$

2.2. The submarine light environment and photosynthetic light harvesting efficiencies

Estimates of downwelling spectral irradiance [$E_d(\lambda)$] at each sample location and season were calculated using the radiative transfer program *Hydrolight* (Mobley, 1989) assuming

Table 1
Definition of abbreviations and symbols

Symbol/abbreviation	Definition	Units
$A_l(\lambda)$	Leaf-specific absorption coefficient	Dimensionless
$A_L(\lambda)$	Leaf absorptance	Dimensionless
$D(\lambda)$	Raw leaf absorbance	Dimensionless
$R(\lambda)$	Leaf reflectance	Dimensionless
$a^*_s(\lambda)$	Optical cross-section	$\text{m}^2 \text{g}^{-1} \text{Chl } a$
$\phi_L(\lambda)$	Leaf-specific photosynthetic light harvesting efficiency	Dimensionless
λ	Wavelength	nm
ΣChl	Total chlorophyll ($a + b$)	$\text{mg g}^{-1} \text{FW}$
Chl a	Chlorophyll a	$\text{mg g}^{-1} \text{FW}$
Chl b	Chlorophyll b	$\text{mg g}^{-1} \text{FW}$
$E_d(\lambda)$	Downwelling plane irradiance	$\mu\text{mol quanta m}^{-2} \text{s}^{-1}$
PAR	Photosynthetically active radiation	$\mu\text{mol quanta m}^{-2} \text{s}^{-1}$

The parenthetic notation (λ) denotes wavelength dependence of certain variables.

local noon solar angles for the sampling dates and latitude (24 N for Lee Stocking Island and 36.5 N for Monterey Bay). Water column Chl a concentrations used for the radiative transfer calculations were selected to be representative of local seasonal conditions: 0.1 mg Chl $a \text{ m}^{-3}$ for the perennially clear waters surrounding Lee Stocking Island in both January and May (Zimmerman and Cummings, unpublished data); 1 mg Chl $a \text{ m}^{-3}$ for Monterey Bay during the “oceanic” season (October), and 10 mg Chl $a \text{ m}^{-3}$ for Monterey Bay during the upwelling season (April) (Pennington and Chavez, 2000). Photosynthetic light harvesting efficiencies (ϕ_L), expressed as the spectrally weighted percentage of $E_d(\lambda)$ absorbed by an average leaf oriented normally to a collimated light source, were calculated for each sampling period and location (Table 1):

$$\phi_L = \sum_{\lambda=400}^{700} \frac{A_L(\lambda) E_d(\lambda)}{E_d(\lambda)} 100$$

3. Results

3.1. Leaf optical properties

Leaf pigment concentrations varied five-fold among plants collected from the high light (mean May turtlegrass $\Sigma\text{Chl} = 0.52 \text{ mg g}^{-1} \text{FW}$) to the low light (mean April eelgrass $\Sigma\text{Chl} = 2.50 \text{ mg g}^{-1} \text{FW}$) environments (Table 2). The differences in pigment concentration were statistically significant, both between tropical turtlegrass and temperate eelgrass, and between low- and high-light sampling periods within both species (Table 3). Ratios of Chl $a:b$, however, were largely unaffected by the light environment and remained slightly above 2.0 for both turtlegrass and eelgrass. The Chl $a:b$ ratio of turtlegrass leaves collected in January (mean Chl $a:b = 2.51$) was significantly higher than the pigment ratios observed in May turtlegrass or in eelgrass (mean Chl $a:b = 2.2$, Tables 2 and 3). Carotenoid concen-

Table 2

Average pigment concentrations, and pigment ratios, of turtlegrass and eelgrass leaves

