

Seasonal photosynthetic patterns of the seagrass *Thalassia testudinum* in the western Gulf of Mexico

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ABSTRACT: Seasonal photosynthetic performance was compared between 2 distinct populations of *Thalassia testudinum* in Texas (USA) during an annual period. The validity of using laboratory leaf incubations to set light requirements was tested by comparison to *in situ* whole-plant measurements of photosynthesis versus irradiance (P vs I). Cosine (2π) and spherical (4π) sensors were used to measure photon flux density (PFD) in laboratory and field experiments, respectively. In addition, differences in PFDs recorded with the different sensors were examined by completing simultaneous *in situ* measurements. This data was used to compare estimates of production based on numerical integration and the daily light saturation period (H_{sat}). Laboratory-based seasonal photosynthetic performance was dependent on temperature and was site-specific. Rates of photosynthesis varied from ca 45 to 345 $\mu\text{mol O}_2$ g dry wt⁻¹ h⁻¹, while dark respiration values ranged from ca 5 to 105 $\mu\text{mol O}_2$ g dry wt⁻¹ h⁻¹. Late spring and summer saturation irradiance (I_k) values derived from laboratory incubations ($I_{k(2\pi)} = 85$ $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) were about 3-fold lower than *in situ* whole-plant measurements ($I_{k(4\pi)} = 290$ $\mu\text{mol photon m}^{-2} \text{s}^{-1}$). Despite the large apparent differences in $I_{k(2\pi)}$ and $I_{k(4\pi)}$ values, integrated production calculated using the 2 estimations were similar because of lower *in situ* 2π cosine PFD values compared to the spherical 4π sensor (ca 50%). However, integrated production estimates using laboratory P vs I data were still 12 to 22% lower than estimates based on whole-plant incubations. Application of the H_{sat} model to the data showed that the predictive capacity varied as a function of water transparency, source of P vs I data and sensor utilized; values were 14 to 100% lower than numerically integrated production. The results underscore the value of *in situ* PFD and entire-plant P vs I measurements for seagrasses, especially under conditions of low water transparency characteristic of estuarine and near shore environments.

KEY WORDS: Seagrass · *Thalassia testudinum* · Production models · Photosynthesis · PFD · H_{sat}

INTRODUCTION

Light is a major factor controlling seagrass growth and distribution and is particularly important in establishing depth limits for growth (Buesa 1974, Wiginton & McMillan 1979, Wetzel & Penhale 1983, Dennison 1987, Duarte 1991). On a worldwide basis, large losses of seagrass areal coverage have been reported as a consequence of decreased light availability (Backman & Barilotti 1976, Cambridge & McComb 1984, Giesen et al. 1990, Onuf 1994). Algal blooms caused by input of excess nutrients, resuspension of bottom sediments, dredging and increased sediment run-off have been

linked to light reduction, causing the decline of seagrass coverage and productivity (Orth & Moore 1983, Cambridge et al. 1986, Goldsborough & Kemp 1988, Pulich & White 1991, Dennison et al. 1993, Onuf 1994).

Seagrass depth limits have been correlated with Secchi depth measurements (Vicente & Rivera 1982), as well as instantaneous and continuous measurements of photon flux density (PFD, 400 to 700 nm; Dennison & Alberte 1985, Zimmerman et al. 1991, Dunton 1994). Seagrass minimum light requirements may also be determined by establishing the relationship between underwater PFD and photosynthetic production through the construction of photosynthesis versus irradiance (P vs I) curves (Kenworthy & Haurert 1991, Batuick et al. 1992, Morris & Tomasko 1993).

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However, the application of the P vs I model to assess seagrass light requirements is complicated by the various methodologies and instruments used to measure PFDs and photosynthesis. A variety of mathematical models used to fit P vs I curves yield different values for photosynthetic parameters (Gallegos & Platt 1981, Fourqurean & Zieman 1991, Frenette et al. 1993, Henley 1993, Zimmerman et al. 1994). In addition, both spherical (4π) and cosine (2π) quantum sensors are used to determine PFD (Drew 1979, Dennison & Alberte 1985, Marsh et al. 1986, Dunton & Tomasko 1994). Since photosynthetic parameters, particularly the saturation irradiance (I_k), are used to determine light requirements based on the daily light saturation period (H_{sat} ; Dennison & Alberte 1982, 1985), the use of the appropriate mathematical model and PFD sensor is critical.

Furthermore, both laboratory and field measurements of oxygen evolution have been used to determine leaf photosynthetic rates (Drew 1978, Williams & McRoy 1982, Marsh et al. 1986, Pirc 1986, Roberts & Moriarty 1987, Pérez & Romero 1992, Dunton & Tomasko 1994). Laboratory photosynthetic measurements based solely on leaf tissue neglect the respiratory demands of non-photosynthetic plant material which can comprise over 80% of seagrass biomass (Caffrey & Kemp 1991, Kraemer & Alberte 1993, Zimmerman et al. 1995). However, few studies have incorporated the respiratory requirements of below-ground tissues in photosynthetic measurements and carbon balance models (but see Zimmerman et al. 1989, 1991, Fourqurean & Zieman 1991, Dunton & Tomasko 1994). Since seagrass light requirements are often derived from laboratory incubations of blade segments where PFD is measured with a cosine quantum sensor, an evaluation of the applicability of these techniques to the field is necessary.

Photosynthetic parameters can follow distinct seasonal patterns (Drew 1978, Libes 1986, Pirc 1986). Therefore, in areas where temperature and PFDs fluctuate widely during the annual cycle, seagrass light requirements may change throughout the year (Dennison 1987). Since the Coastal Bend region of the Gulf of Mexico is toward the northern limit of the range of *Thalassia testudinum* Banks ex König, studies characterizing the seasonal photosynthetic performance of this species reflect physiological characteristics near its temperature tolerance limit.

The objectives of this study were to examine seasonal patterns in P vs I parameters as related to annual fluctuations in temperature, underwater PFD and blade chlorophyll content for 2 distinct populations of *Thalassia testudinum* in Texas. Differences between photosynthetic parameters derived from laboratory and *in situ* photosynthetic measurements were exam-

ined by direct comparison of P vs I data derived through both methods. Likewise, we studied the implications of utilizing laboratory and field-derived saturation irradiance values to determine light requirements. The adequacy of estimating production based on PFD measured with spherical and cosine sensors in conjunction with laboratory or *in situ* P vs I measurements was determined through calculation of daily production estimates based on simultaneous PFD measurements completed *in situ* with both sensors. In addition, the validity of using H_{sat} to estimate production was examined by comparison to production values derived through numerical integration of P vs I curves.

MATERIALS AND METHODS

Study sites. The study focused on 2 spatially isolated populations of *Thalassia testudinum* located at similar depths and about 200 km apart on the south Texas coast (USA). The northernmost population, located at East Flats on the eastern side of Corpus Christi Bay ($27^{\circ}49'N$, $97^{\circ}7'W$; CCB), has been the subject of previous studies on the biology of *T. testudinum* (Czerny & Dunton 1995, Lee & Dunton 1996, 1997). The lower Laguna Madre population ($26^{\circ}08'N$, $97^{\circ}12'W$; LLM) is located east of the Gulf Intracoastal Waterway (GIWW) near South Padre Island and about 15 km north of the Río Grande (Fig. 1).

Sampling at both stations took place between October 1994 and December 1995. Mean depths at CCB and LLM were 110 and 126 cm, respectively. During visits to each site, water samples were collected for determinations of water column dissolved inorganic nitrogen (DIN: $\text{NO}_3^- + \text{NO}_2^-$, NH_4^+) and chlorophyll *a* ($n = 4$). DIN and total water column chlorophyll were measured spectrophotometrically following the methods of Parsons et al. (1984). All values are reported as mean \pm SE.

Photon flux density. Continuous measurements of underwater photon flux density were collected at CCB and LLM from October 1994 to December 1995. An LI-193SA spherical quantum sensor positioned at canopy height (ca 25 cm above the bottom) provided input to an LI-1000 datalogger (LI-COR, Inc., Lincoln, NE, USA) encased in a waterproof underwater housing. Data were collected at 1 min intervals and integrated hourly; the setup was maintained as described in Dunton (1994). The CCB datalogger and sensor were lost in November 1995, hence no data are available after this date.

