The Photosynthetic Response of Several Submersed Macrophyte Species to Light Conditions in the Tidal Freshwater Hudson River

by

Michael T. Harley
Polgar Fellow

Dr. Stuart Findlay
Supervisor
Institute of Ecosystem Studies
Mary Flagler Cary Arboretum
Box AB, Millbrook, New York 12454

ABSTRACT

The response of net photosynthesis to a natural range of light intensities was determined for three common macrophytes of the tidal freshwater Hudson River: Vallisneria americana Michx., Potamogeton perfoliatus L., and Myriophyllum spicatum L. Curves were constructed to describe this relationship, fit by a hyperbolic tangent function that has been used in previous studies. The data were collected from plants grown and incubated in the Hudson River. This was intended to produce results closely corresponding to the light environment of the river in mid to late summer.

The maximum net photosynthetic rates did not differ among species, nor did the compensation points. There was a trend of decreasing maximum net photosynthetic rate for all species over the period of the study. Net photosynthetic output showed a faster response to increasing light in V. americana than in the other two species. As a result, maximum photosynthetic rates were reached in V. americana at significantly lower irradiances than those required to saturate photosynthesis in P. perfoliatus and M. spicatum. This characteristic would give this species a competitive advantage under conditions in which growth is limited by light availability.

Macrophyte distribution data were obtained from the Hudson River between Castleton and the Tivoli Bays by random ponar grabs. There was no clear correlation of depth with

biomass. V. americana was the most abundant of the three species by a wide margin, both in terms of frequency of occurrence and absolute biomass. All three species occupied the same range of depths. These observations were consistent with their determined photosynthetic characteristics. It was suggested that the low irradiance required for the saturation of photosynthesis in V. americana is a factor influencing its abundance in the tidal freshwater Hudson River.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Aquatic vascular plants commonly form dense beds of submersed growth in the shallow waters of estuaries. The great productivity of macrophyte beds in the marine portions of tidal systems has frequently been noted (Wetzel and Neckles, 1986; Flores-Verdugo et al., 1988), but their freshwater counterparts have been historically overlooked. It has recently been demonstrated that the primary productivity of a typical mixed macrophytes bed in the middle Hudson River compares closely to figures quoted for Thalassia seagrass beds (Garritt and Howarth, 1988). The main channel of the Hudson River often experiences net heterotrophic conditions (Cole et al., 1990), and so it is possible that shallow water macrophyte populations could provide a substantial part of the energetic input for the river ecosystem. This notion of large-scale trophic importance (Kemp et al., 1987; Goldsborough and Kemp, 1988; Bianchi and Findlay, 1990) has lead to an intensified interest in the description of what limits the distribution of submersed macrophytes in estuarine systems.

One of the factors leading to the dismissal of submersed macrophytes in river energetics has been that they are typically limited in distribution to small littoral areas along the edges of the main channel (Garritt, 1990). This is largely due to the rapid attenuation of light in even mildly

eutrophic or turbid waters, and to the correspondingly shallow zone in which gross photosynthesis exceeds total respiration (Sand-Jensen, 1989). The amount of suspended solids and phytoplankton in the water column influences the attenuation of light, and in turn affects the depth limit at which macrophytes will be able to accumulate biomass. Any change in the attenuation of incident solar radiation may have an effect on the distribution of submersed macrophytes, and on the primary productivity of the Hudson River ecosystem.

In past studies, the ability of a macrophyte species to photosynthesize through a range of light conditions has been considered one of the primary characteristics determining its distribution in turbid waters (Spence and Chrystal, 1970a; Titus et al., 1975; Dennison, 1987; Goldsborough and Kemp, 1988; Sand-Jensen, 1989; Carter and Rybicki, 1990). This assumption has led to a large body of literature concerning the relationship between light intensity and photosynthetic output in both marine and freshwater plants (Meyer et al., 1943; Van et al., 1976; Barko and Smart, 1981; Fair and Meeke, 1983; Tobiessen and Snow, 1984). The characterization of this relationship has become the traditional means of quantitatively describing a species' "depth tolerance", that is, its ability to grow at low irradiances. However, little work has been done to show how the results of this approach are useful in the explanation of naturally occurring macrophyte distributions in turbid estuarine waters (Carter

and Rybicki, 1990). This methodology is certainly a simplification, and its validity must be considered in each case it is applied.

This study was designed to examine the response of photosynthesis to irradiance (P-I response) in three of the most common macrophytes in the tidal freshwater Hudson River: Vallisneria americana Michx., Potamogeton perfoliatus L., and Myriophyllum spicatum L. Most of the previous freshwater macrophyte work has been done in either in clear water lakes or in the Chesapeake Bay estuary, both of which differ considerably from the Hudson River in many physical and chemical aspects, such as turbidity. This study was conducted with plants grown in the Hudson River, and all measurements of P-I response were made in the river water column itself. The results are, therefore, specific to this estuary. Furthermore, M. spicatum and P. perfoliatus have been the subjects of a number of studies, but this is one of only a few to consider V. americana distribution.