	<i>Thalassia testudinum</i> (Lee Stocking Island, Bahamas)		<i>Zostera marina</i> (Monterey Bay, CA)	
	May	January	October	April
Downwelling irradiance at mid-day (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$)	1100	700	300	50
[Chl <i>a</i>]	0.35 (0.009) ^a	0.59 (0.020) ^b	1.21 (0.086) ^c	1.73 (0.064) ^d
[Chl <i>b</i>]	0.17 (0.005) ^a	0.25 (0.011) ^b	0.53 (0.037) ^c	0.77 (0.030) ^d
[ΣChl]	0.52 (0.009) ^a	0.84 (0.030) ^b	1.74 (0.050) ^c	2.50 (0.045) ^d
[Carotenoid]	0.09 (0.002) ^a	0.13 (0.003) ^b	0.22 (0.015) ^c	0.35 (0.013) ^d
Chl <i>a:b</i>	2.14 (0.028) ^a	2.51 (0.028) ^b	2.27 (0.021) ^a	2.24 (0.036) ^a
Carotenoid: ΣChl	0.21 (0.009) ^a	0.17 (0.009) ^b	0.13 (0.002) ^b	0.14 (0.003) ^b

All pigment concentrations are in units of mg g^{-1} FW. Superscripts indicate statistically identical values as determined by ANOVA and LSD post-hoc analyses (Table 3). Standard errors are listed in parentheses.

trations increased with ΣChl , and the carotenoid: ΣChl ratio of May turtlegrass was higher than the other samples.

The five-fold differences in pigment content between eelgrass and turtlegrass leaves were qualitatively consistent with photoacclimation to different light environments, but they did not translate into similarly large differences in leaf photosynthetic absorptance. The maximum PAR-averaged difference in absorptance (\bar{A}_{PAR}) between samples was 9% ($\bar{A}_{\text{PAR}} = 47\%$ for January turtlegrass, 56% for October eelgrass). The average absorptance of eelgrass leaves from the low-light environment was only 7% higher in the blue (400–500 nm) than the high-light turtlegrass leaves (Fig. 1). The difference increased to 9% in the green (500–600 nm) and 11% in the red (600–700 nm). Observed differences in ΣChl between sampling dates resulted in almost no temporal difference in $A_L(\lambda)$ within turtlegrass or eelgrass leaves.

Table 3

ANOVA results for differences in leaf pigment concentrations and ratios, among all samples

Treatment	d.f.	MS	<i>F</i>	<i>P</i>
[Chl <i>a</i>]	3	25.4	492.8	<0.001
Error	356	0.051		
[Chl <i>b</i>]	3	4.9	395.6	<0.001
Error	356	0.012		
$\Sigma[\text{Chl}]$	3	52.7	479.6	<0.001
Error	356	0.109		
Chl <i>a:b</i>	3	3.2	29.3	<0.01
Error	356	0.108		
[Carotenoid]	3	0.8	454.5	<0.001
Error	356	0.002		
Carotenoid: ΣChl	3	0.09	8.3	<0.01
Error	356	0.011		

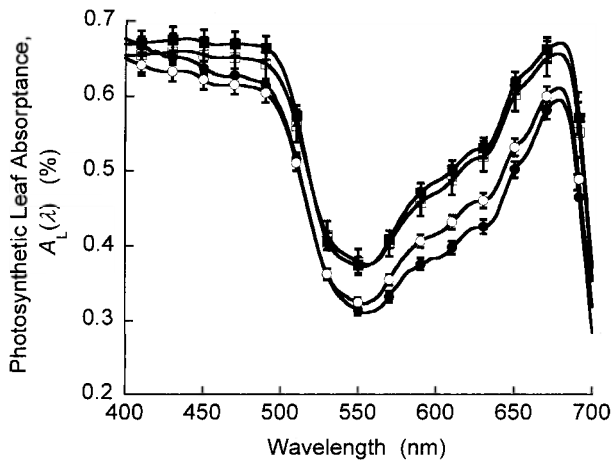


Fig. 1. Average photosynthetic leaf absorbance [$A_L(\lambda)$] for each population, corrected for reflectance and non-photosynthetic absorbance. Error bars represent ± 1 S.E. (●): LSI turtlegrass in May 1998; (○): LSI turtlegrass in January 1999; (■): Monterey eelgrass in October 1998; (□): Monterey eelgrass in April 1999.

The relatively small differences in leaf absorbance between sampling dates and species despite large differences in mean [Chl] produced dramatically different estimates of the optical cross-section [$a_L^*(\lambda)$] for intact leaves, which is a measure of chlorophyll use efficiency (Fig. 2). The optical cross-section for turtlegrass leaves collected in May was nearly two-fold higher than for turtlegrass leaves collected in January, and about five-fold higher than for eelgrass leaves collected in April or October. Within each sample, $a_L^*(\lambda)$ was highest in the blue and lowest in the green.

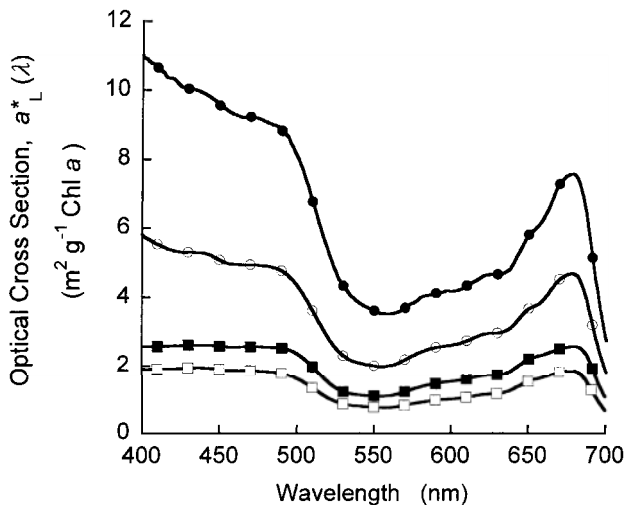


Fig. 2. Average leaf optical cross-section, $a_L^*(\lambda)$. (●): LSI turtlegrass in May 1998; (○): LSI turtlegrass in January 1999; (■): Monterey eelgrass in October 1998; (□): Monterey eelgrass in April 1999.

Optical consequences of the package effect on chl-dependent leaf absorption was clearly illustrated by the relationship between $a_L(\lambda)$ and ΣChl . In the absence of a package effect, $a_L(\lambda)$ would be a linear function of ΣChl , according to Beer's law. The $a_L(\lambda)$ of intact leaves, however, responded non-linearly to leaf ΣChl . The high extinction coefficient for Chl in the blue led to a poorly defined relationship between $a_L(440)$ and ΣChl , an indication that the onset of chl self-shading occurred at relatively low pigment concentrations [Fig. 3(a)]. The non-linear model predicted a transition to optical saturation at 440 nm with ΣChl concentrations as low as $0.12 \text{ mg g}^{-1} \text{ FW}$ (saturation point = $1/\text{exponential parameter}$). In the green region of lower Chl absorption efficiency, $a_L(\lambda)$ showed a stronger overall relation to ΣChl as indicated by r^2 , although the onset of optical saturation also occurred at relatively low pigment concentrations ($0.23 \text{ mg g}^{-1} \text{ FW}$ for 550 nm and $0.31 \text{ mg g}^{-1} \text{ FW}$ for 570 nm). Thus, the differences in chlorophyll content affected photosynthetic leaf absorption more in the green than they did in the blue.

3.2. The submarine light environment and photosynthetic light harvest efficiency

Downwelling irradiance spectra generated by the radiative transfer calculations were typical of measured spectra from these environments (Zimmerman, 2003). The submarine light environment at Lee Stocking Island was brighter and contained a higher proportion of blue (400–500 nm) light than the Monterey Bay environments (Fig. 4). Red light represented a relatively small fraction of the irradiance spectrum in all environments, due to the high absorption coefficient of pure water at wavelengths above 600 nm. The submarine light environment of Monterey Bay was relatively enriched in the green, particularly in April when water column chlorophyll was high (Pennington and Chavez, 2000). Spectral integration across the photosynthetically active region (400–700 nm) yielded instantaneous quantum fluxes at solar noon of $50 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ for Monterey Bay in April, $300 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ for Monterey Bay in October, $700 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ for Lee Stocking Island in January and $1100 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ for Lee Stocking Island in May, a 20-fold difference in PAR between the darkest and brightest environments (Fig. 5).

