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In situ photosynthesis in the seagrass *Halodule wrightii* in a hypersaline subtropical lagoon*

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ABSTRACT: Photosynthesis versus irradiance (P vs I) parameters in the shoalgrass *Halodule wrightii* Ascherson were calculated from measurements of oxygen evolution collected *in situ*, using entire plants in Laguna Madre, Texas, USA. Eleven experimental incubations were performed from May 1989 to April 1991 using pulsed oxygen electrodes that collected data continuously under natural daylight conditions. For comparison with *in situ* measurements of photosynthesis, P vs I parameters were calculated from laboratory measurements on blade segments incubated in a small volume chamber. For field plants, average saturation irradiance (I_k) was 319 µmol m^{-2} s^{-1}, photosynthetic capacity (P_{max}) was 374 µmol O_2 g^{-1} dry wt (dw) h^{-1}, and relative quantum efficiency (α) generally ranged from 0.5 to 1.6 µmol O_2 g^{-1} dw h^{-1} (µmol photons m^{-2} $s^{-1})^{-1}$. Whole plant respiration was 70 µmol g^{-1} dw (leaf) h^{-1}, and compensation irradiance (I_{cp}) was ca 85 µmol m^{-2} s^{-1}. Chlorophyll *a* concentrations averaged 12.8 mg g^{-1} dw, and the mean chl *a*:chl *b* ratio over the 2 yr period was 2.2. For blade segments incubated in the laboratory under similar temperatures to field plants and at corresponding chlorophyll concentrations, P_{max} was not significantly different but α was significantly higher, ranging from 3.4 to 5.3 µmol O_2 g^{-1} dw h^{-1} (µmol photons m^{-2} $s^{-1})^{-1}$. The higher α values resulted in significantly lower estimates for I_k (mean of 101 µmol m^{-2} s^{-1}). The higher α in laboratory plants was largely related to the perpendicular orientation of leaf tissue to a directed light field, which is not reflective of natural conditions for *H. wrightii*. The significant difference in I_k values calculated from incubations performed in the laboratory and field has profound effects on model calculations of H_{sat}, the duration of irradiance-saturated photosynthesis, and thus predictions of the minimum light requirements required to sustain growth in *H. wrightii*. Consequently, the application of laboratory-derived I_k values for *H. wrightii* would result in overestimates of its maximum depth limits and rates of areal primary production.

KEY WORDS: Photosynthesis · Seagrasses · *Halodule wrightii* · Texas · Subtropical · Light · PAR · Photophysiology · Shoalgrass

INTRODUCTION

There are no cornfields in the sea, yet seagrass meadows occur over vast areas and are among the most productive of plant communities (McRoy & McMillan 1977). They provide important structural complexity to coastal habitats and are used both as substrata and food for a wide variety of flora and fauna, including endangered sea turtles (Thayer et al. 1975, Fry & Parker 1979, Bjorndall 1980, McRoy & Helfferich 1980).

In Texas, USA, the occurrence of high finfish production in estuaries dominated by seagrasses and the concentration of overwintering waterfowl in seagrass meadows are no coincidence. In Laguna Madre, which produces more than 66% of the state's annual finfish harvest (Hedgpeth 1967), Hellier (1962) and Odum & Wilson (1962) found a positive correlation between gross photosynthesis (95% of which is seagrass or algal epiphytes) and fish biomass. In addition, Cornelius (1977) found that 4 to 5% of the autumn standing crop of the shoalgrass *Halodule wrightii* in Laguna Madre was consumed by redhead ducks. McMahan (1969) calculated that shoalgrass made up 84 to 89% of the diet for pintail and redhead ducks.

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Despite the large volume of information published on the trophic and functional value of seagrasses, our knowledge of the basic biology of this group is still inadequate to sufficiently predict the effects of environmental perturbations on seagrass growth and productivity (Zimmerman et al. 1991). For example, Laguna Madre is characterized by over 730 km^2 of seagrass meadows composed of 5 different species (Quammen & Onuf 1993) that represent about 85% of total seagrass vegetation in the entire coastal zone of Texas (Onuf pers. comm.). Yet losses of seagrasses in the lower Laguna Madre since the mid-1970s have been documented by McMahan (1969) and Merkord (1978). A vegetational survey in 1988 by Quammen & Onuf (1993) confirmed a 140 km^2 decrease in cover since 1965-67. The decline in seagrass cover has been attributed to light reduction caused by high turbidities that resulted from maintenance dredging (Merkord 1978, Quammen & Onuf 1993, Onuf 1994). In addition, the occurrence of a brown tide algal bloom in Laguna Madre since June 1990 has further stressed seagrass populations through chronic light reduction (Dunton 1994).

It is clear that predicting the effect of chronic reductions in underwater irradiance, as well as efforts to manage the remaining seagrass resources through habitat restoration and the establishment of water transparency criteria, require an accurate knowledge of the plant's photosynthetic light requirements. Such quantitative information becomes extremely valuable when combined with long-term *in situ* measurements of photosynthetically active radiation (PAR). Few studies have addressed photosynthetic carbon production in conjunction with definitive measurements of PAR for accurate calculation of photosynthesis versus irradiance (P vs I) parameters. However, even for species which have been studied extensively, such as *Zostera marina*, measurements of saturation irradiance can vary considerably (e.g. from 35 to 230 µmol photons m^{-2} s^{-1} at 15°C; Drew 1979, Zimmerman et al. 1989). Such variations may be a product of the techniques employed rather than a reflection of actual differences in a species' photosynthetic physiology. This further complicates the use of P vs I parameters in explaining the current distribution of seagrasses from measurements of underwater light fields.

In this study, we examined the photosynthetic rates for entire *Halodule wrightii* plants from *in situ* incubations made periodically over a 2 yr period in Laguna Madre, Texas. We also made concurrent measurements of underwater quantum irradiance to estimate parameters of photosynthetic efficiency and levels of light saturation for this species. Pigment levels within the leaves were also assessed to determine if any variations in P vs I parameters could be related to changes in chlorophyll *a* and *b* (chl *a* and *b*) content. For comparison to field measurements of photosynthesis, leaf segments of *H. wrightii* were also incubated under carefully controlled conditions of light and temperature in the laboratory. The 2 approaches yielded significantly different results and indicated that the use of saturation irradiance values derived from laboratory measurements of photosynthesis may not always be appropriate in the development of models to predict seagrass depth distributions and productivity in the marine environment.