MATERIALS AND METHODS

Construction of the Curve Describing P-I Response

The most common approach to the description of macrophyte photosynthesis has involved the experimental measurement of photosynthetic output through a range of light intensities (Goldsborough and Kemp, 1988). From these data, curves like

that depicted in Figure 1 can be constructed. The vertical axis is a measure of photosynthesis normalized to the dry weight of the macrophyte sample (Goldsborough and Kemp, 1988), its chlorophyll content (Van et al., 1976), or to its leaf surface area (Spence and Chrystal, 1970b). The horizontal axis is a measure of light intensity ("quantum irradiance"), generally expressed in $\mu E*m^{-2}*s^{-1}$, where one Einstein (E) is equivalent to one mole of photons.

The P-I response curve is similar to a typical plot of enzyme reaction velocity against the concentration of its substrate. In fact, some past studies have used the equations common in enzyme kinetics research to describe the macrophyte P-I response (Van et al., 1976). More often, the curve has been fit to the hyperbolic tangent function chosen by Jassby and Platt (1976) in their work with phytoplankton:

$$P=P_{max}*\tanh(\alpha I/P_{max}) \quad (1)$$

Photosynthesis at a given irradiance, I, is equal to the maximum saturated value of photosynthesis multiplied by the hyperbolic tangent of the proportion $\alpha I/P_{max}$. P_{max} is the maximum photosynthetic output approached asymptotically, and α is the initial slope of the curve at low irradiances. I_k is the intensity at which photosynthesis begins to saturate. This has been calculated by the extrapolation of the initial linear portion of the P-I curve to the irradiance at which P_{max} is reached (Fair and Meeke, 1983). The compensation point, I_c, is the irradiance at which net photosynthetic output is zero.

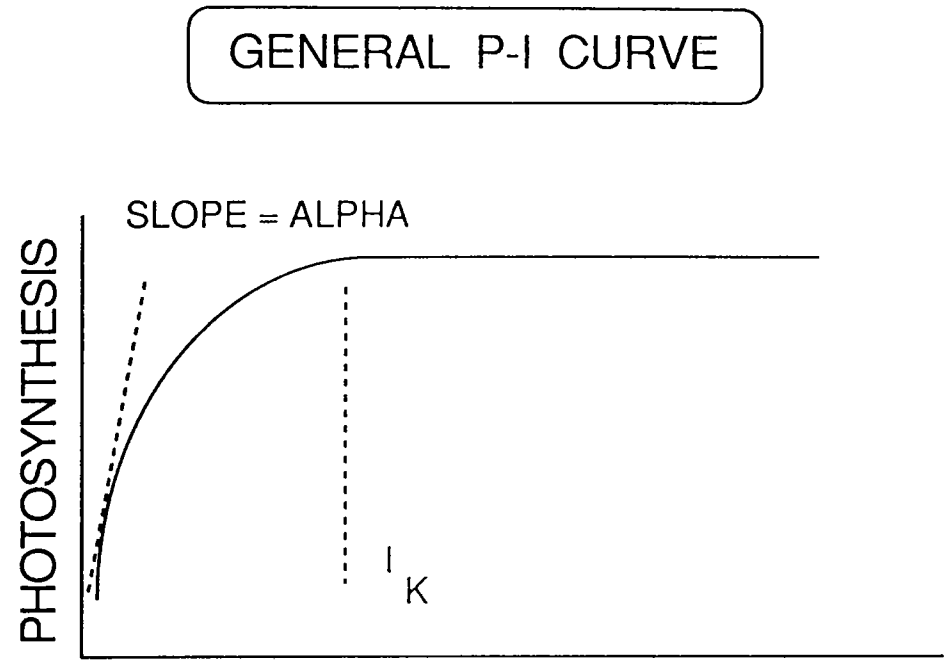

Figure 1. General photosynthesis-irradiance response curve with important parameters shown.

P-I Data Measurement Approach

P-I data have been collected by a variety of methods in previous studies. In order to compare P-I response between several species all the data must be collected under the same conditions, be analyzed similarly, and expressed in the same final form. In this study, the three species of macrophyte were treated identically in all these respects, so that the results would be as directly comparable as possible.

P-I responses vary seasonally due to many factors (Drew, 1978; Wetzel and Neckles, 1986; Dennison, 1987). It is only logical to suggest that the P-I response of a given species might vary geographically. Therefore, a study concerned with the photosynthetic characteristics of macrophytes in the Hudson River, would best collect the data from photosynthetic incubations performed in that river. Laboratory studies utilizing carefully controlled conditions may not correspond well to the natural environment. For example, the neutral density fiberglass screen is often used to adjust irradiance in the lab reduces the intensity of light equally for all wavelengths of photosynthetically active radiation (400-700 nm) (Goldsborough and Kemp, 1988; Twilley and Barko, 1990). This may not recreate the composition of naturally attenuated light in the Hudson River. It has been shown in the Rhode River estuary that as turbidity and concentration of organic compounds in the water column increase, light in the blue-

green range (430-550 nm) begins to penetrate less deeply than does light in the orange range (600 nm) (Pierce et al., 1986). This is contrary to the expected attenuation of light by water. The uneven spectra that often result under natural conditions may not be accurately reproduced in the lab. The production of curves that represent the "natural" P-I response existing in wild macrophyte populations should be based on incubations in naturally attenuated light.