Although observed differences in ΣChl had relatively small effects on spectral absorption coefficients, the submarine light environments were robust predictors of leaf pigment content. Leaf ΣChl decreased five-fold as an exponential function of light (PAR) availability ($r^2 = 0.99$, Fig. 5), which changed by a factor of 20 ($1100\text{--}50 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$).

Despite large differences in chlorophyll concentrations and light environments among species and sampling dates, photosynthetic light harvesting efficiencies (ϕ_L) were relatively constant when evaluated in their native light environments (Fig. 6). The photosynthetic absorbance spectra of turtlegrass leaves captured 50.5 and 50.7% of the downwelling noon PAR in May and January, respectively, in the tropical, clear waters of Lee Stocking Island. Eelgrass leaves captured 54.7% of the downwelling noon PAR for October and 47.6% of the downwelling flux for April in the heavily green-biased waters of Monterey Bay. This convergence to similar light harvesting efficiencies across very different light environments, however, was accompanied by a five-fold difference in leaf [Chl].

Photosynthetic light harvesting efficiencies were also compared in a constant light environment—the turbid, high Chl conditions of Monterey Bay in April—to illustrate the impact of leaf chlorophyll content on light harvesting capacity across habitats. Optical

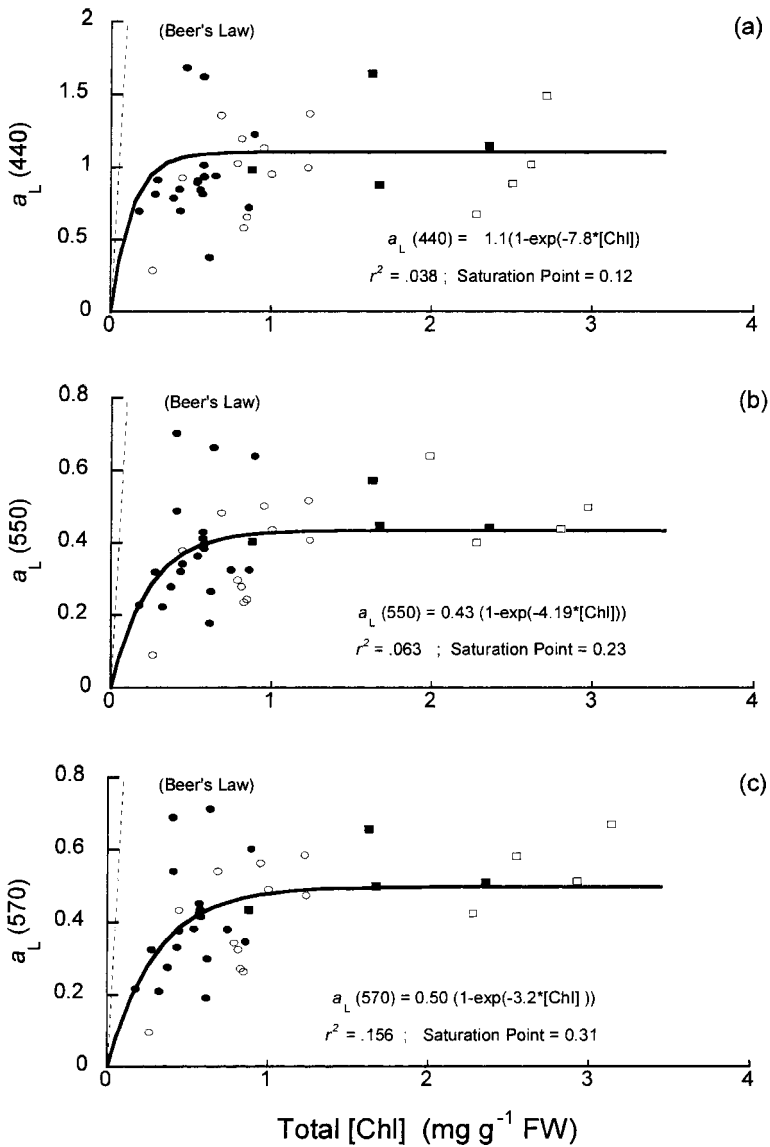


Fig. 3. (a–c): Leaf-specific absorption coefficient, $a_L(\lambda)$, at (a) 440 nm, (b) 550 nm, and (c) 570 nm plotted against total chlorophyll concentrations for all leaves across sites and seasons. Only 20% of the data points are plotted for graphical clarity. Beer's law predictions are represented by dashed lines, and calculated using wavelength-specific extinction coefficients (ϵ , L g⁻¹ cm⁻¹) for Chlorophyll *a*: $\epsilon(440) = 31.16$; $\epsilon(550) = 3.33$; $\epsilon(570) = 8.27$. (●): LSI turtlegrass in May 1998; (○): LSI turtlegrass in January 1999; (■): Monterey eelgrass in October 1998; (□): Monterey eelgrass in April 1999.

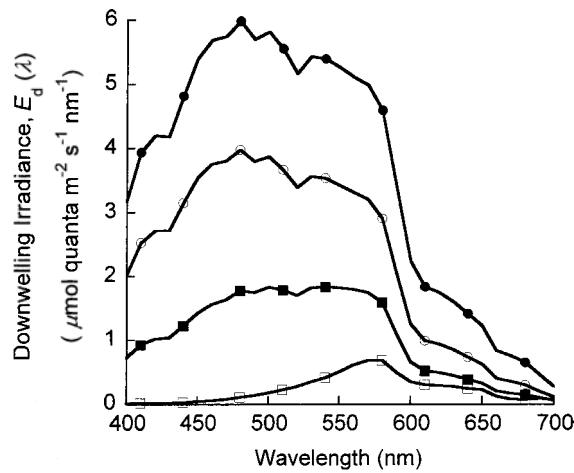


Fig. 4. Estimated downwelling spectral irradiances, $E_d(\lambda)$, at noon for 5 m depth at Lee Stocking Island in (●) May 1998; Lee Stocking Island in (○) January 1999; Monterey in (■) October 1998; Monterey in (□) April 1999.

properties of May turtlegrass with the lowest pigment content ($0.54 \text{ mg Chl g}^{-1} \text{ FW}$) were capable of capturing 40.8% of the downwelling noon PAR in this green dominated environment (Fig. 6). January turtlegrass leaves with 56% more ΣChl ($0.84 \text{ mg g}^{-1} \text{ FW}$) harvested 42.4% of the incident PAR available in the April Monterey Bay environment, representing a 4% increase in photosynthetic light harvesting efficiency. October eelgrass

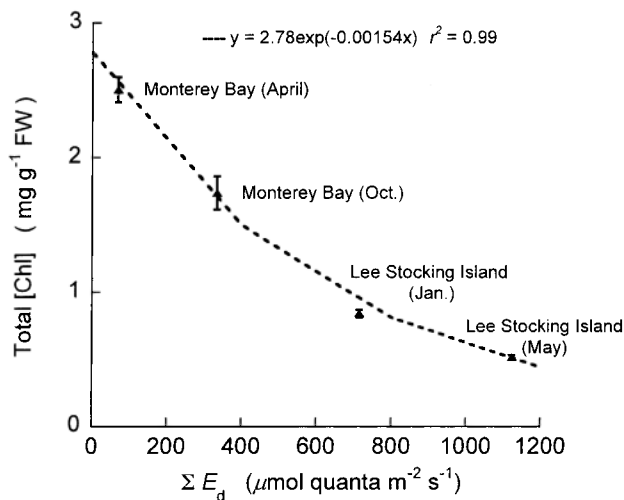


Fig. 5. Total chlorophyll content of seagrass leaves for each sampling date plotted as a function of the clear-sky estimate of downwelling irradiance integrated across the photosynthetically active spectrum (PAR), for local solar noon. Pigment concentration error bars indicate $\pm 1 \text{ S.E.}$