METHODS

***In situ* photosynthetic measurements.** We examined P vs I relationships in a monotypic meadow of *Halo-*

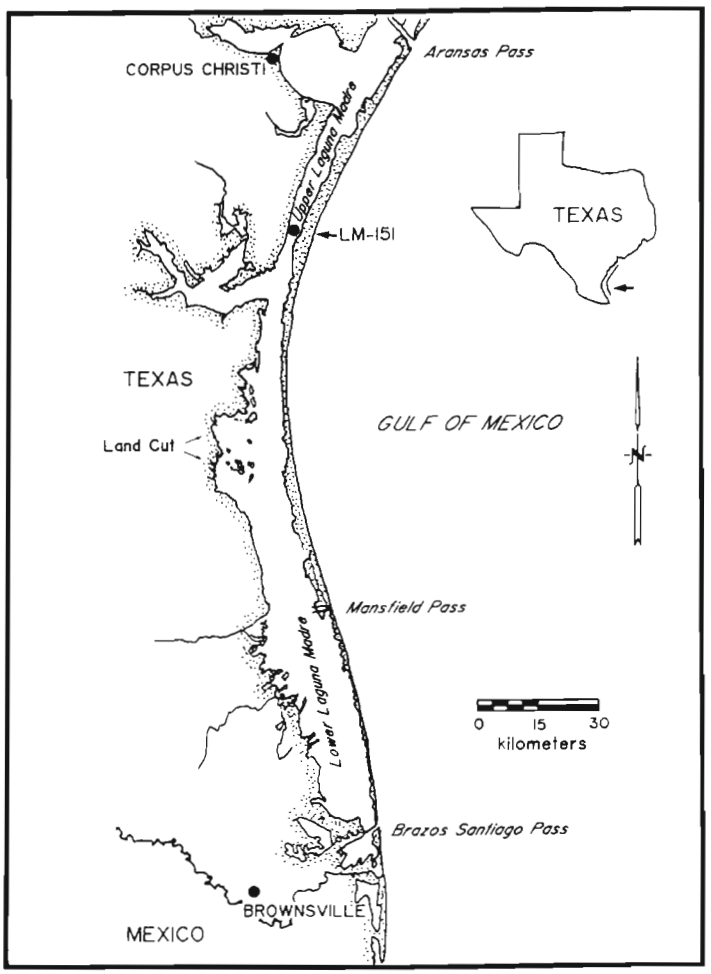

Fig. 1. Location of the experimental study site (LM-151) in the upper Laguna Madre, Texas, USA

dule wrightii in the upper Laguna Madre, Texas (Station LM-151; 27° 21' N; 97° 22' W; Fig. 1). The average depth at this site was 1.3 m (Dunton 1994) which is close to the maximum depth penetration for actively growing populations of *H. wrightii* (1.6 to 1.8 m; Onuf pers. comm.) in upper Laguna Madre.

Experimental incubations were conducted at 2 to 4 mo intervals from May 1989 to April 1991. About 2 wk prior to the *in situ* work, we removed dead leaves, algal epiphytes and drift macroscopic algae within a 2 m^2 area. Algal epiphytes were seldom observed on leaves of *Halodule wrightii* in Laguna Madre, and may be related to the hypersaline conditions and low nutrient concentrations in the upper Laguna (Jewett-Smith 1991). If present, epiphytes were either removed by hand or by clipping the top few centimeters of the oldest blades having the highest concentration of these attached plants. Immediately prior to the deployment of incubation chambers on the seabed, the area was again raked clean of detritus and macroalgae.

Photosynthetic incubations of whole plants were conducted *in situ* using four 5 l chambers placed on the seabed by divers. Clear acrylic plastic chambers were 12 cm in diameter and 45 cm high (Fig. 2). The top of each chamber was permanently sealed and contained a tapered opening for an oxygen probe and a 1.2 cm diameter sampling port plugged with a rubber septum. A small battery-powered submersible pump provided circular water movement within the chamber for 3 min periods at 2 min intervals, as triggered by an external computer running in BASIC. During deployment of the chambers, care was taken to avoid cutting shoots or blades while they were positioned and pressed firmly into the seabed to a depth of 10 cm. Underwater PAR (400 to 700 nm) was measured at 5 s intervals and integrated every 5 min on a continuous basis using an LI-193SA spherical quantum sensor, which provided input to a LI-1000 datalogger (LI-COR, Lincoln, NE, USA). The sensor was placed adjacent to the chambers at canopy level (Fig. 2). Salinity was determined in the field using a refractometer calibrated against an Orion 140 salinometer.

Dissolved oxygen measurements were collected using an Endeco/YSI Type 1125 Pulsed Dissolved Oxygen System. The system utilizes 4 YSI 1128 oxygen electrodes, is flow insensitive, offers high resolution (±0.4 µM), and is capable of collecting continuous measurements of dissolved oxygen and temperature at selectable intervals. For incubations with *Halodule wrightii*, the probes were programmed to collect measurements of dissolved oxygen at 15 min intervals. Chambers were typically deployed by 18:00 h and allowed to equilibrate for several hours prior to data collection. Once oxygen values had stabilized, water samples were collected periodically for oxygen determinations using the Winkler method (Strickland & Parsons 1972) to insure that the probes were operating within calibration (calibrations were conducted in the laboratory prior to the cruise). Constant monitoring of the data output via RS-232 interface to a laptop computer using Endeco software permitted the monitoring of oxygen tensions within the chambers and avoidance of saturating oxygen concentrations. If saturation occurred, oxygen levels were reduced 40 to 50% by bubbling N_2 into the chamber for 2 to 3 min. Any

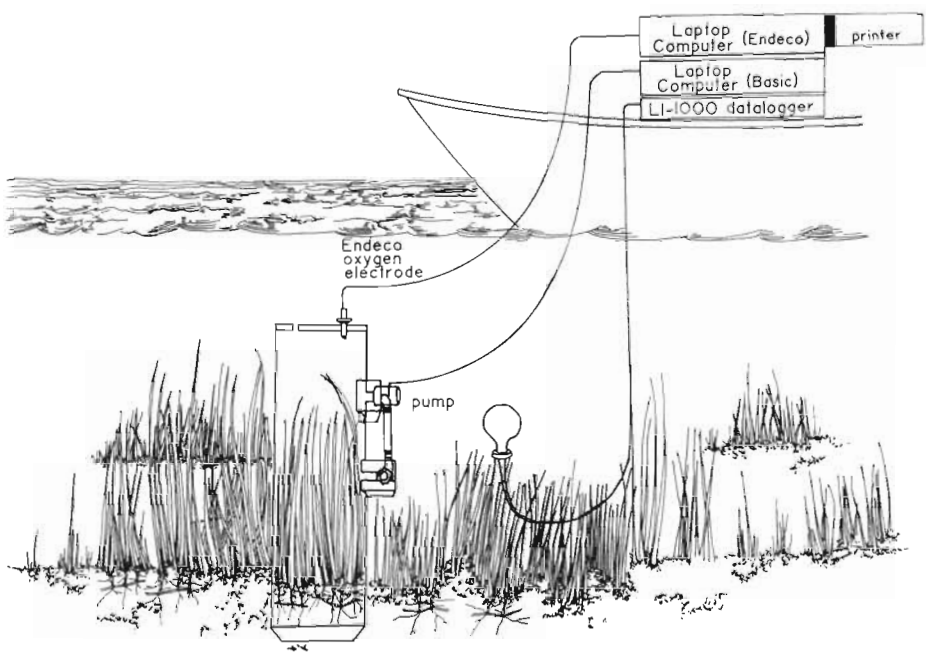

Fig. 2. Photosynthetic oxygen chamber used for *in situ* incubations in Laguna Madre. Four chambers constructed entirely of clear acrylic were employed simultaneously during each incubation. See text concerning details of data acquisition