Seasonal laboratory P vs I . Whole plants were collected from the CCB and LLM stations using a 15 cm coring device. Intact cores were placed in 20 l buckets for transport and gently moved to 80 l aquaria upon

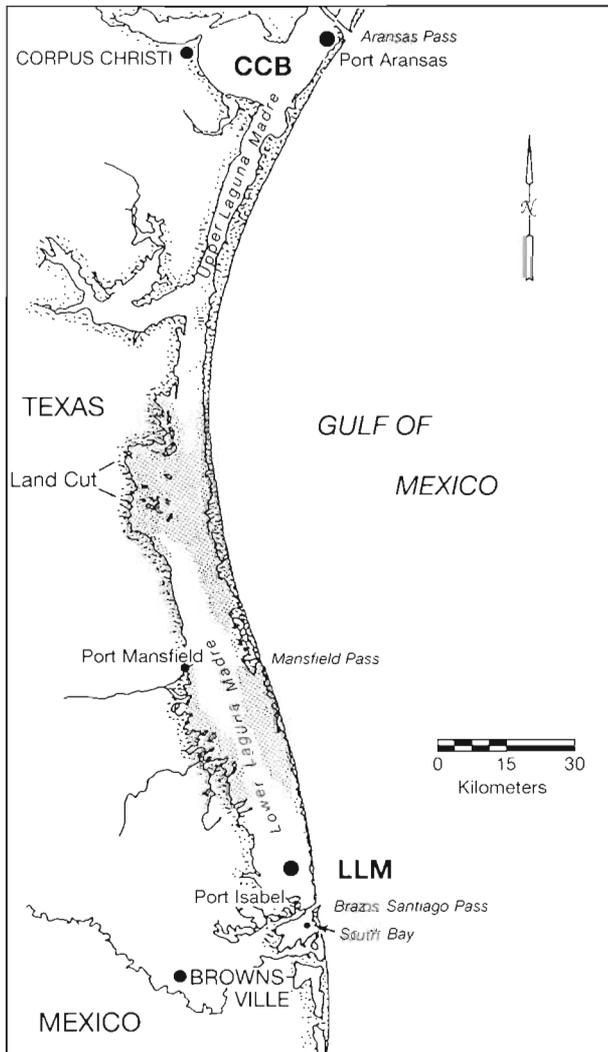


Fig. 1. *Thalassia testudinum* study sites in East Flats, Corpus Christi Bay (CCB) and lower Laguna Madre (LLM), Texas, USA. Stippled areas represent depths less than 1 m

arrival at the laboratory. Plants were maintained within $\pm 2^\circ\text{C}$ of ambient temperatures under flowing seawater and irradiated with approximately $50 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ with overhead fluorescent lights on a 12:12 h light:dark regime.

P vs I incubations were performed at temperatures reflecting *in situ* conditions ($\pm 2^\circ\text{C}$) during 7 periods between November 1994 and December 1995. Collection dates for P vs I material, *in situ* and incubation temperatures are listed in Table 1. Experiments were completed within 5 d of collection ($n = 4$ to 7 blades per site and sampling time); site-specific measurements were made within 3 wk of each other at the same temperature to permit comparison among stations. Although intraseasonal variation in photosynthetic performance may occur within a 3 wk period, water

column temperature and light availability were not observed to change substantially between intervals. Due to technical difficulties with the oxygen electrode system, no data were collected for CCB in November 1994.

Since seagrass photosynthetic rates have been shown to vary with leaf age and position (Mazella et al. 1980), 2 cm blade segments were cut 2 cm above the bundle sheath of the second or third leaf. Blade segments were cleaned of epiphytes by gentle scraping and returned to the aquaria for a 2 h period to reduce wounding effects. Diel cycles in photosynthetic parameters, particularly the maximum rate of photosynthesis (P_{max}), have been documented in phytoplankton (Prézélin 1992), macroalgae (Hanelt et al. 1993) and seagrasses (Kemp et al. 1987). Preliminary data suggested *Thalassia testudinum* displayed a diel rhythm, therefore P vs I runs were completed between 07:00 and 18:00 h to attain an average for daylight hours.

Blade oxygen consumption and evolution rates were measured using a 14 ml chamber fitted with a watertight cap, polarographic oxygen electrode, magnetic stirring mechanism and water jacket for temperature control (Rank Bros, Bottisham, England) as described by Dunton & Tomasko (1994) and Czerny (1994). Light was provided by a tungsten halide lamp and slide projector fitted with neutral density slides (Kodak, Inc.). PFDs were measured with a flat cosine sensor (LI-192SA) inserted into the chamber directly behind the plant material. Photosynthesis was measured at 10 light levels (0, 11, 21, 42, 100, 129, 200, 370, 565 and $890 \mu\text{mol photon m}^{-2} \text{s}^{-1}$). Fresh filtered seawater was used for each incubation and no evidence of CO_2 limitation was observed during the 2 h period. A 6 min stabilization period was allowed for each light level prior to data collection to avoid problems with lacunal gas storage (Dunton & Tomasko 1994). Chamber oxygen consumption rates were not significant relative to blade photosynthesis and respiration rates. No evidence of photoinhibition was observed in laboratory or field experiments (Herzka & Dunton unpubl. data). After completion of a run, blades were dried at 60°C and weighed.

Respiration and photosynthetic rates were calculated through regression analysis and normalized to dry weight of leaf tissue. The Smith-Talling function provided an adequate fit to the data ($r^2 > 0.90$; Smith 1936, Talling 1957):

$$\text{Production} = P_{\text{netmax}} \left(\frac{\alpha I}{\sqrt{P_{\text{netmax}}^2 + (\alpha I)^2}} \right)$$

where P_{max} is the gross maximum rate of photosynthesis calculated as net P_{netmax} + dark respiration (R_d). The maximum rate of photosynthesis is reported on a per

Table 1. Dates of collection, *in situ* and incubation temperature and chlorophyll content of *Thalassia testudinum* blades from lower Laguna Madre (LLM) and Corpus Christi Bay (CCB) used in laboratory *P vs I* experiments. Blade chlorophyll values represent mean \pm SE; gdw: g dry wt; nd: no data

Station	Period	Collection date	Temp. (°C)		Blade chlorophyll	
			<i>In situ</i>	Lab.	mg chl a, b gdw ⁻¹	chl a:b
LLM	1	21 Nov 1994	25	24	nd	nd
LLM	2	2 Feb 1995	17	15	7.36 \pm 0.86	2.91 \pm 0.04
CCB		24 Jan 1995	16	15	6.29 \pm 0.37	2.78 \pm 0.03
LLM	3	12 Apr 1995	25	25	5.30 \pm 0.25	2.92 \pm 0.06
CCB		17 Apr 1995	27	25	6.54 \pm 0.42	2.64 \pm 0.14
LLM	4	2 Jul 1995	30	28	3.90 \pm 0.34	2.85 \pm 0.09
CCB		15 Jun 1995	28	28	4.99 \pm 0.19	2.47 \pm 0.05
LLM	5	27 Jul 1995	31	31	3.92 \pm 0.12	2.75 \pm 0.08
CCB		2 Aug 1995	30	31	4.13 \pm 0.35	2.48 \pm 0.06
LLM	6	27 Oct 1995	26	25	6.29 \pm 0.42	2.79 \pm 0.06
CCB		9 Oct 1995	26	25	7.98 \pm 1.14	3.00 \pm 0.09
LLM	7	13 Dec 1995	18	20	5.29 \pm 0.39	2.65 \pm 0.03
CCB		4 Dec 1995	21	20	4.56 \pm 0.27	3.18 \pm 0.09

gram dry weight and per mg chlorophyll (a, b) basis ($\mu\text{mol O}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$ and $\mu\text{mol O}_2 \text{ mg chl}^{-1} \text{ h}^{-1}$, respectively). *I* represents photon flux density ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) and α is the relative quantum yield of photosynthesis depicted by the linear slope of the light-limited region of the *P vs I* relationship [$\mu\text{mol O}_2 \text{ mg chl}^{-1} \text{ h}^{-1} (\mu\text{mol photon m}^{-2} \text{ s}^{-1})^{-1}$]. Saturation and compensation irradiances (I_k and I_c) were calculated as P_{max}/α and R_d/α , respectively.

