Light response characteristics of net CO₂ exchange in brackish wetland plant communities

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Summary. Photosynthetic responses to incident photon flux density (400–700 nm; PPFD) was studied in a grass community consisting of Spartina patens and Distichlis spicata and a mixed community having the two grasses and a sedge, Scirpus Olneyi. Net community CO₂ exchange and incident PPFD were monitored from dawn to dusk in a large open gas exchange system, and a hyperbolic light response model was fit to the data for each day. Light response curves from five growing seasons were evaluated for seasonal trends in the compensation value, initial slope, and maximum net CO₂ exchange rate calculated from the model at PPFD = 1670 μmol m⁻² s⁻¹.

All response curves were curvilinear. Data from approximately 30% of the 113 days studied fit saturation curves which occurred primarily in spring and fall. Approximately 5% of all curves constructed required a different response curve for the morning and afternoon. These occurred during mid-summer and were interpreted to be evidence of water stress.

The compensation flux density was very high early in the growing season, but rapidly decreased and during the months June, July and August, it averaged near 100 and 120 μmol m⁻² s⁻¹ in the mixed and grass communities. The initial slope and maximum net CO₂ exchange rate increased from early May to maxima in July and declined thereafter. Mid-summer mean values for the mixed and grass communities respectively were 34.3 ± 10.3 mmol mol⁻¹ and 39.1 ± 9.1 mmol mol⁻¹ for the initial slope and 20.3 ± 4.2 mmol m⁻² s⁻¹ and 23.0 ± 3.8 mmol m⁻² s⁻¹ for maximum net CO₂ exchange. Daytime respiration accounted for approximately 20% of maximum gross photosynthesis in both communities.

Photosynthetic efficiency, CO₂ assimilated per unit total incident solar radiation, was approximately 4.1% and 4.7% at dawn or dusk and 2.3% and 2.6% at midday for the mixed and grass community. Gross photosynthesis, maximum photosynthesis plus midday respiration, accounted for 2.7% and 3.0% of total incident solar radiation in the mixed and grass communities.

Introduction

Primary production in tidal wetlands communities is highly variable (Turner 1976). A number of studies have implicated anoxia, salinity, plant nitrogen deficiency, and phytotoxins such as hydrogen sulfide as possible controlling factors (Mendelssohn et al. 1982; Valiela and Teal 1974; Linthurst and Seneca 1981), but our knowledge of the physiological mechanisms by which these factors might regulate photosynthesis and growth is inadequate to explain intraspecific production differences. While we have a preliminary understanding of the photosynthetic system in leaves of species endemic to some wetlands communities (DeJong et al. 1982; Pomeroy et al. 1981; Giurgevich and Dunn 1979) we know much less about how the photosynthetic system operates at the plant community level and we know nothing about the coupling between photosynthesis and growth.

The goal of this study was to characterize community photosynthetic response to incident solar radiation. The study was conducted in two plant communities on a marsh in the Rhode River, a subestuary of the Chesapeake Bay at the Smithsonian Environmental Research Center. Data from this site on community carbon balance, photosynthetic characteristics of individual leaves, and effects of canopy architecture on community photosynthetic efficiency were previously reported (Drake and Read 1981; DeJong et al. 1982; Turitzin and Drake 1981). In this paper I give details of the light response characteristics of photosynthesis for two grass communities. Incident photon flux density (400–700 nm; PPFD) and the change in CO₂ concentration of the air stream as it passed over a section of the plant community enclosed within a large open gas exchange system was measured periodically throughout the day. Results were fit to a hyperbolic model with community CO₂ exchange as dependent variable and PPFD as independent variable. The light response curves were analysed and light compensation value, maximum net CO₂ exchange, and the initial slope of the light response curves were determined for each day studied.

Methods

1. Study site

The study site was the Kirkpatrick marsh on the Rhode River near Edgewater, Maryland (38°53′ N, 76°33′ W). This site is the location for many ongoing studies of the ecology of wetlands and has been the subject of a number of publications which describe its physical and biological make-up. Descriptive aspects of this site relevant to the present study can be found in Drake and Read (1981), DeJong and Drake (1981), and Turitzin and Drake (1981).
Two plant communities were studied: one consisted of the two grasses, *Spartina patens* and *Distichlis spicata*, called the grass community throughout this paper and the other was a mixture of 50–70% of these two grasses and 30–50% of the sedge, *Scirpus Olneyi*, called the mixed community. The two grasses have the C₄ photosynthetic pathway but the sedge does not (DeJong et al. 1982). At the peak of the growing season, the two communities have 0.4–0.6 kg dry weight of aerial biomass per square meter of marsh surface area (Drake and Read 1981) and leaf area index in the range 2.4–4.3 (Turitzin and Drake 1981).