remaining gas bubbles were removed using the 1.2 cm diameter sampling port at the top of the chamber. Plants were incubated under natural daylight conditions, although neutral density shade cloth was occasionally deployed over the chambers to achieve a desired light level. Incubations generally ranged from 0.5 to 1.5 h to maintain a given light level. To assess the effect of phytoplankton on oxygen levels within the chambers, we performed light and dark bottle incubations and obtained total water column chlorophyll concentrations following Parsons et al. (1984). Although the contributions made by phytoplankton were usually insignificant (< 5 % of chamber photosynthesis at P_{max}), the onset of a brown algal chrysophyte bloom in late spring 1990 caused significant increases in chlorophyll concentrations in the upper Laguna Madre (Stockwell et al. 1993). To avoid the necessity of making corrections for the oxygen contributions made by phytoplankton, the water within the chambers was cycled sequentially through 10 and 1 µm filter cartridges for a 15 min period. This procedure effectively reduced chlorophyll concentrations in the chambers to negligible levels.

Photosynthetic rates were calculated from changes in dissolved oxygen concentrations in the chamber over the duration of each incubation. Net chamber photosynthesis was determined from slopes by regression analysis of linear portions of recorded time series at each light level. Chamber respiration rates (for calculation of plant, animal, bacterial and chemical oxygen demand) were determined from incubations conducted the evening prior to the photosynthetic incubation. Respiration by non-seagrass tissues was variable but generally accounted for 10 to 50 % of total chamber respiration. Gross photosynthesis at each light level ($P_{G(I)}$) among the 4 replicate chambers was calculated similarly to that outlined by Fourqurean & Zieman (1991) in which $P_{G(I)}$ represents the sum of net chamber photosynthesis and chamber respiration, normalized to the pigmented shoot and leaf biomass in the chamber (B_{leaf}):

$$P_{G(I)} = \frac{[P_{\text{chamber net}(I)} + R_{\text{chamber}}]}{B_{\text{leaf}}} \quad (1)$$

Gross photosynthetic rates were expressed in units of µmol O_2 g^{-1} dry wt leaf h^{-1}.

***P* vs *I* model calculations.** *P* vs *I* data were fit to the hyperbolic tangent function of Jassby & Platt (1976):

$$P = P_{max} \tanh\left(\frac{\alpha I}{P_{max}}\right) \quad (2)$$

where P_{max} is the light-saturated rate of photosynthesis, α is light-limited slope of *P* vs *I* curve and *I* is the irradiance. This function usually provides the best fit to *P* vs *I* curves based on both goodness of fit and minimizing residuals as reported for phytoplankton and marine macroalgae (Chalker 1980, Coutinho & Zingmark 1987, Geider & Osborne 1992). All curve-fitting was performed statistically on a 486 PC using nonlinear least squares regression techniques (SAS Institute 1987). *P* vs *I* parameters were estimated simultaneously using a derivative-free algorithm (The Dudly algorithm) of Ralston & Jennrich (1978). The saturation irradiance, I_k, was defined as the ratio of the 2 model parameters, α and P_{max}:

$$I_k = \frac{P_{max}}{\alpha} \quad (3)$$

Respiration and calculation of whole-plant compensation irradiance. Estimation of the compensation irradiance for an entire plant (blades and their associated below-ground tissues), required a knowledge of the root:shoot ratios (*RSR*) for *Halodule wrightii* and measurements of leaf and root/rhizome dark respiration rates. During each experimental chamber incubation, we collected blade and root/rhizome material for dark bottle incubations performed at night *in situ*. Samples containing entire blades and root/rhizome tissue were separated and washed immediately after collection and sorted into 4 replicate 300 ml BOD bottles for each tissue type. Two additional bottles were deployed to correct for water column respiration, which normally exhibited negligible oxygen uptake over the 2 to 3 h incubation period. Oxygen concentrations in each bottle were measured using an oxygen electrode or by chemical analysis using the Winkler Method (Parsons et al. 1984). The incubated shoot and root/rhizome tissue was then dried to a constant weight at 60 °C for 24 to 48 h. Results are expressed in µmol O_2 g^{-1} dry wt (dw) tissue h^{-1}.

The apportionment of above- and below-ground tissue was measured from biomass samples retrieved from the 4 experimental chambers used in the *P* vs *I* incubations. Pigmented leaves and shoots (aboveground tissue) were separated from non-photosynthetic shoot and root/rhizome portions; the tissues were washed sequentially through 12 mm and 1.0 mm mesh screens to remove sediments, detritus, and shell material. The pooled material from the 2 components were dried and indices of *RSR* determined. Total plant respiration (R_p) was normalized to 1 g dry wt of leaf tissue and calculated from the respiratory demands of leaf tissue (R_{leaf}) and root/rhizome ($R_{r/r}$) tissue based on the proportion of root/rhizome tissue needed to support that leaf tissue (the *RSR* ratio):

$$R_p = R_{leaf} + R_{r/r}(RSR) \quad (4)$$

Whole plant compensation irradiance (I_{cp}), the light level at which the rate of photosynthetic oxygen evolution (*P*) is equivalent to the total respiratory demands

of the plant (R_p), was then determined mathematically from the hyperbolic tangent function by setting R_p equal to P, substituting I_{cp} for I in Eq. (2) and solving for I_{cp}:

$$I_{cp} = \left(\frac{P}{P_{max}}\right) \coth\left(\frac{\alpha}{P_{max}}\right) \quad (5)$$

Laboratory *P* vs *I* measurements. For comparison with *in situ* measurements of photosynthesis, vegetative shoots were collected from cores gathered at the study site in late April 1993 for laboratory-based metabolic rate measurements. Entire plants (shoots, roots and associated sediment) were placed in holding tanks with continuous running seawater (25 to 26°C) and exposed to ca 100 µmol photons m^{-2} s^{-1} under a daily photoperiod of 12 h light:12 h dark under fluorescent lamps. Leaf segments (3 cm lengths) were cut 2 to 4 h prior to the start of the physiological measurements to minimize the effects of wound respiration (blade tissue turned increasingly brown from cut areas if held >12 h). Plants were incubated within 1 to 3 d of initial collection. We performed the P vs I measurements at 29°C to facilitate direct comparison with field incubations. Five of the eleven *in situ* incubations were conducted at temperatures ranging between 28 and 30°C (mean 29°C) and provided a sufficient sample for statistical comparison at this temperature.