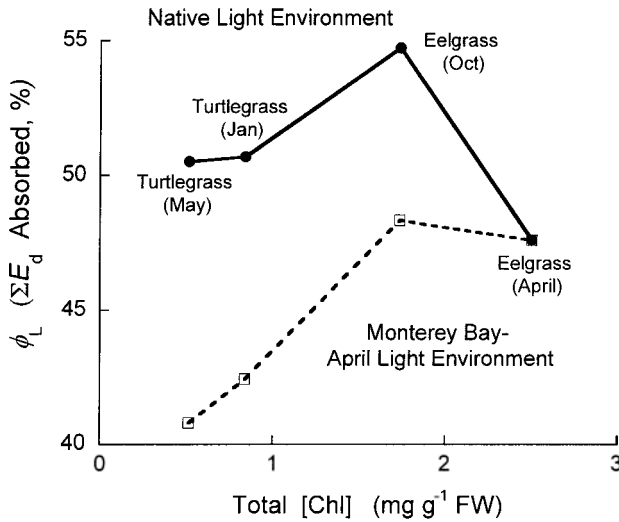


Fig. 6. Leaf-specific photosynthetic light harvest efficiency, ϕ_L , plotted against total chlorophyll content. Filled circles (●) and solid lines represent efficiencies for leaves in their native light environment. Open squares (□) and dashed lines (---) represent efficiencies for leaves in the April (high chlorophyll) light environment of Monterey Bay.

($\Sigma\text{Chl} = 1.74 \text{ mg g}^{-1} \text{ FW}$) improved light harvesting efficiency to 48.3% of incident PAR in this green-dominated light environment, representing an 18.5% higher light harvesting efficiency exhibited by October eelgrass relative to the May turtlegrass leaves. This 18.5% increase in light absorption capacity, however, required five times as much chlorophyll.

4. Discussion

This comparison of pigment content and photosynthetic absorbance of leaves from dramatically different light environments illustrates the adaptive limits of optical plasticity within and among seagrass leaves. The anatomy of turtlegrass and eelgrass leaves are remarkably similar to each other with respect to leaf thickness, chloroplast distribution, and even the developmental sequence leading to mesophyll differentiation (Tomlinson, 1980). Yet, within these structural limitations, seagrass leaf chlorophyll concentrations can vary at least five-fold to produce similar light harvesting efficiencies for plants growing in very different light environments. This acclimation strategy, however, is inefficient with regard to chlorophyll synthesis. The five-fold difference in leaf chlorophyll content observed here produced only a 9% difference in PAR-averaged absorbance, and an 18.5% difference in ϕ_L for the green-enriched light environment of Monterey Bay. In contrast, acclimation to self-shading in the tropical rhodophyte *Ahnfeltiopsis cocinna* (J. Ag.) achieved a similar increase in PAR-averaged thallus absorbance (8%) with only a 30% increase in total phycoobiliprotein content (Beach and Smith, 1996). Raven (1984) suggested that the metabolic

cost of constructing light harvesting complexes containing Chls *a* + *b* + carotenoids was considerably less than the cost of phycobilisome construction. Clearly, seagrasses growing in low light environments possess the metabolic resources to produce high concentrations of leaf chlorophyll, and the low metabolic cost of synthesis may permit photoacclimation strategies that are inefficient in terms of chlorophyll synthesis and utilization.

The strong package effect observed here can be attributed to structural properties of seagrass leaves that restrict chloroplasts to the epidermis which represents less than 20% of the leaf volume (Tomlinson, 1980). In contrast, photoacclimation by terrestrial leaves often is accomplished by changes in the shape and number of palisade layers in the mesophyll, thus altering chloroplast distribution in ways that minimize the package effect (Lee and Graham, 1986; Osborne and Raven, 1986; Poorter et al., 1995). These changes in the anatomy of terrestrial leaves efficiently re-distribute the pigments such that shade-acclimation may actually involve a reduction in area-specific chlorophyll content (Lee et al., 1990). The negative relationship between leaf chlorophyll content and light environment observed here, however, indicates that photoacclimation in seagrasses is more similar to that observed in algal macrophytes (e.g. Henley and Ramus, 1989; Smith and Alberte, 1994) than in terrestrial plant leaves.