Blade chlorophyll content was determined using blade tissue from the same position on a leaf as that used for photosynthetic measurements ($n = 6$). Extractions were completed in *N,N*-dimethyl-formamide (DMF) and processed as described by Lee & Dunton (1997) using the equations of Porra et al. (1989). Blade chlorophyll (a, b) content and chl a:b ratios are presented in Table 1.

In situ P vs I. Whole-plant *P vs I* measurements were conducted in May and September 1995 at LLM. The LLM station was selected for *in situ* measurements because *Thalassia testudinum* blades contain little epiphyte cover and water column chlorophyll concentrations were low during incubation periods.

Four 5 l acrylic plastic chambers fitted with circulating pumps were placed in the monospecific *Thalassia testudinum* bed following the procedure of Dunton & Tomasko (1994). PFDs were measured with a spherical quantum sensor placed at canopy level; previous data indicated that shading due to chambers is minimal (Dunton unpubl. data). Oxygen within the sealed chambers was measured using an Endeco/YSI Type 1125 Pulsed Dissolved Oxygen system similar to Dunton & Tomasko (1994). PFD and dissolved oxygen (μM) were measured simultaneously at 5 min intervals ($n = 4$

to 10 per light level). Underwater pumps ran for 1 min during each 5 min period to provide circulation within the chambers. All instruments were controlled from aboard the research vessel RV 'Etta Armstrong'.

Chamber respiration was measured between 03:00 and 06:00 h for 2 or 3 nights. In addition, dark respiration (R_d) measurements of photosynthetic (green leaf tissue; PS) and non-photosynthetic tissue (sheath, short stem, rhizome, and roots; NPS) were completed during the night using additional chambers and probes. Whole plant samples were collected, sieved and sorted into PS and NPS tissue at least 5 h prior to incubations. Sealed chambers were placed in the water column to maintain ambient temperatures ($n = 2$ or 3).

Chamber oxygen consumption rates were normalized to 1 g dry wt of photosynthetic tissue ($\mu\text{mol O}_2 \text{ g dry wt leaf}^{-1} \text{ h}^{-1}$); respiration rates reflect the whole plant respiratory requirements supported by 1 g dry wt of photosynthetic tissue. Additionally, respiration rates of PS and NPS tissue were calculated and whole-plant respiratory demand ($\mu\text{mol O}_2 \text{ g dry wt leaf}^{-1} \text{ h}^{-1}$) was estimated based on NPS:PS biomass ratios derived from four 15 cm cores sorted and dried as described above. Whole-plant respiration based on PS and NPS respiration rates was compared to total chamber respiration estimates to determine the potential extent of other sources of benthic (i.e. non-seagrass) respiration within the chambers. Water-column respiration was measured with additional capped chambers and found to be negligible in comparison to seagrass oxygen consumption rates ($n = 2$ to 4).

A total of 12 light levels ranging from 0 to 594 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ were used for both May and September *P vs I* curves. For each chamber, measurements of dark oxygen consumption were added to net oxygen evolution to calculate gross production. Because of the variability of field incubations (e.g. Dunton & Tomasko 1994), gross P_{max} was calculated as the mean of the light-saturated photosynthetic rates for all chambers ($n = 3$ May, $n = 4$ September). The relative quantum yield, α , was calculated through regression analysis of the light-limited ($< 215 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$) PFD levels ($n = 4$ May, $n = 5$ September). Saturation and compensation irradiances were derived as in laboratory *P vs I* calculations. Since the photosynthetic parameters for one of the chambers during the incubations in May were unrealistic (e.g. high saturation irradiance and very low relative quantum yield), the remaining 3 chambers were used in all calculations.

Comparison of PFD measurements with spherical and cosine sensors. A setup consisting of a spherical quantum sensor and 2 flat cosine sensors was deployed at CCB for a 10 d period in February 1996. The 2 cosine sensors were positioned 50 cm apart facing the vertically oriented blade surfaces and each other to resemble the orientation of *Thalassia testudinum* blades in the water column. PFD measurements made with the 2 cosine sensors were summed to reflect light availability to both sides of a blade and for comparison with the spherical quantum sensor. All sensors were positioned at canopy height (ca 25 cm) and provided simultaneous input to a datalogger that integrated data hourly.

Modeling integrated production. Estimates of daily integrated production based on *in situ* and laboratory-derived *P vs I* curves and continuous measurements of underwater PFD require model functions to integrate production through time. The Smith-Talling function used to describe laboratory data, as well as the hyperbolic tangent function of Jassby & Platt (1976), did not provide a good fit to the data due to the intrinsic convexity of the light saturation region (data not shown). In order to adequately fit the data, gross P_{\max} and α were input into the Bannister (1979) function recommended by Henley (1993):

$$\text{Production} = P_{\max} \frac{\alpha I}{(P_{\max}^c + (\alpha I^c)^{1/c})}$$

where the value of c controls the convexity of the light saturation region of the *P vs I* curve. As $c \rightarrow \infty$ Bannister's function resolves into the Blackman bilinear function, while $c \rightarrow 1$ results in a rectangular hyperbola (Henley 1993). Values of c for May and September were determined through analysis of residuals calculated as the difference between chamber measurements and model predictions of photosynthetic rates for the same PFD ($c = 4$ for May, $c = 8$ for September). Although the Smith-Talling function (Smith 1936) is equivalent to the Bannister (1979) model when $c = 2$, as mentioned previously it did not provide a good fit in the convex region of the *P vs I* field data.

For comparison of production estimates using both sensor types, PFD measurements during the 10 d period were assumed to be representative of the typical light regime found in a seagrass bed. Laboratory *P vs I* curves were based on incident PFD on one side of the blade; transmittance through blade tissue was measured several times during the course of laboratory incubations and averaged ca 25%. Therefore, one-half the sum of PFDs measured with the 2 cosine sensors ($\text{cosine}_{(\text{avg})}$) was calculated to reflect the average incident light on one side of a blade. Production estimates ($\text{g C g dry wt leaf}^{-1} \text{d}^{-1}$) derived from cosine sensor PFD measurements were all based on $\text{cosine}_{(\text{avg})}$. Gross integrated daily production and H_{sat} production

($P_{\max} \times$ daily light saturation period; Dennison & Alberte 1982, 1985) were calculated using (1) *in situ P vs I* data from September 1995 and PFD measured with the spherical sensor, (2) *in situ P vs I* data and $\text{cosine}_{(\text{avg})}$, (3) the laboratory *P vs I* curve for August combined with $\text{cosine}_{(\text{avg})}$ and (4) the laboratory *P vs I* curve and PFD measurements made with the spherical sensor. Comparison of production estimates derived through the 4 combinations of *P vs I* data and sensors represents all possible methods used to calculate production. Production on a carbon basis was calculated using a photosynthetic quotient of unity.

Statistical analysis. Two-way analysis of variance (ANOVA) was applied to the seasonal laboratory *P vs I* data. Each photosynthetic parameter was treated as a dependent variable with sampling time and site as independent variables. Significance for all tests was set at the $p < 0.05$ level. Levene's test of homogeneity of variance and the Shapiro-Wilks test of normality were used to test ANOVA assumptions (Snedecor & Cochran 1989). Data for laboratory-derived seasonal saturation irradiances (I_k) were square-root transformed to comply with the homogeneity of variance assumption.

Comparison of field and laboratory-collected photosynthetic parameters were completed using an independent Student's *t*-test. *In situ* data for May 1995 were compared with laboratory results from plants collected 5 wk later in early July; incubation and field temperatures were 28°C (Table 1, period 4). Early-September *in situ P vs I* measurements were compared with laboratory results from early August at a temperature of 31°C (Table 1, period 5). Due to logistical constraints, approximately 5 wk elapsed between laboratory and field measurements; however water column temperature remained constant. When necessary, data were log-transformed to meet the assumptions of equal variance and normality.