Oxygenic photosynthesis and respiration rates were measured on leaf segments using a polarographic O_2 electrode in a modified water-jacketed incubation chamber (13 ml vol; Rank Bros., Bottisham, UK). The electrode was calibrated using N_2-purged and air-saturated media. An underwater LI-192SA quantum sensor fitted on one side of the square chamber and connected to a LI-1000 datalogger provided accurate measurement of PFD (photon flux density) within the chamber. Photosynthetic rates were measured at 10 different irradiances using a Kodak slide projector (300 W ELH G.E. bulb) as a light source and slides fabricated from Kodak neutral density filters. Respiration rates were measured in the dark. Initial O_2 concentrations were decreased to about 25% of air saturation by bubbling with N_2 immediately prior to photosynthetic measurements, which proceeded sequentially from the lowest (6 µmol m^{-2} s^{-1}) to the highest (1100 µmol m^{-2} s^{-1}) level of PAR. Rates of dark respiration were performed near levels of oxygen saturation prior to the start of the photosynthetic incubations. Temperature was controlled at 29.0 ± 0.5°C by a refrigerated circulating water bath; a magnetic stirrer insured rapid mixing for both the electrode and the tissue segment. Digital data output was recorded continuously using a Computer Boards A/D converter and Labtech Notebook Software (Ver. 6.3.0) running under MS-DOS on a 286-AT computer. Slopes were determined as described above for incubations that averaged 4 to 6 min. P vs I data were fit to the hyperbolic tangent function (Eq. 2) of Jassby & Platt (1976); leaf compensation irradiance ($I_{c(leaf)}$) was determined similarly as denoted for I_{cp} in Eq. (5).

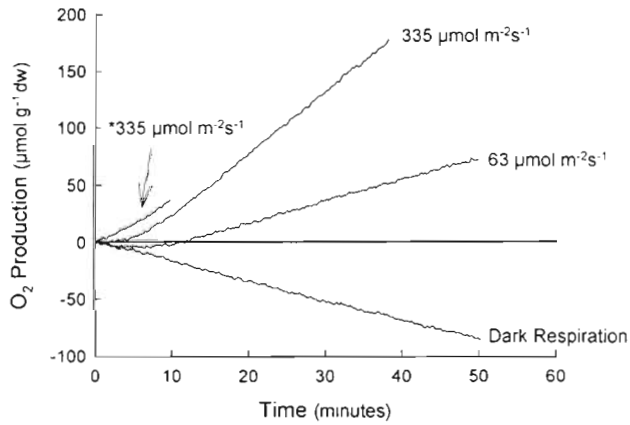

Fig. 3. *Halodule wrightii*. Photosynthetic oxygen evolution and respiratory uptake in blade segments as a function of time at different light levels. Asterisk denotes light level that was not preceded by a 6 min dark period (see text)

Because of concerns about effects of lacunal gas storage on the measurement of photosynthesis, we established a minimal period of stabilization following introduction of blade tissue into the chamber and after establishment of each new light level. The duration of this period was based on a time-course experiment at 3 different light levels, similar to that performed by Drew (1978). The results (Fig. 3) show that a constant rate of oxygen evolution into the incubation chamber was delayed from 1 to 10 min as a function of light level and prior exposure to darkness. The lag period for dark respiration was less than 3 min, but was about 10 min at 63 µmol m^{-2} s^{-1} (following dark respiration) and 4 min at 335 µmol m^{-2} s^{-1} (following a 6 min dark period). However, the lag period dropped to about 1 min at 335 µmol m^{-2} s^{-1} if no dark period preceded the measurement (the linear slopes remained the same). These observations became the basis for the procedure outlined above, in which blade segments were measured at sequential increases in PAR following the measurement of dark respiration with the incorporation of a 4 min stabilization period prior to each measurement.

Measurement of leaf chlorophyll content. Until October 1992, we extracted chlorophylls from leaf tissue by repeated grinding of pre-weighed tissue samples in 90% cold acetone buffered with 0.05% $MgCO_3$ using chilled pestles and mortars with washed sea sand. The extract was made up to a known volume, centrifuged, and absorbances measured at 664 and

647 nm on a Shimadzu UV 160U spectrophotometer. Chl *a* and *b* content was then determined using the equations from Jeffrey & Humphrey (1975) for 90% acetone. After October 1992, we employed an alternative extraction technique utilizing N,N-dimethyl formamide (DMF) which did not require grinding of plant tissue, thus saving time and effort as well as reducing potential sources of error. Pre-weighed tissue samples were extracted overnight in glass screw-cap tubes containing DMF; the resulting extract was measured as described above and chl *a* and *b* content determined using the equations of Porra et al. (1989). Appropriate corrections were made for a turbidity blank at 750 nm in both methods. Comparison of the results using the 2 techniques on blade tissue collected on a variety of occasions yielded no significant differences in chl *a* or chl *b* content (paired *t*-test, $p \geq 0.65$ and $p \geq 0.08$ respectively, $n = 12$).

Statistics. Statistical analyses were performed on a 486 PC using a general linear model procedure (SAS Institute Inc. 1987). Significant differences in chlorophyll content among sampling dates was tested using a 1-way ANOVA. When a significant difference for a main effect ($p < 0.05$) was observed, the means were analyzed by a Tukey multiple-comparison test to determine significant differences among sampling dates. Significant differences in *P* vs *I* parameters were tested using a 2-sample *t*-test.

RESULTS

In situ photosynthesis of entire plants

The *P* vs *I* curves for *Halodule wrightii* plants incubated *in situ* over a 2 yr period in Laguna Madre exhibited marked similarity (Fig. 4). Photosynthetic relationships were explained well by the hyperbolic tangent function of Jassby & Platt (1976), with all curves exhibiting an $r^2 > 0.95$. Incubations conducted throughout the day at a variety of light levels showed, in most instances, no apparent or consistent differences in photosynthetic oxygen production between morning and afternoon periods at similar light levels. No obvious seasonal trends in *P* vs *I* parameters were apparent, despite temperatures that ranged from 12 to 30 °C over the course of this study.