2. Gas exchange measurements
Net ecosystem CO₂ exchange, including assimilation by plants and respiration of roots and soil, was determined by monitoring the change in CO₂ concentration in a stream of air passing over a section of the community enclosed in a plexiglas chamber. Details of the construction and use of this chamber are found in Drake and Read (1981). The measuring circuit included a sampling pump in the field which withdrew streams of air from the inlet and exhaust ports of the chamber and delivered them through stainless steel tubing approximately 50–70 m to a field laboratory where the gas analyzers and related equipment for recording data were housed. Respiration was determined during the daytime in some experiments by covering the chamber with several layers of heavy gage black plastic. Biomass of green tissue was determined by harvesting, drying plants at 60°C for 72 h, and weighing. Gas exchange was monitored for varying periods. In most experiments, the chamber remained over one section of the community for three to five days, and in one experiment, the chamber was kept in place for more than two weeks in order to record the development of photosynthesis during greening of the plant community in early spring. Air was forced through the chamber rapidly enough to change the volume of the chamber every twelve seconds and as a result the temperature of leaves within the chamber tracked the temperature of leaves in the canopy outside the chamber within 2°C (Drake and Read 1981).

3. Photosynthetic photon flux density (PPFD; 400–700 nm)
Incident PPFD within the chamber was measured by a LiCor quantum sensor which had been calibrated against the 400–700 nm band of solar radiation measured by a bank of Eppley radiometers. For calculation of the efficiency of light harvesting by the plant communities PPFD was assumed to be 47.5% of total solar radiation (Stanhill and Fuchs 1977).

4. Data collection and analysis
The output from the gas analyzers, radiometers, and thermocouples, was recorded on strip charts and at three minute intervals on punch tape by an Esterline Angus Data Acquisition System (PD-2064) and reduction of raw data was carried out on a Wang computer. Results from an entire day were used to produce each light response curve which was analyzed for photosynthetic efficiency at low light intensity by evaluating initial slope of the light response curve (A) and for maximum photosynthetic capacity (Pₘ), the rate of net CO₂ exchange at high light intensity. All but a few of the days used in the analysis could be described by a hyperbolic model (eqn 1)

\[ P = \frac{A(I - C)}{1 - B(I - C)} \]  

where \( P \) is net CO₂ assimilation (µmol m⁻² s⁻¹), \( I \) is PPFD (µmol m⁻² s⁻¹), \( A \) is the initial slope of the light response curve (mol mol⁻¹), \( B \) is a mathematical constant (m² s⁻¹ µmol⁻¹), and \( C \) is the compensation value, the value of PPFD at \( P=0 \) (µmol m⁻² s⁻¹). A gives an estimate of maximum photosynthetic efficiency at low intensity, the ratio \(-C/B\) is the asymptote for the curve and gives the maximum possible photosynthetic rate, and \( C \) is the compensation value, the value of PPFD when photosynthesis balances respiration. The value of the constant \( B \) is the slope of the linear dependence of \( P \) upon \( P/(I - C) \) (Fig. 2).

I found no apparent dependence of this constant on season. Mean and standard error for all data collected during the period May through August were \(-1.66±0.13×10^{-3}\) and \(-1.23±0.11×10^{-5}\) m² s⁻¹ µmol⁻¹ for the mixed and grass communities, respectively (Table 2). Horie and Udagawa (1971) discuss the development and application of this model to single leaf and canopy photosynthesis.

Results

1. Time course for net CO₂ exchange and PPFD
Records of the measurement of community photosynthesis and incident photon flux density for three days are shown in Fig. 1.

2. Constants \( A, B, \) and \( C \) for the light response curve
Data as shown in Fig. 1 were averaged for hourly intervals and the ratios of \( P/(I - C) \) were then plotted opposite hourly average values of \( P \). A linear regression was computed and the y intercept was taken as \( A \) and slope as \( B \). The hyperbolic model, its linear transformation, and a plot of the data from Fig. 1 A is shown in Fig. 2 to illustrate the method for obtaining the constants. \( C \) was taken directly from the records of net CO₂ exchange and incident PPFD. The maximum value of photosynthesis (\( Pₘ \)) was computed from the model at a value of 1670 µmol m⁻² s⁻¹ PPFD which is 80% of maximum possible PPFD at this latitude. This value of PPFD was chosen because it could occur at any time during the months May through August when most of the photosynthetic activity occurs and because the value \( Pₘ \) thus computed could be expected to occur. Results are expressed as net CO₂ exchange per unit area of marsh surface. The results reported here include data from 1974 to 1979. In all, 60 days of data collection in the grass community and 53 days in the mixed community were used for the analysis of the light response.

3. Classification of light response curves
The patterns of light response produced by the data in Fig. 1 are shown in Fig. 3. The data in this figure are net CO₂ exchange (\( P \)) and incident PPFD (\( I \)) recorded at 3 min