A PHOTOSYNTHETIC SURVEY OF SEVEN SUBMERSED AQUATIC MACROPHYTE SPECIES FROM LAKE GEORGE, NEW YORK

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SUMMARY

The macrophyte community of Lake George, New York is diverse, composed of 48 submersed species representing a wide range of habitats, depth ranges, and life history strategies. The photosynthetic rates of seven representative submersed aquatic macrophyte species were determined in laboratory studies using a YSI biological oxygen monitor to measure short-term oxygen changes over a range of eight light intensities from 0 to 1000 umol m^{-2} s^{-1} at 20 C. The species examined were: _Elodea canadensis_, _Myriophyllum spicatum_, _Potamogeton amplifolius_, _P. gramineus_, _P. praelongus_, _P. robbinsii_, and _Vallisneria americana_. Comparisons of maximum net photosynthesis, