Field verification of a light-driven model of biomass changes in the seagrass *Halodule wrightii*

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ABSTRACT: Underwater irradiance has frequently been cited as one of the most important, if not dominant, factors that regulates the distribution and productivity of seagrasses. Here we test that hypothesis in the development of a model to predict changes in the biomass of the seagrass *Halodule wrightii* Aschers based on the assumption that light is the dominant factor affecting growth. The model is a time-dependent, mechanistic model developed from above- and below-ground mass-balance and based on data collected in the Upper Laguna Madre, Texas, over a period of 9 yr from 1989 to 1997; the data set is ideally suited to testing the assumptions of the model. The data include regular measurements of above- and below-ground biomass coupled with continuous monitoring of underwater irradiance. Although the Upper Laguna suffered from a persistent brown tide from the summer of 1990 through the spring of 1996, the model was successful in reproducing trends in the observed above- and below-ground biomass. In particular, it captured the rapid recovery of the below-ground biomass as the brown tide bloom declined during spring 1996. Since agreement between the model and data decreases over a period of about 1 yr, some simple data-assimilation techniques were incorporated to help improve model performance. Close agreement between our model and *in situ* biomass measurements of *H. wrightii* collected over a 9 yr period reflect the importance of underwater light intensity as a major abiotic factor regulating seagrass productivity. In addition, the success of the model in predicting both above- and below-ground biomass demonstrates the importance of including both compartments in whole-plant modeling efforts that can be applied to coastal management practices. The demonstrated validity of a predictive whole-plant model for seagrass biomass will provide a valuable tool in the successful management of seagrass resources in coastal areas threatened by decreases in water transparency from anthropogenic impacts.

KEY WORDS: Seagrass · *Halodule wrightii* · Growth model

INTRODUCTION

Seagrass meadows are found in many coastal areas around the world. They help stabilize sediments (Christiansen et al. 1981), provide nursery habitats for fishes (Orth et al. 1984) and contribute significantly to the primary production in coastal and estuarine environments. Seagrasses are regarded as being indicators of the health of coastal ecosystems (Dennison et al. 1993), and recent die-offs occurring throughout the world have caused concern (Robblee et al. 1991, Quammen & Onuf 1993).

About 80% of the 950 km^2 of seagrass meadows in Texas are found in the Laguna Madre (Pulich 1999). A loss of more than 140 km^2 of seagrasses from the Laguna since the 1960s has been attributed to decreases in water transparency arising from maintenance-dredging (Quammen & Onuf 1993, Onuf 1994) and the occurrence of brown tide (Onuf 1996). The loss of seagrasses in Galveston Bay has been partially linked to decreased light levels arising from dredging and eutrophication effects (Pulich & White 1991). Seagrass declines in Florida Bay have been variously attributed to increased eutrophication, reduced photosynthetic capability resulting from infection (Durako & Kuss 1994), stress resulting from increased salinity

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(Zieman et al. 1989) and increasing stagnation from the lack of major storms (Zieman et al. 1989). In many cases, determining the precise cause of the initial decline is hindered by the lack of data prior to and during the decline. Consequently there has been recent interest in using computer models to help identify the reasons for the die-offs and to assist in exploring measures to restore the system.

Several seagrass models already exist. These tend to concentrate on temperate species such as *Zostera marina* (Wetzel & Neckles 1986) and *Potamogeton perfoliatus* (Madden & Kemp 1996). Only 1 published model explicitly addresses the growth and biomass of *Halodule wrightii* (Fong & Harwell 1994, Fong et al. 1997). In general, the modeling of seagrasses presents some interesting challenges, since many of the processes critical to seagrass production ecology are poorly understood. Models that attempt to incorporate these processes often have to rely on semi-empirical formulations which can vary between species and geographical location. For example, the most complex model for *H. wrightii* is the one presented by Fong & Harwell 1994 and Fong et al. 1997). For that model, a semi-empirical relationship between productivity and biomass was developed which, for zero biomass, gives maximum productivity of the plants. Similar problems arise even in compiling the data that form the basis of these relationships. For example, Fong & Harwell (1994) were unable to find data with which they could form a relationship between productivity and temperature for either *H. wrightii* or *Syringodium filiforme*.

Light is foremost among the factors crucial to seagrass production and growth (Zieman & Wetzel 1980) and minimum light levels required to sustain various seagrass species have measured (Duarte 1991, Dunton 1994, Gallegos & Kenworthy 1996, Kenworthy & Fonseca 1996). Estimates of daily production derived from irradiance measurements have previously been made using the H_{sat} model (Dennison & Alberte 1982). This model, although providing an excellent index of daily production, is theoretically flawed (Richardson et al. 1983, Fourqurean & Zieman 1991, Henley 1993, Zimmerman et al. 1994), and would have to be linked to models that convert daily productivity into changes in above- and below-ground biomass. Other factors influencing seagrass growth and production include, for example, nutrient availability and uptake rates (Lee & Dunton 1999), sediment chemistry (Carlson et al. 1994) and disease (Durako & Kuss 1994). Detailed information for many of these is limited.

Even though light is the dominant factor, there are very few long-term measurements of irradiance within seagrass beds. Since 1989 a monotypic meadow of *Halodule wrightii* Aschers in Upper Laguna Madre has been continuously monitored, with regular measurements of above- and below-ground biomass and continuous measurements of underwater irradiance. Since June of 1990, the characteristically clear waters (Pulich 1980) of the Upper Laguna have been affected by a persistent brown tide. The brown tide alga *Aureoumbra lagunensis* (class Pelagophyceae), unknown prior to the summer of 1990, reached cell concentrations exceeding 10^6 ml^{-1} (DeYoe & Suttle 1994). Chlorophyll concentrations during the brown tide rarely fell below 20 mg l^{-1} and reached values as high as 90 mg l^{-1} (Stockwell et al. 1993). This has reduced light levels reaching the seagrass canopy; mean light transmission through the top 1 m of the water column dropped from 47% for the year preceding the brown tide to 19% during its first year (Onuf 1996). Dunton (1996) estimated the minimum light requirements for *H. wrightii* in the Laguna Madre as being 18% of surface irradiance (SI); Kenworthy & Fonseca (1996) estimated the minimum light requirement for *H. wrightii* to lie between 14 and 27% SI (once correction was made for the fact that they measured SI just beneath the water surface). These values are similar to those estimates made by Dunton (1994) based on the significant impact of the brown tide on seagrass growth and production.

Data assimilation is being increasingly used in oceanographic, meterological and marine ecosystem models (Lawson et al. 1995, 1996, Anderson et al. 1996, Vallino 2000). Such techniques can be used to estimate the values of parameters in the model as well as to improve the model's short-term predictive capability. In the former case, model parameters are adjusted until satisfactory agreement is achieved between model results and observations. Differences between model results and observed time-series often increase if the model is run for long periods of time. This can be countered by periodically reinitializing the model using data values, forcing the model back into agreement with the data.

Here, we report on the development of a mathematical model for the growth and biomass of *Halodule wrightii*. There are many approaches to formulating a mathematical model. One is to include as many relevant processes as possible (see Fong & Harwell 1994, Madden & Kemp 1996, Short 1980); this approach is well-suited to data-rich systems such as the Chesapeake Bay (Madden & Kemp 1996). More commonly, it is often better to develop a model that concentrates on only a few dominant processes. We have followed the latter approach. Such a model has the advantage of making it easier to see where the model can be improved and where there are gaps in our knowledge and understanding. Close collaboration between field scientists and modelers can then proceed to help fill these gaps.

The model of *Halodule wrightii* presented here fills a gap in existing models in that it is a whole-plant approach; changes in below-ground biomass are explicitly included. A crucial assumption in the formulation of the model is that light is the dominant factor determining production and growth of the whole plant. The long-term time-series of biomass and irradiance measurements allow us to both test and validate this assumption. Development of the model will also help identify avenues of research important to further development of seagrass models.

METHODS

Data collection. Measurements of plant biomass and underwater irradiance were made at Site LM-151 (27° 21' N, 97° 22' W) in the Laguna Madre, Texas, USA (Fig. 1). Plant biomass samples were collected at 1 to 3 mo intervals from May 1989 to September 1997. Sampling was conducted within a monotypic stand of *Halodule wrightii* Aschers at a depth of 1.3 m.

Estimates of plant biomass were made following the procedures outlined in Dunton (1990, 1994). During each trip, 4 replicate samples were collected using a 9 cm coring device. Samples were thoroughly cleaned of any sediment and other material and separated into

Fig. 1. Location of sampling site (LM-151) situated in the Upper Laguna Madre, Texas, between Corpus Christi Bay and Baffin Bay

above- and below-ground live biomass. For consistency and to avoid uncertainty with respect to the location of plant tissues at the dynamic sediment-water interface, above-ground biomass is defined to include only green-pigmented tissues. This would include all leaf tissues, but excludes horizontal and vertical rhizomes and roots which are not pigmented and normally buried in the sediment. Separation of live and dead material was based on obvious differences in color, buoyancy, and texture of the tissues. The sorted material was dried at 60°C to a constant weight and the results expressed as above- and below-ground biomass (g dry wt m^{-2}) collected in each core.

Measurements of photosynthetically active radiation (PAR) (400 to 700 nm) at the canopy level were collected continuously using a LI-193SA spherical (4π) quantum sensor that provided input to a LI-1000 data-logger (Li-Cor Inc., Lincoln, Nebraska, USA). The data-logger was enclosed in a weighted, clear polycarbonate housing (Ikelite Model 5910, Indianapolis, Indiana, USA) and connected to the sensor cable using a moulded underwater connector (Crouse-Hinds Series 41 Penetrator, La Grange, North Carolina, USA). Stainless-steel bands were used to secure the lid, and the housing was placed within a plastic bag and buried in the seabed to reduce both corrosion and the likelihood of discovery by fishermen. The data-logger was serviced at 2 to 3 mo intervals. The sensor itself was mounted at canopy level (15 to 20 cm above the bottom) on a 3 cm PVC pipe to minimize fouling by drift algae and seagrass leaves. The sensor was cleaned regularly (1 to 3 wk intervals), although fouling was minimal because the brown tide bloom greatly reduced the colonization of fouling organisms due to the persistent low light levels and its high density (1 million cells ml^{-1}; DeYoe & Suttle 1994).

Several gaps, sometimes several days in length, were present in the light record. It is impossible to accurately recover the values of the missing data. The data gaps were filled by first identifying the gap, and then filling it with a data record of the same length taken from the data directly before the gap occurred. Assuming that the statistics of the light field do not change appreciably over time scales of a few days, this procedure will fill the gaps with reasonable values.

The model. The model combines simplicity with the assumption that light is the main factor affecting seagrass growth. Hence, carbon was used as the currency for the model and PAR was the only forcing function. Two compartments were used, one for above-ground biomass and the other for below-ground biomass with transport of material from the above- to the below-ground tissue. Since nutrient uptake was not included, the below-ground compartment was used only for storage. Both above- and below-ground compartments were affected by structural loss and respiration.
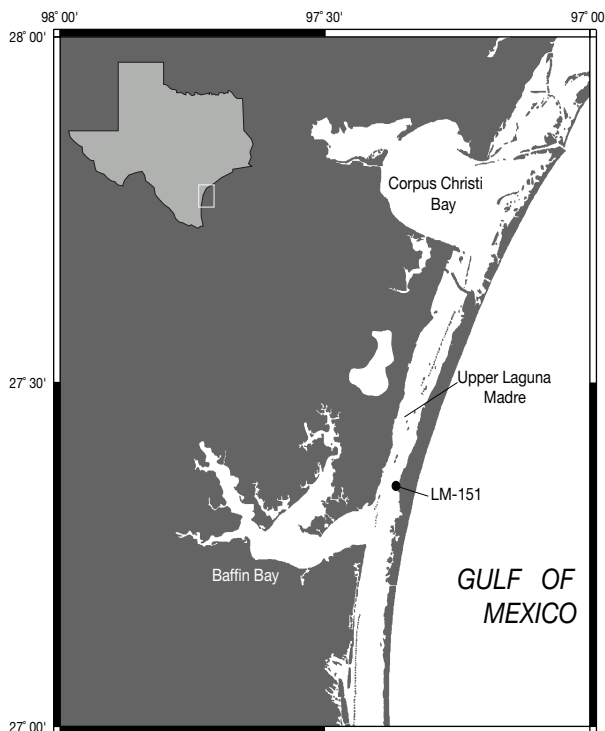
The model uses several parameters (e.g., carrying capacity) whose values are unknown. These were obtained by a least-squares technique using model results and the observed biomass and underwater irradiance measurements from 1989; this year was chosen since it was before the brown tide was observed in Laguna Madre. Both 1996 and 1997 were characterized by low concentrations of brown tide, but these years also represent a period of recovery from prolonged light limitation.