The work of Jassby and Platt was based on data measuring photosynthesis as carbon-14 uptake, a method that, in the short term, can not account for respirational loss of photosynthate. In the measurement of photosynthesis by observation of oxygen evolution, apparent (net) photosynthesis is the result of plant respiration subtracted from gross photosynthesis ($P_{measured}=P_{Gross}-R$). Therefore, equation (1) would best fit ^{14}C data or oxygen data adjusted to represent gross photosynthesis ($P_{Gross}=P_{Net}+R$). This is apparent by the fact that I_c calculated by equation (1) must always equal zero irradiance. When considering net photosynthesis data, such as oxygen evolution measurements, there is no reason why I_c must be zero. If gross photosynthesis equals zero when the irradiance is zero, then net photosynthesis would be expected to be zero at some higher irradiance due to the consumption of oxygen by respiration.

Some macrophyte studies, however, have applied equation (1) to net photosynthesis data (Fair and Meeke, 1983;

Goldsborough and Kemp, 1988). The general shape of the curve fits it well, except for the obligatory value of zero for I_c. This tends to cause the best fit line to overestimate α, while underestimating P_{max}. The hyperbolic tangent model can be used to fit net photosynthesis data, but the errors introduced must be remembered (Fair and Meeke, 1983). These errors occur consistently enough to allow them to be ignored when comparing P-I curves fit the same way. It must be realized, however, that these parameters calculated from net photosynthesis data cannot be compared with parameters for the same species derived from gross photosynthesis data.

When using equation (1), the calculation of I_c must be made by an independent linear regression of the low-irradiance data, in which the x-intercept of the regression line coincides with I_c. Jassby and Platt (1976) determined that this kind of linear regression produces a close fit to the data in the vicinity of the compensation point.

Several macrophyte species have been shown to possess the ability to adapt their P-I response to long term light conditions (Spence and Chrystal, 1970b; Goldsborough and Kemp, 1988; Bowes and Salvucci, 1989). Plants of the same species, but growing at different depths, will have different P-I curves. For this reason, all plant samples used in this study were collected from Hudson River beds with an effort to consistently choose samples from similar depths. This was complicated by variation in depth due to tides. The difficulty

in assuring that all macrophytes originated at similar depths is compensated for by the advantages of using wild grown plants in this study. The end result is the production of P-I curves likely to closely reflect the natural responsiveness of the study species.

Study Site and Time Period

The macrophytes used in P-I data determinations were collected from three beds in the area of the Tivoli Bays site of the Hudson River National Estuarine Research Reserve. All M. spicatum was collected from a bed of mixed composition located between Magdalen Island and the eastern shore of the river, near the northernmost railroad bridge of Tivoli North Bay. All P. perfoliatus was collected from a mixed bed in the river directly adjacent to the southernmost railroad bridge of Tivoli South Bay. V. americana samples were also collected at that site, and from a shallow water bed midstream in the river beneath the Kingston-Rhinecliff bridge.

Incubations were always performed in the main channel of the river, in at least 5 m of water, either directly adjacent to the bed near Tivoli South Bay, or just off the north point of Magdalen Island. All successful incubations ranged in time from July 10, 1991 to September 13, 1991.

Field Measurements of P-I Data

The most convenient method to measure photosynthesis in

the field is by the use of dissolved oxygen measurements. The plant sample is enclosed in a volume of water of known initial dissolved oxygen. After the incubation period, the dissolved oxygen is measured again, and net photosynthesis can be expressed in terms of grams of oxygen evolved. The measurement of dissolved oxygen was done with a Cole-Parmer POM A1 dissolved oxygen meter, supplied by the Bard College biology department. Calibration was made to water saturated air at the temperature of river water before each incubation. This meter was equipped with a probe that could be inserted into standard 300 ml biological oxygen demand (BOD) bottles, so that immediate measurement of the change in dissolved oxygen was possible. The BOD bottles were agitated during the insertion of the probe, to prevent a local oxygen deficiency in the water near the electrode membrane (the Clark oxygen electrode consumes oxygen as it measures it). It was also found to be necessary to change the membrane on the probe before each day of sampling, although this is much more frequently than is normally recommended. Over long periods of incubation, the calibration of the probe would sometimes drift if the membrane had been used on a previous date. This was corrected for by calibrating the probe in water saturated air before and after each measurement. Frequent changing of the membrane effectively eliminated this drift, however.

The bottles containing macrophyte samples were incubated at various depths in the river to collect data from a natural

range of irradiances. This was accomplished by the use of a floatation device, which was a frame approximately 1 m by 1 m square made of 2" diameter PVC pipe. The incubating bottles were attached at various depths along a chain hung vertically through the water column. This chain was anchored to a thin rope, which was tied to the frame such that the chain hung from a point at the center of the square. Floating the bottles from the surface allowed their depth to remain constant despite changes in tidal stage, and the large size of the square allowed the bottles to be unshadowed by the float. In fairly strong currents the chain remained vertical due to the weight of the attached BOD bottles. However, even light currents agitated the bottles enough to prevent the formation of boundary layer stratification in the vicinity of the leaf surface (Goldsborough and Kemp, 1988).

Light intensity was measured through the water column during most days of incubation. This was done with a LI-COR spherical quantum sensor and a LI-1000 datalogger. This instrument measures the intensity of photosynthetically active radiation. In the collection of these data, care was taken to read light intensity as close to the incubating bottles as possible. On a typical day of incubation, light data were collected at intervals through the incubation and a time-weighted average irradiance for each depth was calculated.