Excluding the high P_{max} and I_k values obtained in January 1990, gross P_{max} averaged 374 µmol O_2 g^{-1} dw leaf h^{-1}, and I_k averaged 319 µmol photons m^{-2} s^{-1}

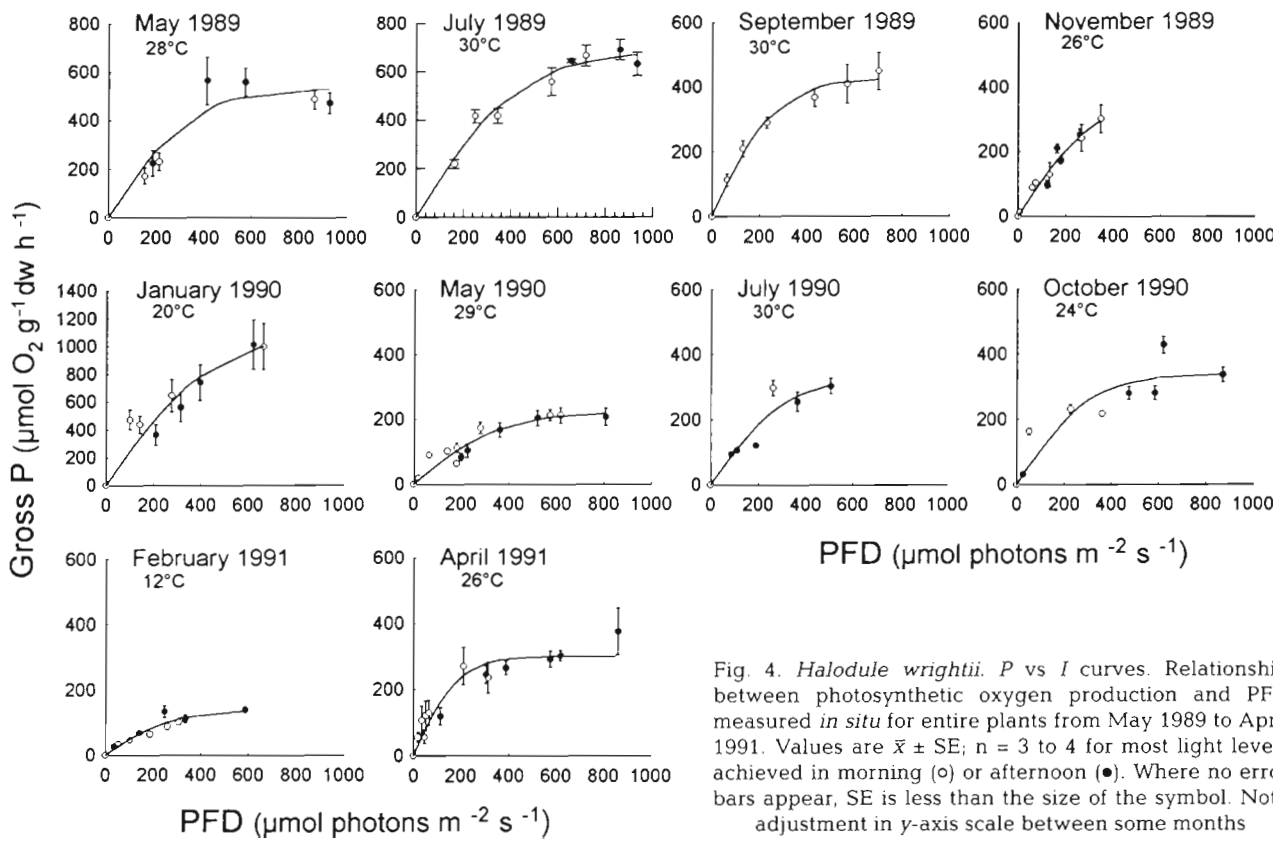

Fig. 4. *Halodule wrightii*. *P* vs *I* curves. Relationship between photosynthetic oxygen production and PFD measured *in situ* for entire plants from May 1989 to April 1991. Values are $\bar{x} \pm SE$; $n = 3$ to 4 for most light levels achieved in morning (○) or afternoon (●). Where no error bars appear, SE is less than the size of the symbol. Note adjustment in *y*-axis scale between some months

Table 1. *Halodule wrightii*. Seasonal variation in the *P* vs *I* parameters for entire plants based on *in situ* measurements of oxygen evolution and root:shoot ratios (*RSR*)

Date	Temp. (°C)	Salinity (‰)	P_{max} (μmol O_2 g^{-1} dw leaf h^{-1})	*R*	α[a]	I_k (μmol m^{-2} s^{-1})	I_{cp}	*RSR*
May 1989	28	45	533	117	1.5	353	177	4.9
Jul 1989	30	47	688	75	1.6	434	119	3.0
Sep 1989	30	48	427	59	1.6	270	93	4.2
Nov 1989	26	45	386	89	1.1	345	100	2.0
Jan 1990	20	39	1104	58	2.4	453	141	5.4
Mar 1990	19	48	–	–	0.6	–	70	2.4
May 1990	29	38	223	76	0.6	365	46	1.7
Jul 1990	30	45	331	116	1.0	321	120	2.1
Oct 1990	24	50	340	72	1.1	306	80	1.4
Feb 1991	12	32	140	75	0.5	286	37	2.6
Apr 1991	26	45	300	62	1.6	189	98	1.3

[a] μmol O_2 g^{-1} dw leaf h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$

(Table 1). No data on these parameters are available for March 1990 since maximum PFD achieved during the entire incubation period was 343 μmol m^{-2} s^{-1} due to low incident PAR under a heavy overcast. The lowest P_{max} value recorded (140 μmol O_2 g^{-1} dw leaf h^{-1}) occurred in February 1991 at an incubation temperature of 12 °C. This contrasts with the high P_{max} value of 1105 μmol O_2 g^{-1} dw leaf h^{-1} the previous January at 20 °C. Values of relative quantum efficiency, α, ranged from 0.5 to 1.6 μmol O_2 g^{-1} dw leaf h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$ excluding the January 1990 value of 2.4. Whole plant respiration generally ranged from about 60 to 90 μmol O_2 g^{-1} dw leaf h^{-1} (average 71 μmol O_2 g^{-1} dw leaf h^{-1}, with 2 abnormally high respiration values (over 115 μmol O_2 g^{-1} dw leaf h^{-1}) recorded in May 1989 and July 1990 (overall average of 80 μmol O_2 g^{-1} dw leaf h^{-1}). Average blade respiration from bottle incubations made during each visit to the study site was 41.5 (SE = 7.3, n = 11) compared to 16.1 μmol O_2 g^{-1} dw h^{-1} (SE = 4.9, n = 11) for root and rhizome tissue. Whole plant compensation irradiance (I_{cp}) averaged 85 μmol m^{-2} s^{-1} for root-shoot ratios that ranged from 1.3 to 4.2, but was much higher for ratios of about 5 or greater. Water salinities varied in response to precipitation and showed little seasonality, ranging from 32 to 52‰.