RESULTS

Water column chemistry

Water column nitrate plus nitrite averaged 0.9 ± 0.1 and $1.1 \pm 0.2 \mu\text{M}$ for CCB and LLM, respectively, while water column ammonium values were 1.3 ± 0.2 and $1.5 \pm 0.2 \mu\text{M}$ (Table 2). Water column chlorophyll concentrations were low during most of the annual period, particularly during *in situ P vs I* incubations at LLM. However, a pelagophyte bloom (brown tide) abundant in the central and northern areas of the Laguna Madre (Stockwell et al. 1993) was found at the LLM station strictly during winter periods. Average water column chlorophyll *a* concentrations in the absence of brown tide were 6.2 ± 0.2 and $1.2 \pm 0.5 \text{ g l}^{-1}$ at CCB and LLM,

Table 2. Physical and water column characteristics at the lower Laguna Madre and Corpus Christi Bay stations during September 1994 through December 1995 (n = 18 to 22). Mean values reported; minimum and maximum values within parentheses. A Student's *t*-test was used to test for significant differences in measurements of DIN and chlorophyll *a* content between stations; same letters indicate no significant difference between sites ($p = 0.05$)

Site	Temp. (°C)	Salinity (‰)	Depth (cm)	NO ₃ ⁻ + NO ₂ ⁻ (μM)	NH ₄ ⁺ (μM)	Chl <i>a</i> (μg l ⁻¹)
CCB	25 (9–33)	31 (25–35)	110 (65–135)	0.9 ^a (0.2–1.4)	1.3 ^a (0.3–4.2)	6.2 ^a (2.1–14.5)
LLM	25 (10–32)	32 (24–37)	126 (100–150)	1.1 ^a (0.2–4.6)	1.5 ^a (0.4–4.9)	1.2 ^b (0.3–4.7)

respectively. Chlorophyll *a* concentrations during the brown tide winter bloom at LLM ranged between 10 and 40 μg l⁻¹. Average temperature, salinity and depth as well as annual minimum and maximum values are reported in Table 2.

Photon flux density

Annual integrated PFD was greater at LLM than CCB. For the period between October 1994 and September 1995, 5800 and 4500 mol photon m⁻² were received at LLM and CCB, respectively. Daily integrated PFD displayed a distinct seasonal pattern at LLM, accentuated by decreased light availability in winter due to the presence of the brown tide algal bloom (Fig. 2). Average daily winter values at LLM ranged between 4 and 10 mol photon m⁻², followed by increasing underwater PFDs during the spring and an annual peak in July at 27 mol photon m⁻². In June, mats of drift algae that frequently traverse the sea bed covered the canopy and spherical sensor at the LLM station during a 2 wk period, decreasing average daily light availability to 12 mol photon m⁻² for that month. Underwater PFD at CCB displayed little seasonal variation and exhibited a smaller annual range than at LLM. Average daily integrated PFD was approximately 10 mol photon m⁻² in winter; highest values occurred in February and July at about 17 mol photon m⁻².

Laboratory *P* vs *I*

Gross P_{max} of *Thalassia testudinum* on a dry weight basis followed a clear seasonal pattern at both stations (Fig. 3a). Maximum photosynthetic rates were high during the early spring and summer months, followed by lower rates coincident with decreasing fall temperatures and very low metabolic activity during winter (<18°C). P_{max} at both stations was approximately 5- to 6-fold higher in the early spring and summer than in

winter, with annual maxima of 272.5 ± 24.8 μmol O₂ g dry wt⁻¹ h⁻¹ at CCB in June and 324.6 ± 24.0 μmol O₂ g dry wt⁻¹ h⁻¹ at LLM in April. Lowest values of P_{max} , recorded at an incubation temperature of 15°C during winter, were 44.3 ± 5.4 and 58.0 ± 3.3 μmol O₂ g dry wt⁻¹ h⁻¹ for LLM and CCB, respectively.

Maximum rates of photosynthesis based on chlorophyll content ($P_{max(chl)}$) displayed a similar seasonal trend (not shown). At both stations, winter $P_{max(chl)}$ ranged between 6.0 and 9.2 μmol O₂

mg chl⁻¹ h⁻¹, while summer minimum and maximum values were 31.5 and 65.5 μmol O₂ mg chl⁻¹ h⁻¹ recorded in April and August, respectively at the CCB station. On a per cm² basis, using a conversion factor of 0.005 g dry wt cm⁻² (n = 20 for both stations during different periods), the maximum rate of photosynthesis ranged between 0.22 and 0.29 μmol O₂ cm⁻² h⁻¹ in winter and 1.37 and 1.63 μmol O₂ cm⁻² h⁻¹ in summer.

Dark respiration followed a seasonal pattern similar to gross P_{max} (Fig. 3b), with a significant Site by Time interaction ($p = 0.048$; Table 3). Winter rates in February at 15°C were very low (5.3 ± 0.7 and 12.0 ± 2.4 μmol O₂ g dry wt⁻¹ h⁻¹ for LLM and CCB, respectively). Dark respiration rates followed *in situ* temperature trends during the year, with the highest annual value observed at the CCB station in August (105.6 ± 8.8 μmol O₂ g dry wt⁻¹ h⁻¹) at a temperature of 31°C. In summer

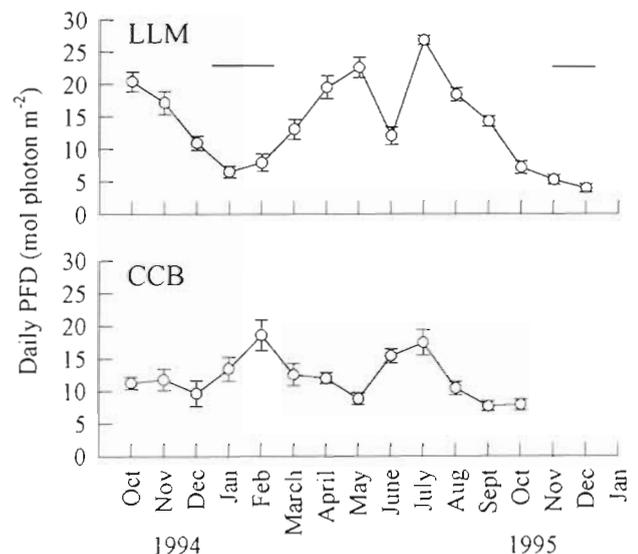


Fig. 2. Average daily integrated underwater PFD at LLM and CCB during the study period. Mean values and standard errors were calculated on a monthly basis. Horizontal lines represent periods during which an algal pelagophyte bloom (brown tide) was intermittently seen at the LLM station