Light profiles were used to determine the light extinction coefficient by the standard exponential equation

(Lind, 1974; Dennison, 1987):

$$I=I_0e^{-kz} \quad (2)$$

I is the quantum irradiance at water depth z, I_0 is the incident irradiance at the surface, and k is the attenuation coefficient. Figure 2 is a typical light profile for the Hudson River on a sunny midsummer afternoon. Such graphs can be used to determine irradiance at a particular depth.

On most days that incubations were done, secchi depth was measured as well. In this study, secchi depth was found to coincide with the depth at which light intensity was 15% of its surface value. On two days, July 10, 1991 and September 13, 1991, light profile data was not collected. Using secchi depths from these dates and extinction coefficients from similar days, light profiles were estimated. From these, the average irradiance that each plant sample was exposed to was calculated.

Collection of Macrophytes and Incubation

Incubations were usually attempted on cloudless days in order to decrease variation in irradiance. Work on partly cloudy days would have required more frequent repetitions of the collection of light data to facilitate the elucidation of average conditions. The typical incubation lasted between one half hour to an hour, and each set of light data took about 10 minutes to gather. This placed practical limitations on frequency of profile data collection. Incubation dates were

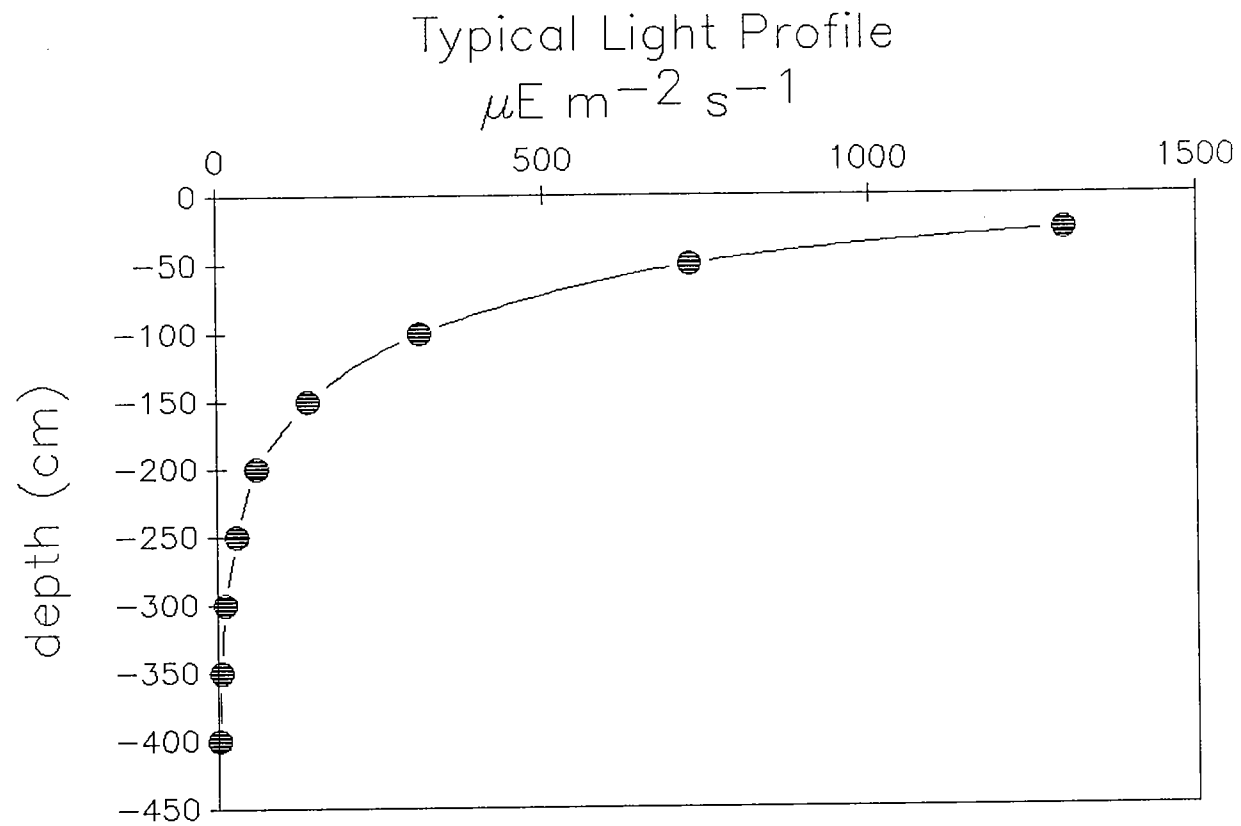

Figure 2. Typical light profile for the tidal freshwater Hudson River.

also chosen in such a way as to avoid unusual light conditions. To that end, incubations were not performed after major storm events. The time of day that incubations took place varied considerably, but the practice of measuring light profiles for each incubation accounted for the resulting variations in the light environment.