Pigment content

Total chlorophyll from *Halodule wrightii* leaf tissue ranged from 7.6 to 19.5 mg g^{-1} dw, with peaks at 19.5 and 19.1 mg g^{-1} dw in January 1990 and May 1991 respectively (Fig. 5). Ratios of chl *a*:chl *b* ranged from 1.3 to 2.9 over the 2 yr period of *in situ* incubations with lower chl *a*:chl *b* ratios (1.3 and 2.0 respectively) corresponding to peaks in total chlorophyll content. The high chlorophyll concentrations and lower chl *a*:chl *b* ratios in *H. wrightii* coincided with the highest P_{max} (January 1990) and lowest I_k (April 1991) recorded over the 2 yr experimental period. Blades collected in April 1993 for laboratory *P* vs *I* experiments exhibited a total chlorophyll concentration of 10.8 mg g^{-1} dw (SE = 0.6,

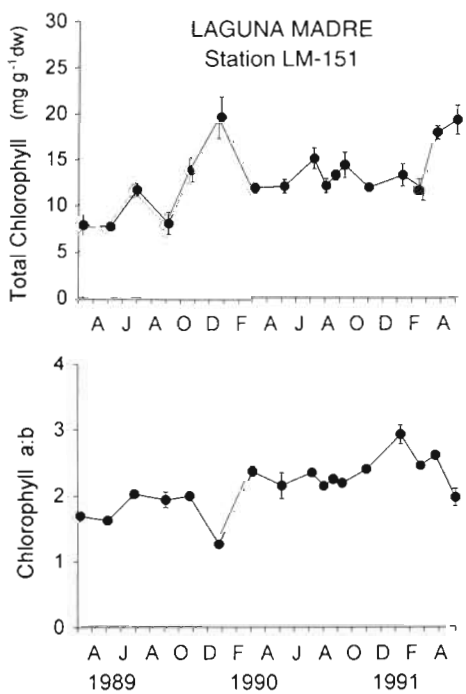

Fig. 5. *Halodule wrightii*. Variations in chl *a* content (upper panel) and chl *a*:chl *b* ratios (lower panel) for plants collected from March 1989 through May 1991 at Station LM-151. Values are $\bar{x}$ ± SE (n = 6). Where no error bars appear, SE is less than the size of the symbol

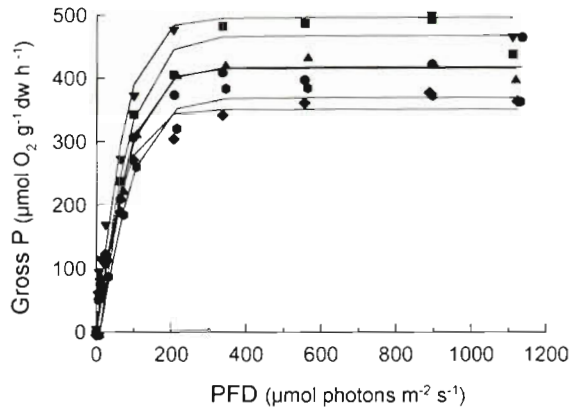

Fig. 6. *Halodule wrightii*. *P* vs *I* curves for 6 replicate blade segments (denoted by different symbols) measured under laboratory conditions at 29°C. Plants were collected in late April 1993 from Station LM-151

n = 6) and a chl *a*:chl *b* ratio of 2.6, which were not significantly different ($p > 0.05$) from measurements collected during the 2 yr experimental period.

Laboratory measurements of photosynthesis using blade segments

Six *P* vs *I* curves were generated from individual blade segments of *Halodule wrightii* plants collected from Station LM-151 in late April 1991 (Fig. 6). Photosynthetic measurements made at 29°C in the laboratory were described well by the hyperbolic tangent function of Jassby & Platt (1976), and r^2 was >0.95 for each of the curves.

A summary of the calculated *P* vs *I* parameters is shown in Table 2. Gross P_{max} values ranged from 356 to 491 µmol O_2 g^{-1} dw leaf h^{-1}, similar to the range in P_{max} values derived from entire plants *in situ* (Table 1). However, I_k values ranged from 90 to 110 µmol m^{-2} s^{-1}, ca one-third the average of *in situ* incubated plants. Similarly, values of α averaged ca 3 times greater for blade segments [range 3.4 to 5.3 µmol O_2 g^{-1} dw leaf h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$] than in whole plants incubated *in situ* (range 0.5 to 2.4). Since I_k is empirically derived from estimates of P_{max} and α, and P_{max} values were relatively the same between the 2 experimental approaches, the lower I_k values for blade segments can be ascribed to the 3-fold increase in α. The higher values of α for blade segments is not related to total leaf chlorophyll concentrations and chl *a*:chl *b* ratios, which were nearly the same as recorded from leaf tissue of entire plants incubated *in situ*. Statistical comparisons of the *P* vs *I* parameters obtained between plants incubated in the field and of blade segments measured under laboratory conditions yielded values of I_k, $I_{c(leaf)}/I_{cp}$, and α that were significantly different ($p < 0.05$) between the 2 approaches.

DISCUSSION

Photosynthetic light requirements of seagrasses: comparison of techniques

Efforts to gain a more thorough and accurate understanding of the minimum light requirements necessary to sustain growth in seagrasses has focused on plant carbon budgets and the energy demands of below-ground plant tissues (Zimmerman et al. 1989, Fourqurean & Zieman 1991, Olesen & Sand-Jensen 1993). The importance of below-ground tissues in estimating light compensation points (I_c) was demonstrated by Olesen & Sand-Jensen (1993), who found the I_c for growth of entire eelgrass *Zostera marina* plants at 21°C was considerably higher (47 µmol m^{-2} s^{-1}) than compared to leaves alone (30 µmol m^{-2} s^{-1}). Estimates of leaf I_c for eelgrass have been reported even lower (from 10 to 17 µmol m^{-2} s^{-1}) at similar temperatures (Dennison & Alberte 1982, Marsh et al. 1986).

The incorporation of below-ground biomass, which often accounts for up to 85% of the biomass of many seagrasses (Eleuterius 1987, Lindeboom & Sandee 1989, Dunton 1990, Fourqurean & Zieman 1991), can therefore have a profound impact on estimates of I_c for entire plants, and hence on H_{comp}, the duration of time

Table 2. *Halodule wrightii*. Comparison of average *P* vs *I* parameters gathered from entire plants incubated in the field at 28 to 30°C (see Table 1) versus blade segments examined under controlled laboratory conditions at 29°C. Values are $\bar{x} \pm$ SE

Parameter	Entire plants (field) (n = 5)	Blade segments (lab) (n = 6)	Comparison of *P* vs *I* parameters
P_{max} (µmol O_2 g^{-1} dw leaf h^{-1})	441 ± 80	421 ± 21	p = 0.82
α [µmol O_2 g^{-1} dw h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$]	1.3 ± 0.2	4.2 ± 0.3	p = 0.0004
I_k (µmol m^{-2} s^{-1})	349 ± 27	101 ± 4	p = 0.0008
I_c (µmol m^{-2} s^{-1})	111 ± 21	22 ± 2	p = 0.0001

Table 3. Variation in I_k and I_c values as a function of the experimental approach employed for measurement of photosynthesis in eelgrass *Zostera marina*. nd: not determined