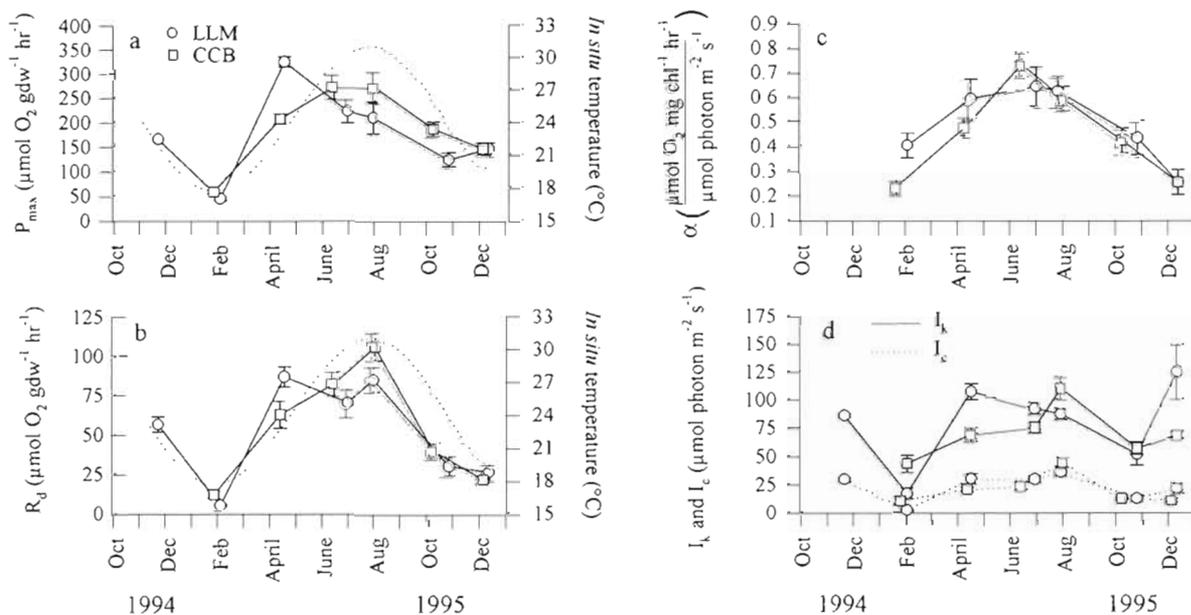


Fig. 3. *Thalassia testudinum*. (a) Gross maximum photosynthetic rate, (b) dark respiration, (c) relative quantum yield, and (d) saturation and compensation irradiances, derived from laboratory incubations of blade material during the study period. Dotted lines indicate approximate *in situ* temperature during the year as derived from non-linear regression of average daily measurements collected at 6 min intervals at a sampling platform located approximately 4 km from the LLM site. Values represent means \pm SE ($n = 4$ to 6)

30 to 40% of gross P_{max} was consumed by dark respiration, not counting nocturnal respiration. During the winter and fall periods of low metabolic activity dark respiration accounted for 10 to 25% of P_{max} .

Regression analyses of P_{max} and R_d versus temperature indicated that although the majority of the variability for both parameters was explained by temperature, respiration rates were determined by temperature to a greater extent ($r^2 = 0.80$ and 0.64 for R_d and P_{max} , respectively).

Relative quantum yield on a chlorophyll (*a*, *b*) basis displayed lowest values in winter, followed by increasing α throughout the spring and summer (Fig. 3c). In February, relative quantum yields were 0.23 ± 0.03 and $0.40 \pm 0.05 \mu\text{mol O}_2 \text{ mg chl}^{-1} \text{ h}^{-1}$ ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) $^{-1}$ at CCB and LLM, respectively. Peak values were recorded in mid summer (June/July), when α was 0.64 ± 0.08 and $0.73 \pm 0.05 \mu\text{mol O}_2 \text{ mg chl}^{-1} \text{ h}^{-1}$ ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) $^{-1}$ for LLM and CCB, respectively. Estimates of α decreased in late summer through early winter, approximating winter lows in December 1995. Statistical analysis indicated a correlation between $P_{max(\text{chl})}$ and α ($r^2 = 0.62$; $\alpha = 0.0064 P_{max(\text{chl})} + 0.24$).

Saturation and leaf compensation irradiances reflected seasonal trends in other photosynthetic parameters (Fig. 3d). Values were higher in the early spring and summer months than during fall and winter, with the exception of abnormally high I_k values at the LLM station during December 1995 and November 1994 attributed to unusually low values of relative quantum

Table 3. ANOVA table for laboratory P vs I parameters with site and time as independent variables

	Source	SS	df	MS	F-ratio	p-value
P_{max}	Site	36230	1	36230	1.8	0.188
	Time	298726	5	59745	29.3	0.000
	Site \times Time	65796	5	13159	6.5	0.000
	Error	95646	47	2035		
Respiration	Site	355	1	355	1.5	0.220
	Time	56896	5	11379	49.4	0.000
	Site \times Time	2810	5	562	2.4	0.048
	Error	10824	47	230		
α	Site	0.001	1	0.001	0.061	0.806
	Time	0.949	5	0.190	11.500	0.000
	Site \times Time	0.208	5	0.042	2.508	0.043
	Error	0.779	47	0.017		
I_k (square-root transformed)	Site	0.7	1	0.7	0.5	0.466
	Time	149.2	5	29.8	24.0	0.000
	Site \times Time	51.8	5	10.4	8.3	0.000
	Error	58.5	47	1.2		
I_c	Site	24.2	1	24.2	0.5	0.502
	Time	7133.8	5	1426.8	27.0	0.000
	Site \times Time	843.5	5	168.7	3.2	0.015
	Error	2483.5	47	52.8		

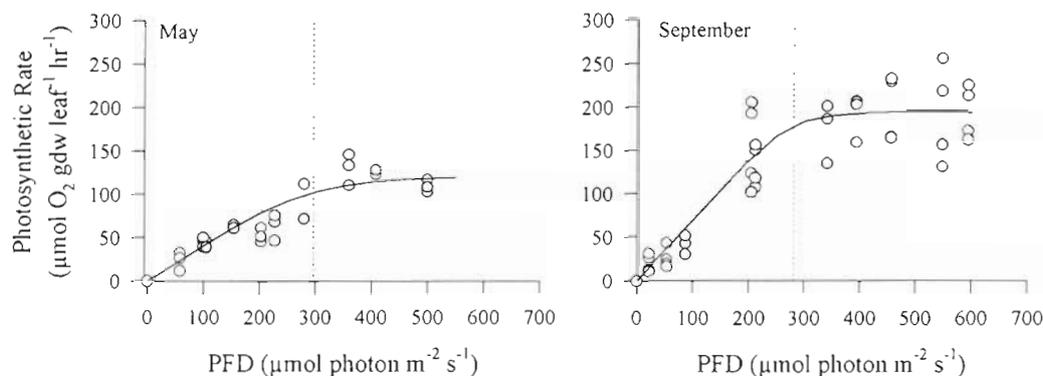


Fig. 4. *Thalassia testudinum*. Photosynthesis vs irradiance curves derived *in situ* at LLM in May and September 1995 using chambers placed in the seagrass bed. Model functions derived using the Bannister (1979) function are plotted as solid lines; dashed lines represent the saturation irradiance

yield. Winter and fall estimates of I_k for both stations ranged between 17 and 69 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Peak I_k values were 107 at LLM in April and 110 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ at CCB in August. The compensation irradiance ranged from 2 and 8 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in winter to annual maxima of 44 and 36 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in August, for CCB and LLM respectively.

Two-way ANOVA indicated a significant Time by Site interaction for P_{max} , R_d , α , I_k and I_c (Table 3), indicating the magnitude of changes in maximum rates of photosynthesis were not consistent over time at the 2 stations. Values of P_{max} , R_d and I_k for the LLM population peaked in the early spring (April), while the same photosynthetic parameters for the CCB population reached an annual maximum during summer months (July to August). Hence, there appeared to be approximately a 2 mo lag period in seasonal maxima of P_{max} , R_d and I_k .