Underwater irradiance measured at canopy level was used in both the development and calibration of the model. For simulations where model results were compared to field observations of biomass, measured *in situ* light data were used. Additional simulations were made using a synthetic annual light cycle in which the SI on a given day was calculated by averaging data from a time-series of SI measured in the Laguna Madre between August 1994 and February 1997. Values for the same time on the same Julian day each year were averaged to produce a time-series of 1 yr in length. Because of the non-integer number of years in the original time-series and the fact that some days had some data missing, each average was from between 2 and 4 data values. Light irradiance at the plant canopy level was calculated using Beer's law:

$$I(z) = I(0) \exp(-kz) \qquad (1)$$

where $I(0)$ is the SI, $I(z)$ the irradiance at depth z within the water column, and k is the attenuation coefficient whose value was chosen for each particular simulation. Effects of scattering at the air-water interface were taken into account assuming a flat interface and using Fresnel's equations (Kirk 1994). The specific gross production (P) at irradiance I was then calculated using a Jassby-Platt parameterization (Jassby & Platt 1976):

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

Table 1. Parameter values used in the model. Production and respiration values were converted from oxygen to carbon assuming photosynthetic and respiration efficiencies of 1. Values for structural loss were determined from personal observation in the field. See 'Methods' and Table 3 for explanations of the parameters

Parameter	Value	Source
$P_{\max}$	422 mmol O_2 g dry wt^{-1} h^{-1}	Dunton (1996)
I_k	319 mmol m^{-2} s^{-1}	Dunton (1996)
R_a	41.5 mmol O_2 g dry wt^{-1} h^{-1}	Dunton & Tomasko (1994)
R_b	16.1 mmol O_2 g dry wt^{-1} h^{-1}	Dunton & Tomasko (1994)
M_a	0.004 d^{-1}	
M_b	0.0004 d^{-1}	

where I_k is the saturation irradiance and $P_{\max}$ the maximum specific production. Values for $P_{\max}$ and I_k were obtained from measurements made within the Laguna Madre (Dunton & Tomasko 1994), and are shown in Table 1 with other parameters used in the simulations. Self-shading within the plant canopy limits the total amount of production at high shoot densities. This was modeled using a logistic function to modify Eq. (2) to give

$$P(I,C_a) = P_{\max} \tanh\left(\frac{I}{I_k}\right)\left(1 - \frac{C_a}{\kappa}\right) \qquad (3)$$

where C_a is the above-ground biomass. The parameter κ is the carrying capacity of the canopy and was determined using a least-squares technique as described above.

Sinks of carbon within a unit area of seagrass bed include respiration, leaf loss, mortality of above- and below-ground material, grazing etc. Measurements were available for plant respiration (see R_a, R_b in Table 1). All other loss rates were combined into 'structural loss'. Both respiration and structural loss for both the above- and below-ground compartments were assumed to depend linearly on the biomass of each compartment. For example, above-ground respiration and structural-loss rates had the forms $R_a C_a$ and $M_a C_a$ respectively. Values that were used for the respiration rates (R_a and R_b) and specific structural-loss rates (M_a and M_b), are shown in Table 1.

Temperature can significantly affect the rates of physiological processes such as photosynthesis and respiration (Thornley & Johnson 1990). The water column was assumed to be well mixed, with a temperature, T, at time t determined from:

$$T(t) = 21.0 + 9.0 \sin\left(\frac{2\pi t}{365} - \frac{\pi}{2}\right) \qquad (4)$$

This expression was obtained by fitting a sine function to data taken from Lower Laguna Madre (Brown 1997). Photosynthetic parameters and respiration rates for *Halodule wrightii* have been measured over a range of temperatures, both in the laboratory and *in situ* (Dunton & Tomasko 1994). Comparisons between *in situ* and laboratory measurements for *Thalassia testudinum* showed that *in situ* whole-plant production measurements are more reliable than laboratory measurements (Herzka & Dunton 1997). Unfortunately, *in situ* measurements for *H. wrightii* show considerable variability. For example, estimates of $P_{\max}$ at 22°C can be 5 times greater than those measured at 30°C (Dunton 1996). Consequently, we modeled the temperature dependence of production and respiration using an Ahrrenius formulation (Thornley & Johnson 1990):
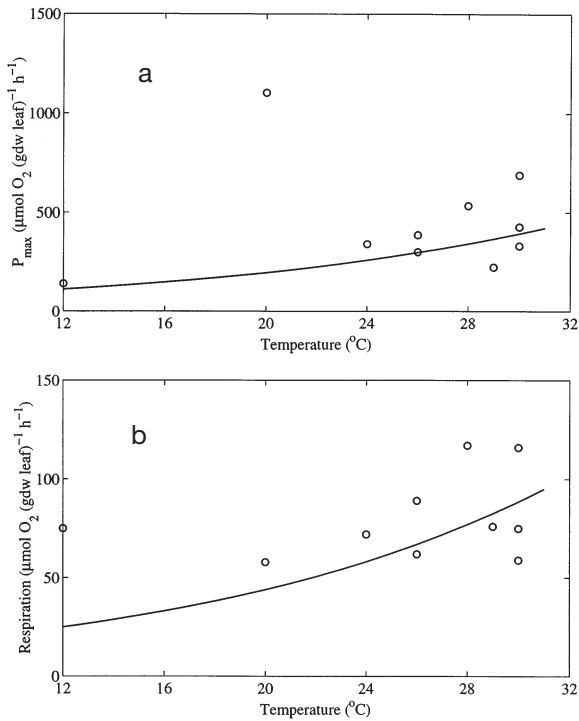
Fig. 2. Comparison of observed and theoretical changes of maximum gross production (P_{max}) and respiration with changing temperature. (O) Data from Dunton & Tomasko (1994); line: model formulation based on the Ahrrenius formulation

$$\Gamma(T) = \Gamma_0 \exp\{\zeta[T(t) - T_0]\} = \Gamma_0 \exp(\zeta \Delta T) \quad (5)$$

where Γ is the physiological parameter of interest (e.g., respiration), T is the temperature and Γ_0 is the value of Γ measured at temperature T_0 (in this case 31°C). In this study, the parameter $\zeta = 0.07$ was chosen such that $Q_{10} = 2$, a value typical of marine organisms (Valiela 1995). With the exception of an outlier (a high P_{max} at 22°C), there is generally good agreement between the data collected by Dunton & Tomasko (1994) and the Ahrrenius formulation (Fig. 2).

The below-ground biomass of *Halodule wrightii* can account for as much as 60 to 80% of the total plant biomass (Dunton 1996). This below-ground material is supported by photosynthetically produced carbon (Smith et al. 1984, Caffrey & Kemp 1991, Ralph et al. 1992) which is stored in the rhizome and used to maintain the plant during periods of low photosynthetic production (Pirc 1989, Lee & Dunton 1996). Little is known about how seagrasses allocate resources, although carbon is stored in the rhizomes as carbohydrates (Pirc 1985, Dawes & Guiry 1992). Transport of material occurs both vertically between leaves and rhizomes (Dawes & Lawrence 1979, 1980, Pirc 1985, Dawes & Guiry 1992, Lee & Dunton 1996, 1999) and horizontally along the ramet (Lee & Dunton 1999). In

Table 2. Values of the 3 parameters obtained by calibration of the model with observational data for the year 1989. See 'Methods' and Table 3 for explanations of the parameters

Parameter	Value
κ	667.0 g dry wt m^{-2}
τ	0.34
δ	0.001

the simple model used here, only transport from the above- to the below-ground component is considered. Various formulations for transport in both directions were examined, but only the simple model used here resulted in convergence between the data and the model results. The formulation we used assumes that transport is proportional to the gross production of the plant

$$\text{Transport} = \tau P(I, C_a) \quad (6)$$

The value of τ obtained from model calibration is given in Table 2.

Seagrasses release dissolved organic carbon (DOC) into the sediments (Moriarty et al. 1986) and this can provide an additional loss of carbon from the plant. For the sake of simplicity, we again assumed that the rate of DOC loss was proportional to gross production with a proportionality factor δ determined from model calibration (see Table 2).

The resulting equations determining the evolution of the above-ground (C_a) and below-ground (C_b) biomass were

$$\frac{dC_a}{dt} = (1 - \tau)P(I)e^{k\Delta T}C_a\left(1 - \frac{C_a}{\kappa}\right) - R_a e^{k\Delta T}C_a - M_a C_a \quad (7)$$

$$\frac{dC_b}{dt} = (\tau - \delta)P(I)e^{k\Delta T}C_a\left(1 - \frac{C_a}{\kappa}\right) - R_b e^{k\Delta T}C_b - M_b C_b \quad (8)$$

The model was programmed using Matlab (Matlab is a trademark of The Mathworks Inc. Natick, MA) and run on a Digital Alpha UNIX workstation. Several parameters (τ, κ and δ) whose values are unknown are used in the model. These were obtained using the constrained nonlinear optimization routine contained in the Matlab optimization toolbox[1], using model results and the observed biomass and underwater irradiance measurements from 1989, before the brown tide was observed in Laguna Madre. The bloom abated in 1996 and 1997, allowing the plants to recover from prolonged light-limitation. The results of

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[1]The optimization routine used a sequential quadratic programming method in which estimates of the Hessian and Lagrangian were updated at each iteration (Grace 1993)

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Table 3. Symbols and parameters used in present study

Symbol	Parameter	Measure
t	Time	d
I_0	SI	μmol m^{-2} s^{-1}
$I(z)$	Irradiance at depth z	μmol m^{-2} s^{-1}
z	Water depth	m
k	Water column attenuation	m^{-1}
ζ	Parameter in temperature relation	
P	Gross production	μmol O$_2$ g^{-1} dry wt h^{-1}
P_{max}	Maximum gross production	μmol O$_2$ g^{-1} dry wt h^{-1}
I_k	Saturation irradiance	μmol m^{-2} s^{-1}
C_a	Above-ground biomass	g dry wt m^{-2}
C_b	Below-ground biomass	g dry wt m^{-2}
κ	Carrying capacity	g dry wt m^{-2}
T	Temperature	°C
R_a	Above-ground respiration	μmol O$_2$ g^{-1} dry wt h^{-1}
R_b	Below-ground respiration	μmol O$_2$ g^{-1} dry wt h^{-1}
M_a	Above-ground mortality	d^{-1}
M_b	Below-ground mortality	d^{-1}
δ	DOC release	As fraction of production

this model calibration are shown in Table 2. Once calibrated, the model was run both with and without the assimilation of field biomass data to reset the model at the beginning of each 1 yr simulation. When run without data assimilation, the differential equations (Eqs. 7 & 8) were solved using initial conditions for C_a and C_b and underwater irradiance as the sole forcing function.

Simple data-assimilation techniques were used to minimize drift between model results and observations. To do this, the model was started as before, solving Eqs. (7) & (8) using the same initial conditions for C_a and C_b and forcing the model with the observed underwater irradiance. The equations were integrated for a 1 yr simulation period; C_a and C_b were then re-initialized using the first observed values of that year. The equations were again integrated for 1 yr and the process repeated. Table 3 summarizes the symbols and parameters used.

RESULTS

Field data and model calibration

The underwater irradiance (Fig. 3) showed a strong seasonal signal as well as a decline from 1990 through
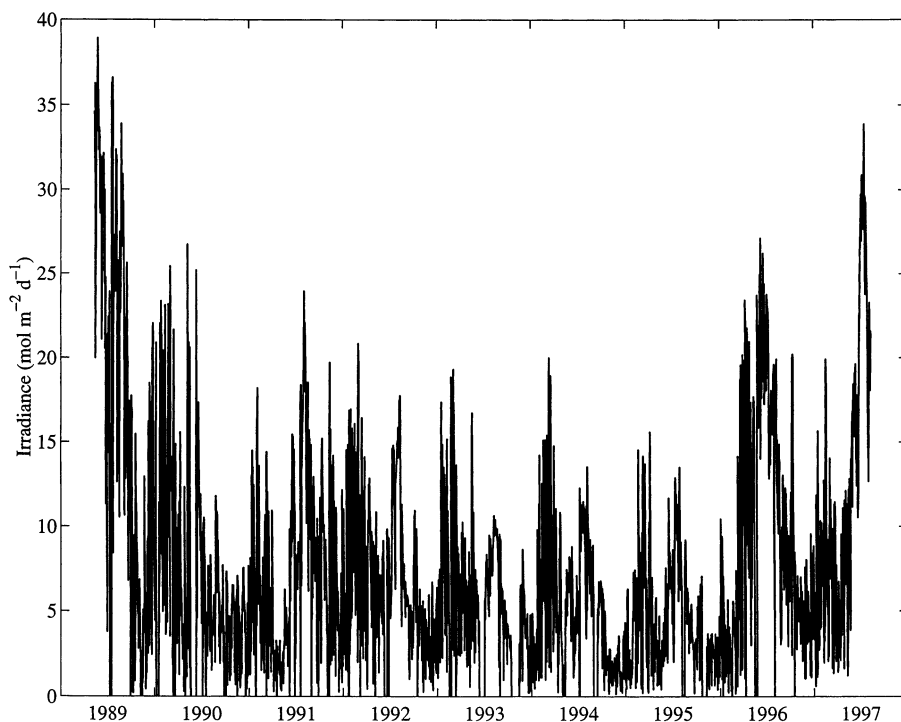

Fig. 3. Daily irradiance (PAR, mol photons) measured at the canopy level at Site LM-151 from May 1989 through August 1997. A long-lived brown tide algal bloom resulted in lowered irradiances from 1990 through 1995
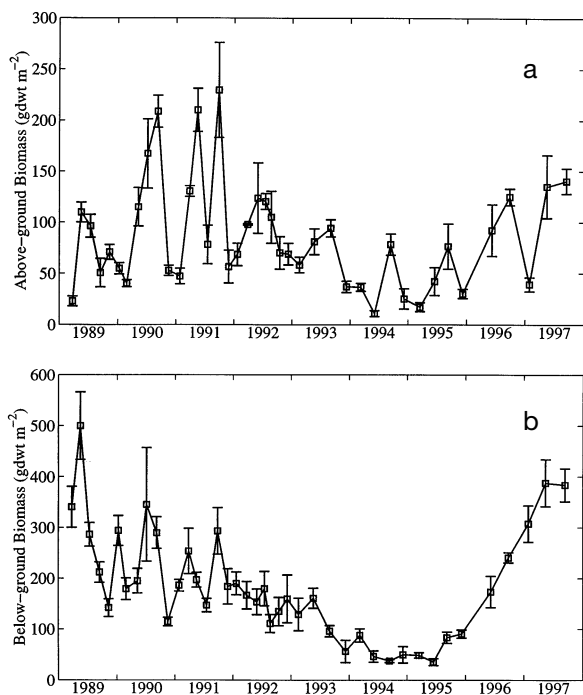
Fig. 4. *Halodule wrightii.* Biomass at Site LM-151 between March 1989 and September 1997. Error bars: ±SE. Both (a) above- and (b) below-ground biomass showed declines attributed to decreased light levels; the below-ground biomass showed a faster recovery than the above-ground biomass as the brown tide decreased in 1995

1995 as a result of the brown tide. In 1989, 1 yr before the brown tide bloom began, underwater irradiance peaked at 38.9 mol photons m^{-2} d^{-1}. During the brown tide, peak irradiances fell steadily, reaching a minimum of 15.6 mol photons m^{-2} d^{-1} in 1995. By late 1997, following abatement of the bloom, values as high as 33.8 mol photons m^{-2} d^{-1} were recorded. Abatement began in winter 1995/1996, as reflected in the subsequent 18 mo period in which canopy-level irradiances were comparable to those before the onset of the brown tide.

The above- (Fig. 4a) and below-ground biomass (Fig. 4b) of *Halodule wrightii* also showed both a seasonal cycle and a decline. The above-ground biomass first showed the effect of reduced irradiance between 1991 and 1992, when the peak biomass dropped from 229 to 124 g dry wt m^{-2}. The maximum annual above-ground biomass continued to decline, reaching a minimum of 76 g dry wt m^{-2} in 1995 before returning to values similar those seen in 1989. The below-ground biomass followed a slightly different pattern, with a continuous decline from a maximum of 500 g dry wt m^{-2} in 1989 to 90 g dry wt m^{-2} in 1995. In 1996 and 1997, the below-ground biomass recovered rapidly, reaching a peak of 387 g dry wt m^{-2} in 1997. The total plant biomass behaved in a manner similar to the

below-ground material, with a peak value of 610 g dry wt m^{-2} in 1989 followed by a steady decline to a maximum of 166 g dry wt m^{-2} in 1995.

After calibration, the model was run while being forced with the observed underwater irradiance for the years 1990 to 1997 (Fig. 3). Above- and below-ground biomasses measured in January of 1990 were used as initial values for the model. The model results showed a clear seasonal signal and tracked the decline of both the above- (Fig. 5a) and below- (Fig. 5b) ground biomass between 1992 and 1996.

Three separate periods were apparent when the model results did not agree well with observed biomass. For the first 2 yr (1990 and 1991) the model under-predicted both the above- and below-ground biomass. The model did not replicate the variation that is seen in the measured above-ground values. For example, towards the end of 1990, the observed biomass dropped from over 200 g dry wt m^{-2} to approximately 50 g dry wt m^{-2} (Fig. 5a), whereas the peak in the model results was approximately 120 g dry wt m^{-2}. The measured below-ground values showed a similar variation to those above-ground, but these were also not reflected in the model results. Instead, the below-ground model results showed a steady decline from 300 to approximately 100 g dry wt m^{-2}.

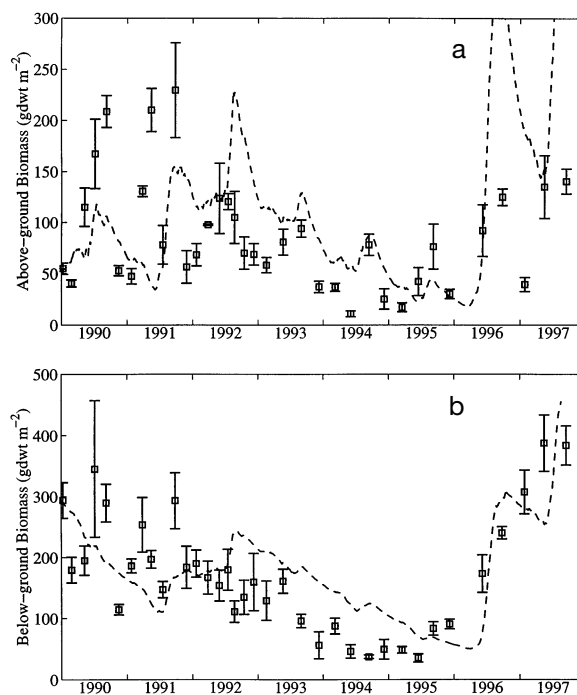Observed and simulated biomass were in better agreement between 1992 and 1995. During this period,

Fig. 5. *Halodule wrightii.* Comparison between observation (□, ±SE) and model (dashed line) output of (a) above- and (b) below-ground biomass over the period 1990 to 1997
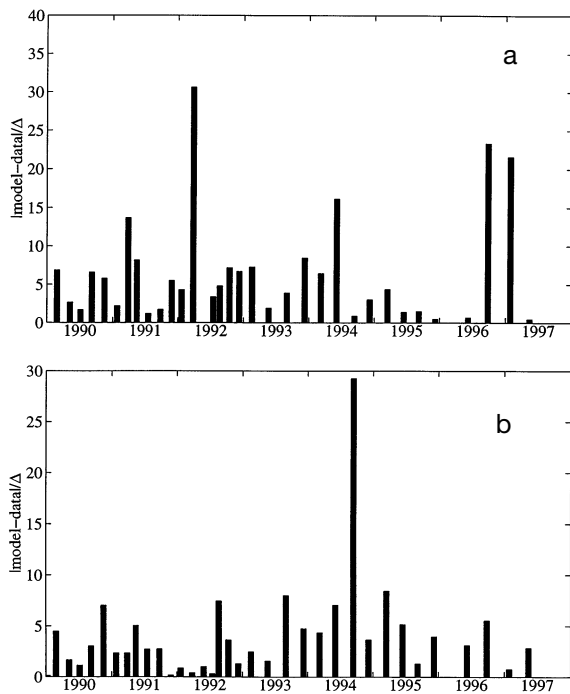
Fig. 6. *Halodule wrightii.* Absolute value of the residuals between the model and data normalized to the standard error of each data point (a) above- and (b) below-ground. Each bar on the plot shows how close the modeled biomass is to the measured value in units of the standard error of that measurement

the reduced irradiances resulting from the brown tide were having an apparent impact on the seagrass. The model generally over-predicted both above- and below-ground biomass, but tracked the rate of biomass decline well. The recovery of the below-ground biomass in 1996 and 1997 was also captured accurately by the model (Fig. 5b). However, the model strongly over-predicted the above-ground biomass during the same period (Fig. 5a).