I_k (μmol m^{-2} s^{-1})	I_c	Temp. (°C)	Technique	Location (USA)	Source
230	28	15	Bottles, 7 cm leaf segments, Winkler	California	Drew (1979)
100	10	20	Rank Bros. O_2 electrode chamber, 2 cm blade segments	Woods Hole, MA	Dennison & Alberte (1982)
348	nd	20	Large chambers *in situ*, entire plants, ^{14}C uptake	Chesapeake Bay, VA	Wetzel & Penhale (1983)
65–120	15–25	20	Rank Bros. O_2 electrode chamber, 2 cm blade segments	Woods Hole, MA	Dennison & Alberte (1985)
78	17	20	Rank Bros. O_2 electrode chamber, 2 cm blade segments	Woods Hole, MA	Marsh et al. (1986)
35	nd	15	Small-volume chamber, blade segments, O_2 electrode	San Francisco Bay, CA	Zimmerman et al. (1991)

that PAR is above compensation irradiance. In this study, our estimates of whole plant compensation irradiance (I_{cp}) for *Halodule wrightii* were also considerably higher than that of blade I_c (Table 2). However, the reasons for this difference cannot be attributed solely to the inclusion of below-ground tissue respiration in the calculation of I_{cp}, since blade respiration of laboratory incubated plant segments was often greater than the respiration values calculated for entire plants measured *in situ*. The higher respiration for 3 cm blade segments may be due to a cumulative wounding effect that is minimized when using entire leaves in 300 ml BOD bottles. However, the effect of elevated leaf segment respiration on I_{cp} is minimized by the higher photosynthetic response of leaf tissue in laboratory incubations. The greater photosynthetic response of blade segments at limiting light levels cannot be attributed to changes in leaf chlorophyll content, which have remained virtually unchanged between 1989 and 1993 (present paper and Dunton unpubl. data). The photosynthetic performance of blade segments of *H. wrightii* from other sites in south Texas at 30 °C have also been nearly identical to the response depicted in Fig. 6 for this species (Czerny 1994).

The measurement of photosynthesis in the laboratory, in which a small blade segment of *Halodule wrightii* was positioned perpendicular to a directed light field, resulted in high relative quantum efficiencies (α). Plants incubated *in situ* under a naturally diffuse underwater light field exhibited lower values of α. In the absence of any significant difference in chlorophyll concentration, field- and laboratory-incubated plants exhibited similar rates of light-saturated photosynthesis (Table 2). Consequently, I_c and I_k values for laboratory-incubated plants are significantly lower.

Values of <3 μmol m^{-2} s^{-1} for I_c at temperatures of 10 °C or less have been reported for eelgrass (Marsh et al. 1986), whose lower depth boundary corresponds to 11% of surface irradiance (Dennison 1987, Olesen & Sand-Jensen 1993). However, I_c values for growth in some common macroalgae are also close to this range (0.3 to 2.5 μmol m^{-2} s^{-1}), yet their minimum light requirements are nearly an order of magnitude lower, 0.12 to 0.61% of surface PAR (Markager & Sand-Jensen 1992). Similarly, values of 35 μmol m^{-2} s^{-1} for saturation irradiance (at 10 to 15 °C) for eelgrass (Marsh et al. 1986, Zimmerman et al. 1991) are lower than reported for arctic kelp (Dunton & Jodwalis 1988), whose total annual quantum dose of irradiance is probably received by most seagrass communities within a 1 wk summer period (Dunton 1994).

The apparent differences in the minimum light requirements needed to sustain growth and achieve light-saturated photosynthesis are largely explained by the experimental techniques employed, as shown in this study and as summarized in Table 3 for *Zostera marina*. In eelgrass, I_c and I_k values were generally lowest when blade segments were oriented perpendicular to a directed light field, usually within a small stirred chamber (e.g. Marsh et al. 1986, Zimmerman et al. 1991). In contrast, I_c and I_k values were considerably higher when whole leaves or blade segments were incubated in bottles or large chambers which were not purposely aligned to incoming PAR (Drew 1979, Wetzel & Penhale 1983), as also shown in this study. Estimations of H_{sat}, the duration of irradiance-saturated photosynthesis (Dennison & Alberte 1982), may therefore vary widely. The use of laboratory-derived P vs I parameters may lead to an overestimation of photosynthesis as argued by Fourqurean & Zieman (1991), or to prediction of maximum depth

limits that are not observed in the field (Zimmerman et al. 1991).

Continuous measurements of underwater irradiance near the maximum depth limits of *Halodule wrightii* clearly indicate that the depth limits and productivity of *H. wrightii* cannot be explained using *P* vs *I* parameters derived from our laboratory experiments using blade segments (Dunton 1994). Evidence for this conclusion is based on observations from 3 different estuarine systems in south Texas. Compilation of data presented in this paper and *P* vs I measurements collected at 2 other locations in Texas (Dunton unpubl. data), have established $I_{k\,(field)}$ and I_{cp} values for *H. wrightii* of 315 and 80 µmol m^{-2} s^{-1} respectively. Based on this information, Dunton (1994) found that the onset of a brown algal bloom in late spring 1990 in Laguna Madre (Stockwell et al. 1993) dropped $H_{sat\,(field)}$ values from 5 to about 2 h. The decline in H_{sat} also coincided with a 24 to 46% decrease in spring leaf elongation rates and a steady decline in total plant biomass to less than half pre-brown tide levels; in contrast $H_{sat\,(lab)}$ values exhibited little change (remaining at or above 6 h) when derived from laboratory *P* vs *I* parameters ($I_{k\,(lab)}$ = 101 µmol m^{-2} s^{-1}). At the deep edge of a seagrass bed in Corpus Christi Bay, $H_{sat\,(field)}$ during spring and summer generally averaged 3 to 5 h compared to >7 h for $H_{sat\,(lab)}$; in San Antonio Bay, a *H. wrightii* bed disappeared when $H_{sat\,(field)}$ dropped to <2 h over an 8 mo period but $H_{sat\,(lab)}$ values remained well above 5 h (Dunton 1994). In all 3 examples noted above, $H_{sat\,(lab)}$ values were either largely insensitive to declines in water transparency to which *H. wrightii* responded, or provided unrealistic estimates of H_{sat} for populations living near their maximum depth. In conclusion, although laboratory measurements of photosynthesis using blade segments are invaluable in addressing specific physiological questions [e.g. temperature effects on photosynthesis (Marsh et al. 1986), inorganic carbon uptake effects on photosynthesis (Durako 1993)] extrapolation of laboratory *P* vs *I* parameters to field populations may not provide the accuracy required to successfully model seagrass production from *in situ* measurements of PAR.

Photosynthetic performance in *Halodule wrightii*

We observed little variation in *P* vs *I* parameters in *Halodule wrightii* over the 2 yr experimental period. This is most likely a consequence of the small temperature range of most incubations (between 24 and 30°C), the lower resolution of this approach in the measurement of photosynthetic oxygen evolution and the corrections required for chamber oxygen demand (compared to controlled laboratory experiments). In one instance we conducted *P* vs *I* measurements at 12°C (early February 1991), and found that P_{max} values dropped to 140 µmol O_2 g^{-1} dw leaf h^{-1}, compared to the overall average of 374 µmol O_2 g^{-1} dw leaf h^{-1}. The large decrease in light-saturated photosynthesis in *H. wrightii* at 12°C is a consequence of reduced metabolic activity caused by the temperature dependence of the dark reactions of photosynthesis, as reported in several studies on seagrasses (reviewed by Bulthuis 1987).