For each incubation, one species of macrophyte was collected at one of the described sites. Approximately the top 20 cm of new growth was used, and if possible, apical sections were chosen. Samples of macrophyte were generally collected in water between 1 m and 1.5 m deep. Some attention was given to tidal stage by collecting plants from the shallower end of that range during low tides, and collecting from deeper water during high tides. The samples were gently rubbed free of epiphytic growth and rinsed in river water. These plant sections were then stored, protected from light, in river water for at least one half hour. This was meant to minimize the release of previously stored oxygen from internal air spaces into the water during incubation. Although longer equilibration times have been used in some studies (Spence and Chrystal, 1970a), a period of one half hour has been recommended for both P. perfoliatus (Kemp et al., 1986) and M. spicatum (McCracken et al., 1975). These species contain small lacunae, so that gas storage is never great. Trial incubations in the dark showed that oxygen was rarely released by non-photosynthesizing macrophytes. The use of short lengths

of plant with cut ends has been noted to decrease lacunal release of oxygen as well (Drew, 1978).

BOD bottles that had never been exposed to Winkler reagents were filled in the field with Hudson River water of known initial dissolved oxygen concentration. Care was taken not to leave air bubbles in the bottles. The water was always collected the evening before the day of incubation from the main channel of the river adjacent to the village of Tivoli. It was filtered through glass fiber paper (effective pore size of 1 micron) to remove algae and other water column microorganisms, and then stored open to the air, in the dark, until the next day.

Small lengths (approximately 10 cm each) of macrophyte leaves that had been collected and prepared as described above were inserted into the water-filled BOD bottles. These bottles were immediately attached to the floatation device described and lowered into the river. At each incubation depth three plant samples were placed: two in replicate "light bottles" from which net photosynthesis was determined, and one "dark bottle", wrapped in aluminum foil, from which respiration rate was measured as the decrease in dissolved oxygen. In addition, each incubation included three dark bottles containing only filtered river water. These were "blanks" used to confirm that bacterial respiration was negligible.

In early trials, a wide range of incubation depths were experimented with. A successful incubation was one in which

several bottles ended up in the range of saturated photosynthesis, and at least one bottle was distributed below the depth where I_c occurred. In the majority of incubations, bottles were distributed in groups of three or four (two light bottles, one dark, and sometimes a blank) at six depths: 25, 100, 150, 200, 300, and 400 cm. These depths proved to span the desired range of irradiances. At 400 cm, there was an irradiance of approximately 5-10 $\mu E*m^{-2}*s^{-1}$, which was less than 1% of the surface value on all days of incubation. This light intensity proved to be less than the I_c value for all three species.

During the incubation, water temperature was measured through the water column. Temperature has been shown to have an effect on photosynthetic output (Drew, 1978; Tobiessen and Snow, 1984). At the beginning and end of each incubation light data were collected. Depending upon the length of the particular incubation and the uniformity of cloud cover, various numbers of additional light profiles were sometimes taken.

Initial experiments determined that the appropriate time for incubation would be less than one hour for 10 cm sprigs of macrophyte. The Hudson River water used for incubation was initially an average of 89% oxygen saturated throughout the study period. Therefore, longer incubation would have lead to dissolved oxygen concentrations approaching or exceeding saturation. This was undesirable due to the possibility of

oxygen-induced inhibition of photosynthesis. Also, oxygen saturated conditions can result in gas coming out of solution, forming bubbles in the incubation vessels. This gaseous oxygen would not be included in measurements of dissolved oxygen, and so photosynthesis would be underestimated. For this reason, bottles containing air bubbles at the end of the incubation period were excluded from subsequent analysis.

At the end of the incubation period, the bottles were retrieved and dissolved oxygen concentration was measured immediately after removal of the each plant sample. The dissolved oxygen meter calibration to water saturated air was checked before each set of measurements. The macrophytes were brought back to the lab and each was divided into a portion frozen for later chlorophyll determination, and a portion which was dried to constant weight in a 70°C oven. Chlorophyll analysis has not yet been carried out, and so the photosynthesis data collected has been normalized only to grams dry weight of macrophyte.

Collection of Biomass and Distribution Data

A separate phase of this study was begun in late summer in order to gather information describing the Hudson River distributions of the three macrophyte species for which P-I response had been measured. Dr. David Strayer, working at the Institute of Ecosystem Studies (IES) in Millbrook, NY, had been conducting a bivalve abundance study in the freshwater

Hudson beginning in July 1991. That study employed a nine inch square Ponar grab to take benthic samples at random distances across twelve Hudson River transects. The sites ranged through the freshwater and brackish water portions of the river. The southernmost site was 100 m north of the Newburgh-Beacon bridge, and the northernmost site was near the Port of Albany. The day, time, and depth were recorded for each grab, and the complete contents of each were stored frozen for later sorting.

Those grab contents were used in this Polgar study to estimate macrophyte biomass per unit area at each of the sites. This method of sampling may result in an underestimation of biomass, especially due to the discontinuity common in submersed beds, and the elongate nature of macrophyte stems compared with the small volume of the grab. The main interest of this work, though, is the determination of abundances and distributions of three species of macrophytes relative to each other. If the Ponar grab underestimates biomass, it would do so consistently. Therefore, the absolute accuracy of this method in determining biomass per unit area of river bottom is of little concern.

One day of sampling with the same nine inch Ponar grab was spent as part of this study (September 6, 1991). The work was done in the mixed bed adjacent to the southernmost bridge of Tivoli South Bay, already described above. The work was restricted to water less than five meters deep at low tide on

that day. Strayer's grabs were completely random, so that the majority of them were in water much deeper than five meters, well beyond the photic zone in this turbid river. These shallow water data were intended to provide enough resolution in order to precisely define the maximum depth at which each species occurs.