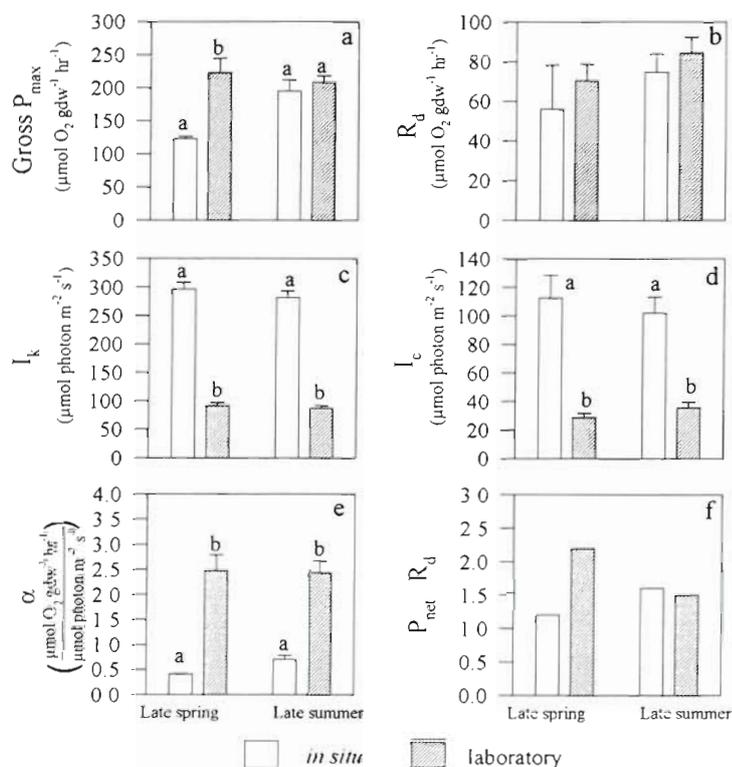


Fig. 5. *Thalassia testudinum*. Comparison of laboratory and field-derived photosynthetic parameters for the LLM station. *In situ* data for May 1995 was compared with laboratory data collected 5 wk later in early July; incubation and field temperatures were 28°C. September *in situ* P vs I measurements were compared with laboratory results from August at a temperature of 31°C (Table 1). Letters represent presence or absence of significant differences between methods within a study period as determined with a Student's t -test ($p = 0.05$). Statistical analysis was not deemed appropriate for estimates of R_d because whole-plant estimates are based on average PS and NPS dark respiration rates corrected for root to shoot ratios (Table 4), and the source of variation is not equivalent

In situ P vs I

Photosynthetic parameters derived from whole-plant incubations displayed similar values in May and September, with the exception of gross P_{max} , which averaged $122 \pm 4 \mu\text{mol O}_2 \text{ g dry wt leaf}^{-1} \text{ h}^{-1}$ at 28°C in May and $195 \pm 17 \mu\text{mol O}_2 \text{ g dry wt leaf}^{-1} \text{ h}^{-1}$ at 31°C in September (Fig. 4). When compared to laboratory-derived values, a significant difference in gross P_{max} was found in late spring ($p = 0.015$), but not in late summer ($p = 0.5$; Fig. 5a).

Respiration rates of photosynthetic tissue were 7 to 8 times higher than for non-photosynthetic tissues (Table 4). Calculations of whole-plant dark respiration based on tissue-specific R_d and NPS:PS biomass ratios was higher in September than in May, at 74.5 and 55.9 $\mu\text{mol O}_2 \text{ g dry wt leaf}^{-1} \text{ h}^{-1}$, respectively. As mentioned previously, a second estimate of plant respiration based on chamber oxygen consumption per gram dry weight of leaf tissue within each chamber resulted in similar whole-plant respiration rates (Table 4), indicating that community respiration excluding seagrasses was negligible for the purposes of this study. Estimates of R_d derived from laboratory incubations of blade segments were

Table 4. *Thalassia testudinum*. Dark respiration estimates based on (1) chambers in seagrass bed and (2) separate incubations of photosynthetic (PS) and non-photosynthetic (NPS) tissue at LLM. Chamber respiration was calculated as oxygen consumption within each chamber normalized to dry wt photosynthetic tissue. Whole plant R_d represents the respiration supported by 1 gdw (g dry wt) of PS material based on the relative biomass of non-photosynthetic and photosynthetic tissues (NPS:PS in gdw gdw⁻¹)

	Chamber respiration ($\mu\text{mol O}_2 \text{ gdw leaf}^{-1} \text{ h}^{-1}$)	R_d PS ($\mu\text{mol O}_2 \text{ gdw}^{-1} \text{ h}^{-1}$)	R_d NPS ($\mu\text{mol O}_2 \text{ gdw}^{-1} \text{ h}^{-1}$)	NPS:PS	Whole-plant R_d ($\mu\text{mol O}_2 \text{ gdw leaf}^{-1} \text{ h}^{-1}$)	Net $P_{\text{max}}:R_d$
May	46.4 ± 6.3	26.0 ± 2.5 (n = 2)	3.7 ± 2.5 (n = 2)	8.0	55.9 ± 22.5	1.2
Sep	68.8 ± 2.2	34.7 ± 0.2 (n = 2)	4.3 ± 1.0 (n = 3)	9.2	74.5 ± 9.3	1.6

about 12 to 20% higher than whole-plant respiration rates (Fig. 5b). $P_{\text{net}}:R_d$ ratios were 1.2 and 1.6 for May and September (Table 4).

Saturation irradiances were similar in May and September, averaging 297 and 281 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ for May and September, respectively. *In situ* estimates of I_k were over 3-fold higher than those calculated from laboratory experiments; differences were highly significant ($p < 0.001$; Fig. 5c). Likewise, whole-plant compensation irradiances were over 3-fold higher than laboratory estimates (Fig. 5d). *In situ* estimates of relative quantum yield were 40% lower in May than September (Fig. 5e). Laboratory estimates significantly overestimated relative quantum yield ($p < 0.001$).

Spherical and cosine PFD measurements

During the 10 d period of sensor deployment at CCB there were no major storm or wind events, and hourly PFDs displayed similar trends (Fig. 6a). The spherical quantum sensor detected maximum daily PFD between ca 900 and 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The daily maximum for the sum of the 2 cosine sensors (i.e. light available for photosynthesis to both sides of a *Thalassia testudinum* blade) was between ca 400 and 500 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$. Regression analysis indicated a strong correlation between the measurements of PFD made with spherical and cosine sensors ($r^2 = 0.96$; Fig. 6b); the sum of PFD for the 2 cosine sensors was approximately one half that measured with the spherical quantum sensor.

Integrated and H_{sat} production estimates

Laboratory and *in situ* P vs I data for the late summer were used in conjunction with underwater PFDs during a 10 d period of high water clarity to generate production

estimates. With the exception of results based on *in situ* P vs I and $\text{cosine}_{(\text{avg})}$, the H_{sat} model underestimated integrated production by about 10 to 15% for a given P vs I model and sensor (Table 5). The highest production estimates were obtained using the laboratory P vs I curve and spherical sensor PFDs; production was about 25% higher than for the combination of *in situ* P vs I data and spherical sensor PFDs as well as laboratory P vs I data and $\text{cosine}_{(\text{avg})}$. As expected, due to the low PFD values associated with $\text{cosine}_{(\text{avg})}$ and high saturation irradiance of the *in situ* P vs I curve, these

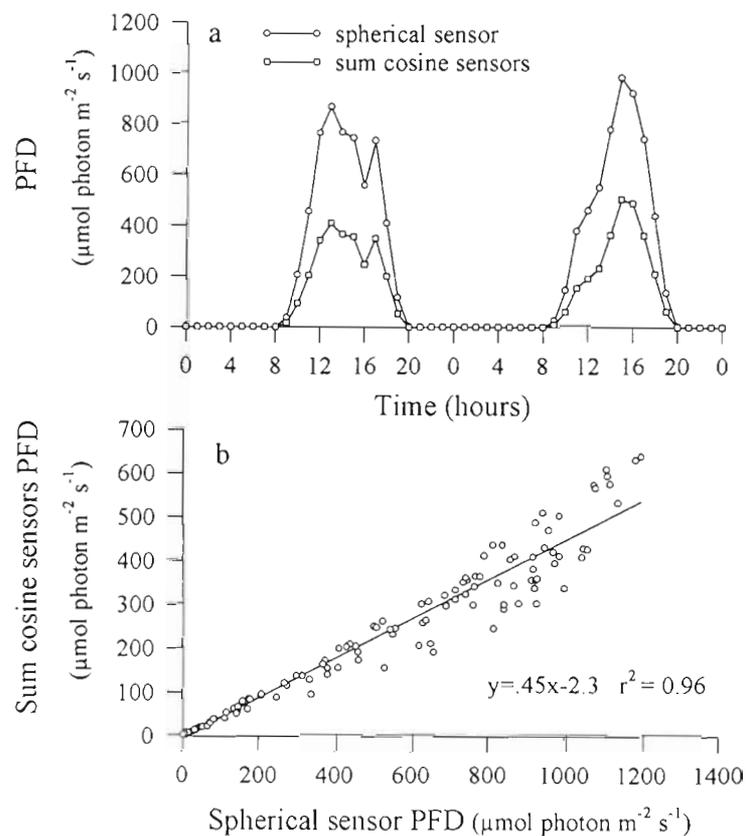


Fig. 6. (a) Simultaneous measurements of underwater PFD made with a spherical and 2 cosine sensors for a 10 d period in January 1996. The first 2 d of data are shown; the remaining days displayed very similar patterns. (b) Regression analysis between measurements made with a spherical sensor and the sum of the 2 cosine sensors