The restriction of chloroplasts to thin layers in seagrass leaves is somewhat reminiscent of shade-adapted terrestrial leaves (Lee et al., 1990). As in macrophytic algae, however, the chloroplasts are restricted to the epidermis and there is no spongy mesophyll. This chloroplast distribution is likely the consequence of a submerged existence in which primary gas exchange occurs across the leaf surface. Although the restriction of chloroplasts into two thin, dense layers may be advantageous in low light environments, it reduces the total number of chloroplasts that can be distributed throughout the leaf. It also exposes chloroplasts to very high-light intensities, particularly in shallow tropical environments, thereby increasing the probability of photoinhibition (Björkman, 1981; Osmund, 1987; Lee et al., 1990). Thus, the large differences in leaf chlorophyll content observed here may be a necessary consequence of the anatomical restrictions imposed by a submerged aquatic existence on chloroplast distribution within seagrass leaves.

Despite the structural restrictions on chlorophyll distribution that produces strong package effects, seagrass leaves (even those with relatively little chlorophyll) are relatively efficient light capturing organs. The photosynthetic pigments of seagrass leaves can absorb 48–56% of the incident PAR, even in green-enriched light environments. If non-photosynthetic absorbance (~23–29%) is included, the total seagrass leaf absorbance is similar to the leaves of higher plants (Givnish, 1987) and thalli of macrophytic algae (Smith and Alberte, 1994). Light absorption efficiency may be enhanced in seagrass leaves by mesophyll structures that promote internal light scattering, effectively increasing the pathlength through the leaf (Vogelman, 1993). Although internal scattering has not been measured in seagrass leaves, high indices of refraction at the lacuna/tissue boundary should promote scattering, thereby increasing the photon pathlength and probability of absorption.

The package effect within the leaf depends on the absorption coefficient of the pigment, in addition to its distribution. The optical cross-section of chlorophyll, an indicator of this package effect, is much lower in the green than in the blue or red. This spectral difference is most pronounced in the tropical turtlegrass where a_L^* varied from $>10 \text{ m}^2 \text{ g}^{-1}$ Chl *a* in the blue to $<4 \text{ m}^2 \text{ g}^{-1}$ Chl *a* in the green. The increased pigment concentrations of the temperate

eelgrass resulted in a spectral flattening of this optical cross-section. All leaves exhibited similar efficiencies at absorbing the incident PAR in their native environments, but the October eelgrass leaves were 18.5% more efficient at light absorption in the green-enriched light of Monterey Bay than were the turtlegrass leaves characterized by low pigment content. Thus, large increases in leaf chlorophyll content may be inefficient with regard to the cost of pigment synthesis, but they do improve light harvesting efficiency of the entire leaf, particularly in submarine environments dominated by green light.

The plasticity of seagrass leaves with regard to chlorophyll content may play a significant role in the ability of these submerged aquatic plants to colonize shallow tropical banks as well as turbid waters of temperate and boreal environments. Since this range in photoacclimation can also be observed in red and brown seaweeds, the cost of photoacclimation appears relatively easy to offset by the gain in light harvesting efficiencies. Thus, although the package effect has significant impacts on the optical properties of seagrass leaves, chlorophyll use efficiency does not appear to play a strong ecological or evolutionary role in seagrass survival.

A number of reasons have been proposed for the notoriously high-light requirements of seagrasses including carbon demand by non-photosynthetic below ground tissues (Fourqurean and Zieman, 1991; Kraemer and Alberte, 1993), and direct carbon limitation of photosynthesis (Durako, 1993; Beer and Koch, 1996; Zimmerman et al., 1995, 1997; Invers et al., 2001). This study demonstrated that photosynthetic light harvesting by seagrass leaves is only slightly lower than other macrophytes, aquatic or terrestrial. Although seagrasses may be vulnerable to displacement by algal competitors, the optical properties of seagrass leaves do not appear to create a dramatic disadvantage with respect to light harvesting in submerged aquatic environments.

Acknowledgements

We thank D. Kohrs and S. Wittlinger for assistance with seagrass leaf collections and laboratory analyses, R. Maffione for *Hydrolight* computations of the submarine light fields and P. Falkowski for critical comments and suggestions that significantly improved this study. Funding was provided by the Environmental Optics Program, Office of Naval Research, as part of the CoBOP DRI (Award No. N00014-97-1-0032).

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