Agreement between the model and the observations are variable but reasonably acceptable, with some notable exceptions (Fig. 6). The largest peaks (e.g., 1992: Fig. 6a) correspond to those points that have very small standard errors (cf. Fig. 5a). On the whole, the model appears to predict above- and below-ground biomass to within 5 to 7 SE.

Model sensitivity: initial conditions and minimal light requirements

Incorporating data assimilation into the model by using measured biomass to re-initialize the model at the start of each year greatly improved the agreement between model results and data (Fig. 7). Again, the

same 3 time periods are apparent. Sudden jumps or discontinuities are evident in the model results (e.g., between 1992 and 1993). These are artifacts of re-initializing the model biomass at the start of each year. In 1990, the model results were identical to those without data assimilation (Fig. 5) since both models used the same initial conditions.

Differences between model results for which data assimilation was and was not used become apparent in 1991. The former produced lower above-ground bio-mass which better tracked the observed values. Agreement with below-ground biomass data was also improved (e.g., cf. Figs. 5 & 7). In addition, the use of data assimilation reduces the residuals, especially for the period 1992 to 1997 (e.g., cf. Figs. 6 & 8).

The minimum light requirements for *Halodule wrightii* were estimated by running the model for 1 yr using different, constant light-attenuation coefficients and forcing the model using the surface light (Fig. 9). If *H. wrightii* received only 10% SI throughout the year, plant biomass rapidly decreased (Fig. 10). For 15% SI, there was some gain in biomass during the summer, but plant biomass at the end of the year was lower than at the start of the year. The results for 20% SI were
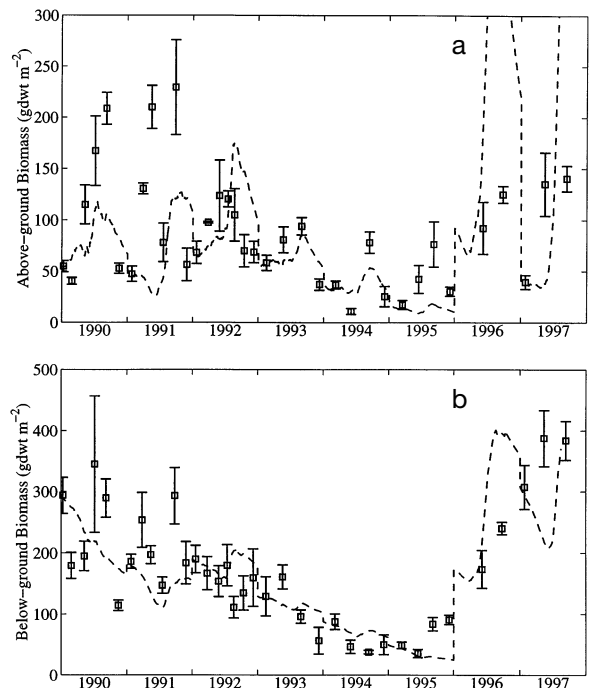

Fig. 7. *Halodule wrightii.* Comparison between observation (□, ±SE) and model (dashed line) output of (a) above- and (b) below-ground biomass over the period 1990 to 1997. This model differs from that in Fig. 5 in that data-assimilation techniques have been incorporated into the model. Comparison with Fig. 5 shows better agreement between the Fig. 7 model and data, especially for the period 1992 to 1995

similar to those for 15 % SI, except that there was a slight net increase in biomass during the course of the year. This indicates that the minimum light requirement for *H. wrightii* lies between 15 and 20 % SI, in
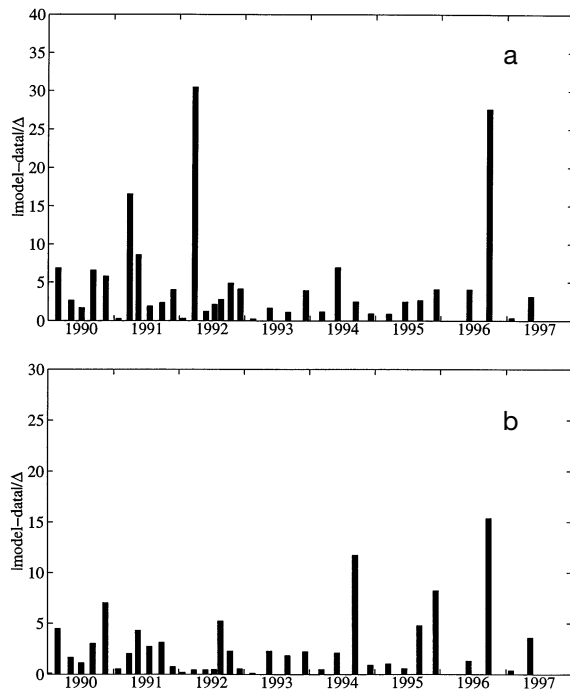

Fig. 8. *Halodule wrightii.* Absolute value of the residuals between the model with data-assimilation and data normalized to the standard error of each data point (a) above- and (b) below-ground
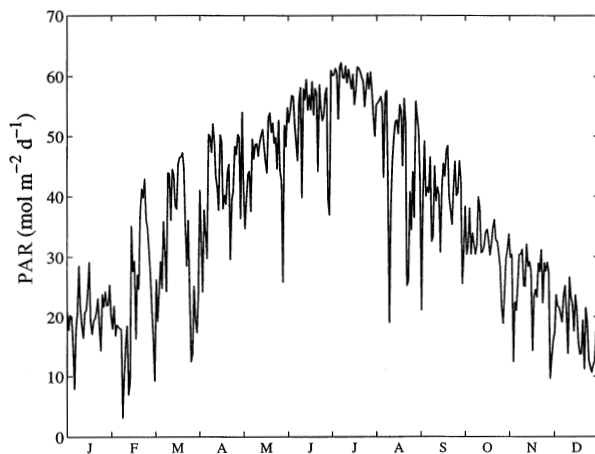

Fig. 9. *Halodule wrightii.* Daily SI (PAR, mol photons) for 1 yr. Data are a composite of surface irradiances measured in Lower Laguna Madre between August 1994 and February 1997. Values were obtained by averaging data measured on the same day from each year. Missing data were not replaced, so the number of data values used for each average varied
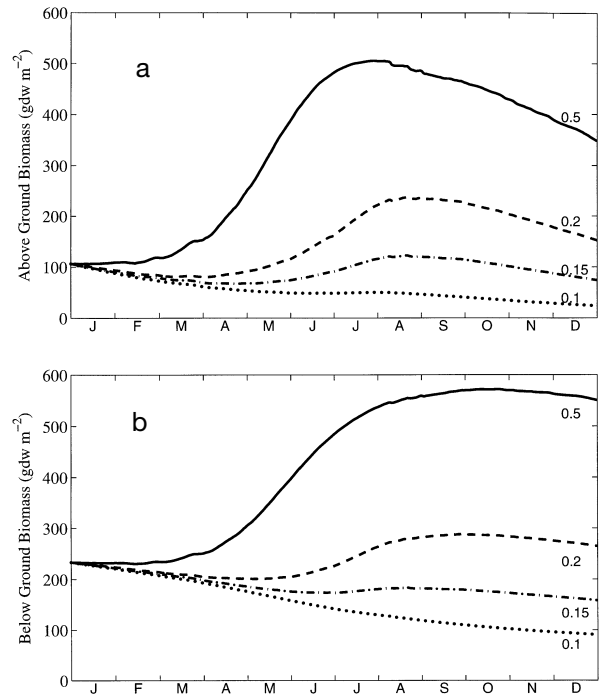

Fig. 10. *Halodule wrightii.* Light requirements for growth. Biomass modeled (a) above- and (b) below-ground obtained using various fractions of surface irradiance (SI): continuous line = 50 % (k = 0.46) SI at canopy level; dashed line = 20 % (k = 1.07) SI at canopy level; dash-dotted line = 15 % (k = 1.26) SI at canopy level; dotted line = 10 % (k = 1.54) SI at canopy level

agreement with previous observations for *H. wrightii* in Laguna Madre (Dunton 1994, 1996, Onuf 1996). The case for 50 % SI is shown for comparison in Fig. 10.

DISCUSSION

Model validity and overall performance

The model we have presented is based on the assumption that light is the dominant factor determining seagrass growth and production (Zieman 1980). Given this, the model shows good agreement with the observed above- and below-ground biomasses during the period 1990 to 1997 (Fig. 5). PAR was used as the sole environmental forcing. However Zimmerman & Mobley (1997) have put forward persuasive arguments that light 'quality' (i.e., spectral information) is also important for seagrass health. In particular, models based solely on PAR predict higher production than spectral models, particularly for high concentrations of water-column chlorophyll (P. Eldridge pers. comm), because both phytoplankton and seagrasses make use of the same region of the light spectrum. Unfortunately very little information is available for the spectral ab-

sorbance properties of seagrass leaves, making a full
spectral model difficult to implement at this time. In
addition, such a model would require spectral ab-
sorbance characteristics of the suspended material in
the water column. Some progress has been made
towards developing such a model by calibrating stan-
dard parameterizations for the spectral attenuation
coefficients for a particular region (Gallegos & Ken-
worthy 1996).

The model does not uniformly over-predict or under-
predict the observed biomass (Fig. 5). During the early
part of the simulation (1990 and 1991), the model
under-predicts both the above- and below-ground bio-
mass; during the later part (1996 and 1997), the model
over-predicts the above-ground biomass; during the
central part of the simulation (1992 to 1995), the model
over-predicts both above- and below-ground biomass.
This variation in model performance suggests that
some or all of the parameters held constant throughout
the simulations may in fact vary with time. The lack of
variation in these parameters will be partly compen-
sated for in the values of τ, δ and κ obtained from opti-
mization. This is because the model will not reproduce
changes in biomass arising from changes in P_{max} and
I_k. Thus, any such changes in biomass can contribute
to the determination of values for the other parameters.

One dramatic feature of the observed biomass is the
rapid recovery of the below-ground biomass as the
brown tide decreased in 1995 and 1996. The model
captures this, but over-predicts the recovery in the
above-ground biomass (Fig. 5a). Given the fact that the
model was calibrated using data only from 1989, it is
encouraging to see agreement between the model and
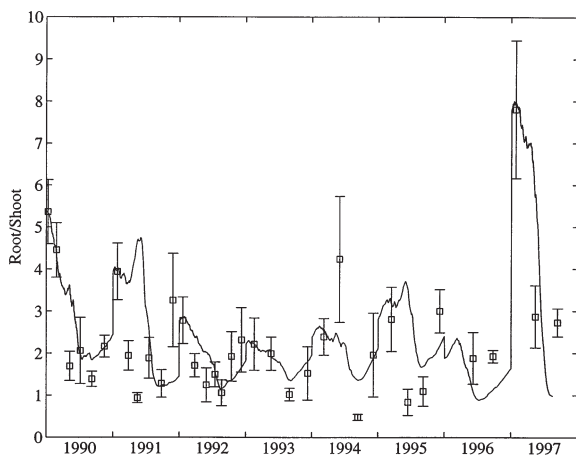field data for the increase in below-ground biomass.

Fig. 11. Ratio of below- to above-ground (Root/Shoot) biomass
for the observations (□) and the model results with data as-
similation (line). Error bars represent standard errors derived
from those of the biomass measured above- and below-
ground, calculated using standard propagation of errors

The over-prediction of the above-ground biomass is
troublesome, and may be the result of several factors.
One is the fact that, as mentioned above, the photosyn-
thetic and respiration parameters were taken as con-
stants.

Data-assimilation techniques have been used in this
to work both estimate the values of certain parameters
(Table 2) and to improve the predictive capabilities of
the model (Fig. 7). Using data assimilation to calibrate
a model requires a large amount of high-quality data
in a model that accurately reflects the mechanics of
the system being studied. Considerable care must be
taken, since different optimization techniques can pro-
duce very different parameter values (Vallino 1998).
This emphasizes the need for modeling and field pro-
grams that are complementary.

We also used data assimilation to help improve the
predictive capabilities of the model. The method of re-
initializing the model every year was crude. Without
data assimilation, the simulation results diverge from
the observations (Fig. 5). With data assimilation, how-
ever, the model is periodically brought back into step
with the data (Fig. 7). It appears from Fig. 7 that the
model drifts from the observed results after a period of
≤1 yr, that this is the period over which the model most
accurately predicts the observed biomass.

Much of the biomass of *Halodule wrightii* lies below
ground and is in a dynamic state. The ratio of below
to above-ground biomass provides an indicator of
the resource allocation of the plant. The model
with data assimilation reproduces the observed ratio
well (Fig. 11). This would indicate that even though a
crude model of resource allocation has been used,
when combined with a data-assimilation technique, a
reasonable prediction of the resource allocation can
be made.

The model is successful in predicting observed
changes in above- and below-ground biomass over the
course of a year using observed light data. This sug-
gests that the model can be used to examine the effects
of idealized changes in light using the synthetic SI and
imposed values of the attenuation coefficient *k*. Sea-
grasses require a minimum level of light for mainte-
nance and growth (Duarte 1991). For *Halodule wrightii*
this has been estimated from field work as lying
between 15 and 18% of SI (Dunton 1996, Kenworthy &
Fonseca 1996). The model predicts a similar range
(Fig. 10); however this was produced by assuming that
light attenuation (*k*) in the water column was constant
throughout the year. In reality, average monthly values
for *k* fluctuated, and in the Upper Laguna Madre lay
between approximately 0.2 m^{-1} and 2 between 1989
and 1993.