Table 5. *Thalassia testudinum*. Mean \pm SE daily integrated and H_{sat} production (values given in mg C g dry wt leaf⁻¹ d⁻¹) calculated through use of laboratory (blade segments) and *in situ* P vs I (whole plant) curves for August and September 1995, respectively, in combination with continuous measurements of underwater PFDs made with spherical and cosine sensors during a 10 d period of relatively high water transparency. Numbers in parentheses represent daily period of light saturation in hours. A photosynthetic quotient of unity was assumed

Sensor	P vs I model applied:			
	Integrated production		H_{sat} production	
	Laboratory $I_k = 87$	<i>In situ</i> $I_k = 281$	Laboratory $I_k = 87$	<i>In situ</i> $I_k = 281$
Cosine _(avg)	19.1 \pm 0.53	11.6 \pm 0.7	17.5 \pm 0.9 (7.0)	1.6 \pm 1.0 (1)
Spherical	25.3 \pm 0.3	21.7 \pm 0.4	24.0 \pm 0.8 (9.6)	18.7 \pm 0.6 (8.0)

values drastically underestimate production. Since production is not typically calculated in this fashion, it will not be discussed further.

DISCUSSION

Seasonal variations in P vs I parameters

Seagrasses inhabiting estuarine systems are subject to biotic and abiotic factors that may be highly site-specific. Evaluation of photosynthetic performance during a single time period by exposing plants to a temperature range reflective of the natural environment can provide information regarding the limits of physiological temperature tolerance, the optimum temperature for photosynthesis, effects of temperature on photosynthetic parameters and the interaction between varying light and temperature regimes (Bulthuis 1983, Pérez & Romero 1992, Massini et al. 1995). However, this approach disregards natural variation in seasonal characteristics such as blade chlorophyll content and chl $a:b$ ratios, acclimation and the potential presence of internal annual rhythms (Ott 1979, Wiginton & McMillan 1979). Therefore, the characterization of P vs I parameters on a seasonal basis under a temperature regime reflective of *in situ* conditions provides a more meaningful representation of trends in photosynthetic performance (Drew 1978, 1979, Pirc 1986, Dennison 1987, Dunton & Tomasko 1994). In this study, the photosynthetic performance of 2 distinct populations of *Thalassia testudinum* in the western Gulf of Mexico was examined during 7 distinct seasonal periods between November 1994 and December 1995 as a function of underwater PFD, *in situ* temperature and blade chlorophyll content.

Underwater light can be highly estuary- and site-specific, as reported by Zimmerman et al. (1991) for *Zostera marina* L. beds in San Francisco Bay and Dunton (1994) for *Halodule wrightii* in 3 Texas estuaries. In this

study, the LLM site received greater integrated underwater PFD than CCB during the April through October summer period. Underwater light at the LLM site also exhibited a more predictable seasonal pattern and wider range in average daily PFD on a monthly basis (4 to 27 mol photon m⁻²) than CCB (8 to 17 mol photon m⁻²; Fig. 2). Greater average water column chlorophyll values at CCB (exclusive of brown tide; Table 1) and the presence of brown tide at LLM during the winter periods are 2 factors that contributed to differences in monthly and annual PFDs.

Laboratory incubations of blade material at temperatures reflective of *in situ* conditions indicated distinct seasonal trends in photosynthetic parameters; gross P_{max} , $P_{\text{max(chl)}}$, R_d , α , I_k and I_c were lowest in winter, increased with higher water column temperatures in the early spring and peaked in the spring or summer months. In a seasonal study of photosynthetic performance of *Cymodocea nodosa* (Ucria) Aschers. in Spain, Pérez & Romero (1992) found higher P_{max} and I_k values in summer than in winter. Other studies have also examined seasonal patterns in photosynthetic performance (Drew 1978, Libes 1986, Pirc 1986). Regression analysis of P_{max} and R_d vs temperature indicated a correlation with *in situ* temperature ($r^2 = 0.64$ and 0.80 , respectively). The dependence of P_{max} and R_d on temperature has been reported previously in the seagrass literature (see Bulthuis 1983, 1987 for review).

Annual peak values of gross P_{max} , R_d and I_k at CCB appear to lag LLM by about 2 mo; maximum values for LLM were detected in the early spring (April) and in summer (July/August) for the CCB population. The LLM station is located about 200 km southwest of CCB, therefore subtle differences in water column temperature, nutrient availability, daily light period or underwater PFD may trigger the annual peaks in maximum photosynthetic rates at different times at each station, which may be in turn associated with the maximal growth period. Drew (1978) found higher gross photosynthetic rates in spring at 17°C than in summer at 25°C for *Posidonia oceanica* (L.) Delile in Malta, while *Cymodocea nodosa* displayed the opposite pattern. The data presented here supports the hypothesis that accurate characterization of photosynthetic performance and determination of light requirements demands site-specific measurements.

Photosynthetic parameter values reported in this study are within the range of those reported in the literature for *Thalassia testudinum* in Florida, Texas and Cuba for both laboratory and *in situ* measurements of P vs I (Table 6). At incubation temperatures

Table 6. *Thalassia testudinum*. Photosynthesis versus irradiance parameters. Units for the relative quantum yield (α) are $\mu\text{mol O}_2 \text{gdw}^{-1} \text{h}^{-1} (\mu\text{mol photon m}^{-2} \text{s}^{-1})^{-1}$. The maximum rate of photosynthesis is presented in terms of gross values unless noted otherwise. For Dawes & Tomasko (1988) and Fourqurean & Zieman (1991) all data for each parameter were pooled. All conversions assumed a photosynthetic quotient of unity. nps: non-photosynthetic tissue; wp: whole plant

	Temp. (°C)	P_{max} ($\mu\text{mol O}_2 \text{gdw}^{-1} \text{h}^{-1}$)	R_d ($\mu\text{mol O}_2 \text{gdw}^{-1} \text{h}^{-1}$)	α	I_k ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$)	I_c ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$)	Method	Sensor	Source
Blade segment incubations									
CCB, TX	31	270	106	2.45	110	44	O ₂ evol.	2 π	This study (late summer)
LLM, TX		208	85	2.44	87	36			
CCB, TX	30	255	62	4.3	84	nd	O ₂ evol.	2 π	Czerny (1994)
Lassing Park, FL	26	94 (net)	nd	nd	nd	nd	O ₂ evol.	2 π	Koch (1994)
West Central Florida	30	231	78	2.6	62	35	O ₂ evol.	2 π	Dawes & Tomasko (1988)
Cuba	27	235	134	nd	nd	nd	¹⁴ C	nd	Buesa (1974)
Whole shoot/whole plant incubations									
LLM, TX	31	195	35 leaf 4.3 nps 7.3 wp	0.7	281	107	<i>In situ</i> whole plants	4 π	This study (late summer)
Florida Bay, FL	25–30	375	14 leaf 3.3 nps 4.9 wp	0.9	407	nd	Lab. whole shoots; O ₂ evol.	2 π	Fourqurean & Zieman (1991)
Redfish Bay, TX	27–35	122 (net)	nd	nd	250	nd	Lab. ¹⁴ C fixation	Pyrhelio- meter	Williams & McRoy (1982)
Puerto Rico		273 (net)	nd	nd	190	nd			
Florida	~30	60.5 (net)	nd	nd	nd	nd	<i>In situ</i> ¹⁴ C	Pyrano- graph	Bittaker & Iverson (1976)

between 25 and 30°C, gross P_{max} ranges between ca 200 and 375 $\mu\text{mol O}_2 \text{g dry wt}^{-1} \text{h}^{-1}$, while dark respiration rates for blade tissues range between ca 80 and 105 $\mu\text{mol O}_2 \text{g dry wt}^{-1} \text{h}^{-1}$. During low temperature periods (<18°C) maximum photosynthetic and dark respiration rates may be up to one-sixth of the rates found during spring and summer for blade tissue (Czerny 1994, this study).