All plant material was thawed, sorted by species and dried to a constant weight in a 70°C oven. This weight was later converted to biomass per square meter of river bottom.

RESULTS

Temperature and Light Conditions

The water column at all the sites during the study was isothermal to a depth of five meters. No temperature measurements were taken at greater depths. On only two occasions, the warmest day of incubation (July 22, 1991) and the last day of incubation (September 13, 1991), was there any deviation from this pattern. In each case, the top 0.5 meter of the river was warmer than the water below it. These differences were slight, 0.3°C on the earlier date and 0.4°C on the later. This variation was considered insignificantly small. Previous studies comparing temperature to photosynthesis show considerable effects between the low temperatures of spring waters (5°C to 17°C), and those of summer (20°C and above) (Drew, 1978; Titus and Adams, 1979).

At low spring temperatures, differences as small as 5°C have had significant effects on the photosynthesis of P. crispus L. (Tobiessen and Snow, 1984). This sensitivity to small temperature changes has not been observed under warmer conditions. It is clear that the variation of less than 1°C described above need not be considered.

The variation in water temperature over the study period was similarly small. All temperatures in July and August ranged between 24.9°C and 27.0°C, a difference of 2.1°C. During the incubation on September 13, 1991 water temperature was measured at 23°C, increasing the variation to 4°C. Based on the discussion above, all variations in temperature during this study were taken as insignificant.

Light extinction coefficients similarly varied little over the period of the study, ranging from 1.61 m^{-1} to 1.97 m^{-1}, with a mean of 1.76 m^{-1} (S.E.=0.0392). The full summertime range of extinction coefficients occurring at these sites is in no way represented by these numbers, which are the product of sampling biased by a selectivity for days distant from major storm events.

P-I Curve Data

The P-I data collected were fit by the Statgraphics statistical package (version 2.6), using a nonlinear regression of the data according to equation (1). The fit determined both α and P_{max} simultaneously. Figure 3 is a

representative P-I curve for M. spicatum, in which the observed data are shown with the regression line. The points graphed as negative oxygen production are either dark bottles or light bottles incubated below I_c. Figures 4 and 5 are sample curves for P. perfoliatus and V. americana respectively.

The hyperbolic tangent model fit the P-I data with a general underestimation of P_{max} and an overestimation of the low irradiance portion of the curve, as was expected. These errors can be seen in Figures 3, 4, and 5. However, the nature of the fit to the net photosynthesis data is consistent, and so the parameters calculated are useful for comparative purposes. There was no evidence of photorespiration in the P-I data, even at the highest irradiances.

The linear regressions used to determine I_c, as described above, produced best fit lines which had slopes that correlated closely to α calculated by the simultaneous nonlinear fit (R^2=0.957, n=11). The use of a linear regression is an acceptable method to estimate I_c from net photosynthesis data. Resulting values of I_c are included in Table 1, which also shows the P-I parameters as determined by the nonlinear fit, and I_k, calculated as described above. Respiration of each macrophyte species varied widely within each incubation data set. This has been shown to occur in P. perfoliatus (Goldsborough and Kemp, 1988). However, the average respirations of each species in this study were

similar, ranging from 1.7-1.9 mg O_2 per gram dry weight of plant (gdw) per hour.

Table 1. Parameters of photosynthesis-irradiance response curves for all incubations.

Date	Plant	P_{max} (mg O_2*$g^{-1}h^{-1}$)	α	I_k ($\mu E*m^{-2}s^{-1}$)	I_c
7/10	M. spicatum	12.2	0.0430	452.1	71.3
8/6	M. spicatum	1.4	0.0087	173.2	114.4
8/7	M. spicatum	6.4	0.0420	293.0	40.3
8/8	M. spicatum	5.4	0.0146	446.2	108.1
Mean		6.4	0.0270	341.1	83.5
7/12	P. perfoliatus	13.8	0.0500	424.1	29.3
7/22	P. perfoliatus	15.3	0.0570	487.5	73.4
8/5	P. perfoliatus	5.7	0.0310	250.1	53.6
Mean		11.8	0.0460	387.2	52.1
7/12	V. americana	8.5	0.0560	279.1	82.3
7/22	V. americana	11.6	0.1370	192.1	25.5
8/2	V. americana	8.3	0.1210	143.9	2.3
9/13	V. americana	6.2	0.1400	100.2	11.6
Mean		8.6	0.1140	178.8	30.4

Biomass-Distribution Data

A linear regression of biomass against depth for the combined Ponar grab data of all three species showed poor correlation (r^2=0.147), as did similar regressions for each individual species. Several methods were employed to adjust for tidal effects, based on tide tables and recorded times of sampling. None of these improved the correlation, though. Biomass was almost equally distributed through all depths at which macrophytes occurred. This made the data of little use in the determination of accurate depth limits of distribution. However, a rough estimate of that depth limit can be made for macrophytes in general. This is useful for comparison to the

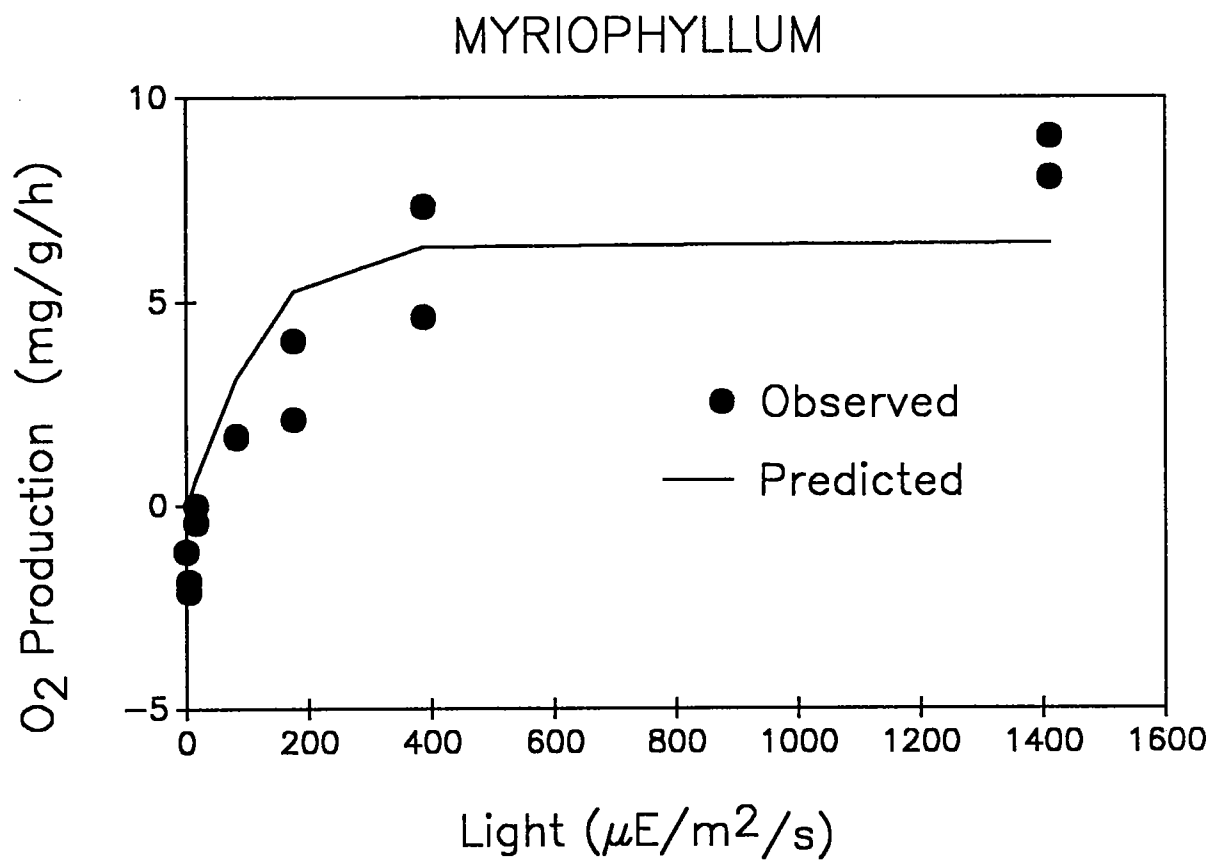

Figure 3. Representative photosynthesis-irradiance data for M. spicatum, with best fit line determined by equation (1).