The calibration of the model produced values
(Table 2) for the carrying capacity (κ), transport rate

from above- to below-ground tissues (τ) and the rate of exudation of DOC (δ). The carrying capacity ($\kappa = 667$ g dry wt m^{-2}) is larger than the maximum above-ground biomass observed (approximately 250 g dry wt m^{-2}). However, the model is driven entirely by light and there are many other factors (e.g., nutrient uptake) that can affect the total biomass an area can sustain. It is possible however that this high value for the carrying capacity explains in part the high values for the modeled above-ground biomass in 1996 and 1997.

How long can *Halodule wrightii* tolerate chronic levels of low light? No changes in seagrass distribution were detected in the Upper Laguna Madre between surveys made in 1988 and 1992 (Onuf 1996), but between 1992 and 1995 more than 9.4 km^2 of seagrass vegetation had been lost at depths >1.4 m. At depths <1.4 m, biomass decreased substantially and the plants relied heavily on stored carbon reserves (Dunton 1994). When the brown tide declined in 1996 and 1997, *H. wrightii* was able to recover quickly. This is especially true of the below-ground biomass, which returned to almost pre-brown tide levels within 18 mo.

Toward a whole-plant model: resource allocation and carbon sinks

The ability of *Halodule wrightii* to respond rapidly to favorable light levels may help it survive periods of low light levels. Even though average light levels dropped as low as 9% SI during the brown tide, there were periods where as much as 50% SI reached the bottom (Dunton 1994, Onuf 1996). During the early period of the brown tide, the seagrass presumably used previously stored material for maintenance (Dunton 1994). As this material was depleted, the plants would find it harder to survive. If the rapid increase in below-ground biomass seen at the end of the brown tide is indicative of an allocation strategy of the plant, then the plant may be able to use short periods of high light to replenish these reserves, allowing it to survive longer at low average light levels.

Photosynthesis in seagrass leaves must support not only the leaf tissue but also considerable non-photosynthetic below-ground biomass. Therefore, the plant must be able to transport carbon from the leaves to the roots and rhizomes. Measurements of translocation for *Halodule wrightii* are scant and varied. For example, Moriarty et al. (1986) found that under optimal irradiance, 6 to 26% of the carbon fixed by the leaves had been translocated to the below-ground tissues after 3 h. After 4 h, 7% had been translocated, and after 6 h the proportion had risen to 28%. These values should be compared with the value we obtained for transport between above- and below-ground material. The cali-

bration of the model produces a value of $\tau = 34\%$ of gross primary production. This value is higher than that seen in the experiments, but represents transport in only 1 direction, rather than the net transport to below-ground material that was measured by Moriarty et al. (1986). In addition to vertical transport, translocation will also occur horizontally. Terrados et al. (1997) estimated that growth at the apical meristem of a *Cymodocea nodosa* rhizome was supported by resources originating from shoots further than 50 cm from the growth site. So, to properly represent the dynamics of carbon (and nutrients) within the plant, models of seagrasses must include translocation of resources to adequately account for the use of the plants resources. Some success has been achieved in modeling transport in terrestrial plants (Wilson 1988). These models often require a good knowledge of carbon and nitrogen dynamics in the plant as well as a parameterization of flow resistances.

The 1-directional linear model of transport we have used is obviously a major simplification. Although transport from above- to below-ground tissue is considered, flow in the opposite direction is not. Consequently, the model does not allow for the usage of material stored in the rhizome to supplement photosynthetically produced carbon during times of low irradiance. The model assumes that transport occurs only from the above- to the below-ground tissue. This is obviously unrealistic. Seagrasses can use material stored in the rhizome during periods of stress. For example, rhizome carbohydrate concentrations in *Thalassia testudinum* increase during the summer and decrease during the winter and spring (Lee & Dunton 1996). The summer increase has been attributed to production and storage of starch, while the decreases have been linked to utilization of these reserves for maintenance and growth (Dawes & Lawrence 1980, Lee & Dunton 1996). One might suspect that this would cause the model to predict a more rapid decrease in biomass when PAR is low. However, the simulations do not seem to indicate this (Fig. 5). A possible reason is that this loss of carbon is being counterbalanced in the model by an overproduction arising from using PAR instead of a spectral model.

The exudation of DOC from the below-ground tissue was also determined during the calibration of the model. This value ($\delta = 0.001$) is much lower than that observed by Moriarty et al. (1986), indicating that further development of the model is required in this area. In oligotrophic environments, seagrasses appear to compensate for nutrient limitation by increasing root surface area to facilitate nutrient uptake (Lee & Dunton 1999). Evidence for significant release of DOC by below-ground tissues was demonstrated by Ziegler & Benner (1998) in the Lower Laguna Madre. They noted

that the heterotrophic activity of the water column was fueled by release of DOC from seagrass-dominated sediments. These observations also agree with those of Lee & Dunton (1999), who found that over 50% of the nitrogen taken-up by *Thalassia testudinum* was re-released by the plant. The excess carbon predicted in our model may reflect our underestimate of below-ground tissue exudation of DOC into sediments, which appears to be significant. Consequently, this model provides the framework for combining hypothetical models with experimental work that can contribute to our overall understanding of seagrass productivity.

CONCLUSIONS

In contrast to previous seagrass models, our approach to the development of a quantitative and reasonably accurate production model for the subtropical seagrass *Halodule wrightii* was unique in several respects.

First, the model is relatively simple. It does not take into account many of the complex relationships associated with nutrient loading and light attenuation caused by phytoplankton, epiphytes, and benthic algae. It is specific to the Laguna Madre, which despite the persistence of a long-lived brown tide algal bloom, is a hypersaline lagoon of oligotrophic character. Consequently, the importance of biological interactions are minimized and physical factors (e.g., light and temperature) become most important.

Second, the model takes a whole-plant approach. The dominance of below-ground tissues with respect to total seagrass biomass has long been recognized but seldom considered in physiological or ecological studies. Since below-ground tissues appear to play critical roles in the biogeochemical processes that occur in the sediments, as well as regulate processes in the overlying water column, it is important to include this component in seagrass models. From a resource management perspective, the inclusion of below-ground tissues is critical for a predictive model.

Third, our model links theoretical and empirical knowledge with 9 yr of actual field measurements collected on a regular basis. The field data provided an unprecedented opportunity to validate model predictions, identify gaps in our knowledge, and reassess the role of various processes that contribute to our ability to apply models in coastal resource management. The results of this joint effort revealed that subsequent seagrass modeling efforts should not ignore the sizable below-ground component or the role of light as a major abiotic factor, especially in nutrient-limited environments. The predictive power of seagrass models as tools for effective management decisions appear to be largely based on our ability to provide accurate estimates of water-column light attenuation and fundamental knowledge of the physiological characteristics of seagrasses.

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