Since *Thalassia testudinum* displays higher light and respiratory requirements when *in situ* temperatures are high, anthropogenic activities that reduce water clarity should be avoided during these periods. Onuf (1994) associated seagrass loss in the Laguna Madre with maintenance dredging of the Gulf Intracoastal Waterway and suggested that reduced light availability was detectable as far as 1.2 km from dredged sites. Due to the high light requirements of *T. testudinum* during the spring and summer, dredging may have serious impacts on seagrass populations over large areas.

Blade-segment compared to whole-plant P vs I

The maximum rate of photosynthesis was not significantly different between whole-plant and laboratory-based estimates in late summer; however, significant

differences were found for the late spring comparison. On the other hand, no significant differences were found in blade or whole-plant dark respiration rates. While laboratory incubations of blade segments do not include the respiratory requirements of non-photosynthetic tissue (Caffrey & Kemp 1991, Fourqurean & Zieman 1991, Table 4), gross production can be overestimated due to wounding effects which increase respiration rates. The lack of a significant difference between the 2 approaches may be due to an overestimation of R_d based on cut blade segments.

Relative quantum yield values from *in situ* incubations were approximately 5-fold lower than α derived from blade segment incubations. Additionally, laboratory experiments tended to severely underestimate I_k ; *in situ* measurements were 3 times higher. In a direct comparison of *in situ* and laboratory-derived photosynthetic parameters for *Halodule wrightii*, Dunton & Tomasko (1994) found similar results. Likewise, Fourqurean & Zieman (1991) reported high I_k and low α values for *Thalassia testudinum* in Florida (Table 6); their experimental setup simulated a seagrass canopy by incubating various shoots within chambers. High values of I_k and low relative quantum yields based on shoot and whole-plant incubations have been reported previously for *T. testudinum* (Williams & McRoy 1982, Fourqurean & Zieman 1991), *Zostera marina* (Wetzel

& Penhale 1983), *Cymodocea nodosa* (Pérez & Romero 1992) and *H. wrightii* (Dunton & Tomasko 1994).

Within a lush seagrass canopy, epiphyte cover and self-shading can drastically affect the light available for photosynthesis (Short 1980, Pérez & Romero 1992, Massini et al. 1995). Tomasko (1992) found that *Halodule wrightii* increased rhizome growth and shoot formation rates when surface PFD was decreased using a 'canopy' of *Thalassia testudinum* blades as opposed to neutral density screening. The response was attributed to differences in spectral composition caused by seagrass shading. Consequently, self-shading will not only decrease light availability, but will also result in differences in spectral composition of light throughout the canopy. Therefore, estimates of α and I_k derived from incubations of *T. testudinum* blade segments with a unidirectional light source are not reflective of the natural environment found within a seagrass canopy. Extrapolation from the laboratory to the natural environment should be exercised with caution, particularly when calculating daily periods of saturation (H_{sat}) or setting minimum light requirements.

Spherical and cosine sensors: integrated production estimates

Estuarine underwater PFD is usually measured with a spherical quantum sensor due to the diffuse nature of the light field (Kirk 1994). Gallegos (1993) suggested that biological considerations should determine whether spherical (4π) or flat cosine sensors (2π) are appropriate for monitoring underwater PFD in seagrass meadows. He suggested a spherical sensor should be used in the case of a solitary seagrass shoot exposed to a diffuse light field (such as that found toward the edge of a bed), while a flat sensor is suitable for an emerging shoot that can be viewed as a 'flat surface'.

Integrated production estimates based on spherical and cosine_(avg) sensor derived PFDs combined with summer *in situ* and laboratory-based *P vs I* data, respectively, were in agreement with each other (19 and 25 mg C g dry wt leaf⁻¹ d⁻¹; Table 5). Estimates of gross production within this range result in leaf growth rates of about 1.2 g dry wt m⁻² d⁻¹ (Herzka 1996, J. E. Kaldy unpubl. data) when whole-plant respiration is taken into account. However, integrated production estimates based on laboratory *P vs I* data and spherical sensor PFD measurements tended to overestimate production by ca 25%. Estimates of production based on the H_{sat} model displayed a similar trend, although production estimates were about 10 to 15% lower than integrated production for the 10 d period of favorable water clarity (Table 5). Since P_{max}

derived from blade and whole-plant incubations was not significantly different for the September *P vs I* data utilized, differences in integrated and H_{sat} production are attributed to the lower relative quantum yield [0.70 vs 2.44 $\mu\text{mol O}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$ ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)⁻¹] and higher saturation irradiance (281 vs 87 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) of *in situ* versus laboratory data, respectively.

Differences in production estimates derived through numerical integration or the H_{sat} model should be greater during extended periods of low water transparency, when $\text{PFD} < I_k$. In order to test this hypothesis, a 10 d period of low water clarity recorded at the CCB station (28 October through 6 November 1995) was chosen to model production. During this time period, underwater PFD at CCB did not exceed 175 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ during any one day as a result of northern fronts leading to overcast skies and sediment resuspension.

Cosine_(avg) was calculated as:

$$\text{Cosine}_{(\text{avg})} = \frac{\text{PFD}_{(\text{spherical})} \times 0.45}{2}$$

where 0.45 is the slope of the equation derived from regression analysis of PFD measured with a spherical and sum of 2 cosine sensors in January 1996 (Fig. 6b).

Integrated production based on laboratory *P vs I* data combined with spherical sensor PFD measurements were 2.5 times higher than production calculated using *in situ P vs I* data (Table 7). Production based on cosine_(avg) and the laboratory *P vs I* data was 22% lower than estimates based on *in situ P vs I* data and PFD measured with the spherical sensor. The general pattern agrees with the estimates of production based on the period of high water clarity (Table 5), although the overestimation of production resulting from the combination of laboratory *P vs I* data with scalar PFD was much more drastic during the low water transparency period. Due to the intrinsic assumption of the H_{sat} model, which states that production = 0 when $\text{PFD} < I_k$, production under conditions of limited light

Table 7. *Thalassia testudinum*. Mean \pm SE daily integrated and H_{sat} production (values given in mg C dry wt leaf⁻¹ d⁻¹) calculated for a 10 d period of low water transparency at CCB. Numbers in parentheses represent the daily light saturation period in hours. A photosynthetic quotient of 1.0 was assumed

Sensor	<i>P vs I</i> model applied:			
	Integrated production		H_{sat} production	
	Laboratory	<i>In situ</i>	Laboratory	<i>In situ</i>
	$I_k = 87$	$I_k = 281$	$I_k = 87$	$I_k = 281$
Cosine _(avg)	3.8 \pm 0.6	1.1 \pm 0.2	0.0 (0)	0.0 (0)
Spherical	12.1 \pm 1.5	4.9 \pm 0.82	7.2 \pm 2.1 (2.9)	0.0 (0)

availability may be severely underestimated (Fourqurean & Zieman 1991, Zimmerman et al. 1994). Hence, production calculated based on the H_{sat} model and 10 d period of low PFDs severely underestimated integrated production. The model clearly fails for estuarine systems with variable (i.e. non-sinusoidal) or low-light regimes.

In conclusion, underwater light availability for seagrass maintenance and growth is site-specific, and should be monitored continuously to provide an accurate representation of the underwater light environment. Although blade incubations of *Thalassia testudinum* in the laboratory can provide useful physiological information regarding seasonal patterns in photosynthetic performance, laboratory estimates of I_k based on blade segments may significantly underestimate light requirements, particularly if applied to PFD measurements made with spherical quantum sensors. Therefore, erroneous predictions of depth limits and seagrass productivity may result. Combining laboratory P vs I data with cosine_(avg) sensor light measurements can underestimate production compared to estimates based on whole-plant P vs I and spherical PFD measurements by about 10% during periods of high water clarity and 25% during periods of low light. The results of this study support the importance of 'whole-plant' studies of plant metabolism and *in situ* light measurements.

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