In contrast, the extremely high P_{max} measured at 20°C in January 1990 (1104 µmol O_2 g^{-1} dw leaf h^{-1}) corresponded with a peak in total leaf chlorophyll and low chl *a*:chl *b* ratios. The significant increase in blade chlorophyll followed a precipitous drop in underwater PAR during the preceding months (Dunton 1994). A second peak in blade chlorophyll content in May 1991 was also associated with extremely low values of underwater irradiance (Dunton 1994) and a lower I_k value. Increases in chlorophyll content in aquatic plants has been associated with significant correlations in both α (Goldsborough & Kemp 1988) and P_{max} (Nielsen & Sand-Jensen 1989). These observations indicate that *Halodule wrightii* may possess some capacity for photosynthetic adjustment in response to its underwater light environment as reflected by changes in *P* vs *I* parameters. Such adjustments have been well documented in experimental manipulations with underwater irradiance for *Zostera marina* (Dennison & Alberte 1985). Additionally, seagrasses from deep edges of meadows typically have higher chlorophyll content than plants from shallow edges (Drew 1978, Wiginton & McMillan 1979, Dennison & Alberte 1982, 1985, Dawes & Tomasko 1988).

We observed no differences in photosynthetic production between morning and afternoon incubations at similar light levels. However, *Halodule wrightii* was not normally exposed to levels of PAR above 800 µmol m^{-2} s^{-1} and failed to show any clear signs of photoinhibition at higher light levels. In contrast, Libes (1986) noted a depression in afternoon photosynthesis in *Posidonia oceanica* that were incubated *in situ*, but attributed this response to the high light conditions that occurred during the day when plants were frequently exposed to an irradiance equivalent to 1400 µmol m^{-2} s^{-1}.

The light-saturated rates of photosynthesis for *Halodule wrightii* reported here are in the range of values reported for *Halodule* spp. in previous studies using bottles or large incubation vessels *in situ* (Williams & McRoy 1982, Morgan & Kitting 1984, Lindeboom & Sandee 1989, Zieman et al. 1989) or under artificial light (Beer & Waisel 1982). For *H. wrightii*, Williams & McRoy (1982) noted that P_{max} ranged from about 250 to 340 µmol C g^{-1} dw leaf h^{-1} for Texas plants, and from about 250 to 1580 µmol C g^{-1} dw leaf h^{-1} for Puerto

Table 4. Comparison of light-saturated rates of gross photosynthesis among seagrasses, freshwater angiosperms, and terrestrial plants based on rates of oxygen evolution. Asterisks denote rates of carbon production that were converted to oxygen based on a photosynthetic quotient of unity

Species	Temp. (°C)	P_{max}, µmol O_2 h^{-1}: g^{-1} dw	cm^{-2}	mg chl^{-1}	Source
Seagrasses					
Cymodocea nodosa	25	–	2.0	65.0	Drew (1979)
Halodule wrightii	29	441	–	34.5	This study
Halophila stipulacea	25	–	0.8	62.5	Drew (1979)
Phyllospadix torreyi	15	–	2.5	48.3	Drew (1979)
Posidona oceanica	17	–	0.8	23.3	Drew (1979)
Ruppia drepanensis	16	67*	–	54.6*	Garcia et al. (1991)
Thalassia testidinum	30	239	–	67.5	Dawes & Tomasko (1988)
Zostera marina	15	–	1.3	26.7	Drew (1979)
Zostera marina	20	91.2	0.5	28.2	Dennison & Alberte (1982)
Freshwater angiosperms					
Elodea canadensis	15	161	0.1	19.4	Nielsen & Sand-Jensen (1989)
Myriophyllum spicatum	15	285	0.1	28.1	Nielsen & Sand-Jensen (1989)
Potamogeton crispus	15	562	0.2	32.8	Nielsen & Sand-Jensen (1989)
Terrestrial plants					
Shade plants	25	–	0.8*	9.2*	Björkman (1981)
Sun plants	25	–	2.1*	39.5*	Björkman (1981)

Rico plants. In Florida Bay, Zieman et al. (1989) reported leaf production in *H. wrightii* ranging from 126 to 277 µmol C g^{-1} dw h^{-1}. In studies of *H. uninervis* in the Red Sea, Beer & Waisel (1982) reported an I_k value of 300 µmol m^{-2} s^{-1}, $I_{c\,(leaf)}$ values of 20 to 40 µmol m^{-2} s^{-1}, and P_{max} values of 21 µmol O_2 mg chl h^{-1}. Interestingly, we found light-saturated rates of photosynthesis, expressed per unit chlorophyll content, for *H. wrightii* and other seagrasses similar to values reported for other aquatic plants and in terrestrial leaves (Table 4). However, photosynthetic production in submerged aquatic macrophytes per unit biomass or surface area is usually lower than in terrestrial plants, as noted by Nielsen & Sand-Jensen (1989), because of the thinner leaves and thus lower chlorophyll content possessed by submerged plants. The chlorophyll content and chl *a*:chl *b* ratios presented in this paper for blade tissue of *H. wrightii* are in general agreement with results for a variety of seagrasses (Drew 1978, Wiginton & McMillan 1979, Dennison & Alberte 1982, Garcia et al. 1991, Zimmerman et al. 1991).

The measurements of photosynthetic production presented here provide a more realistic estimate of the *in situ* physiological light requirements for *Halodule wrightii*. *In situ* measurements are valuable because they take into account problems relating to self-shading (Pérez & Romero 1992) and natural variations in underwater irradiance. These estimates are useful in calculating net carbon balances under different light regimes and in theoretical calculations of the minimum daily quantum requirements of *H. wrightii* based on models that utilize parameters of H_{sat} and H_{comp}. Mean ratios of net photosynthesis to dark respiration (P_{net}:R), useful indicators of plant productivity (Bowes & Salvucci 1989), generally ranged from 2 to 4 for *H. wrightii*, slightly lower than blade P_{net}:R ratios reported for *Zostera marina* (Zimmerman et al. 1991). However, P_{net}:R values for *H. wrightii* include the respiratory demands of below-ground tissue as well as leaves. Based on our observations of the depth distribution and productivity of *H. wrightii* in Texas estuaries, the P vs I parameters derived from whole plant incubations are more realistic than laboratory-derived values and can be used reliably in models that address seagrass production and their minimum light requirements. However, uncertainty with respect to the carbon demands and role of below-ground tissue continue to compromise our ability to effectively manage seagrass populations that are increasingly subjected to chronic reductions in underwater light.

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