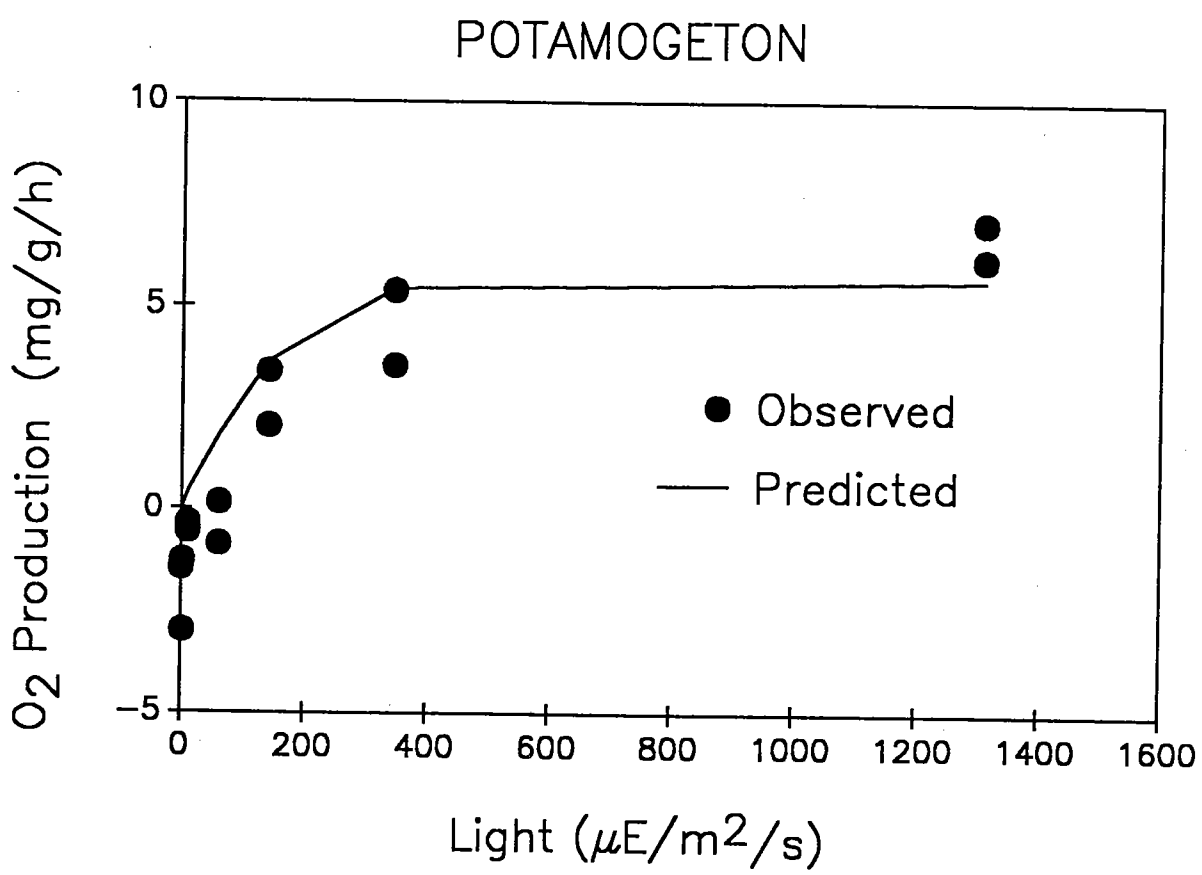

Figure 4. Representative photosynthesis-irradiance data for P. perfoliatus, with best fit line determined by equation (1).

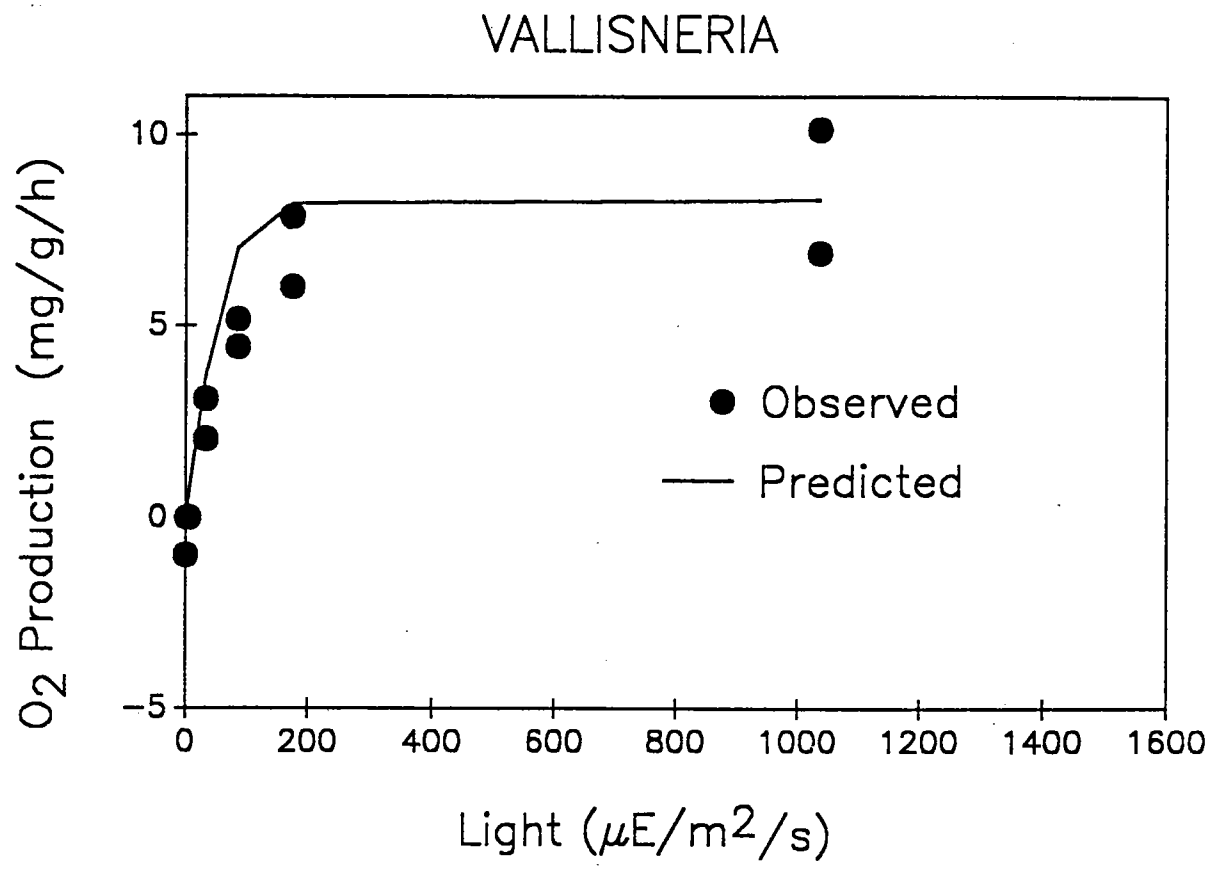

Figure 5. Representative photosynthesis-irradiance data for V. americana, with best fit line determined by equation (1).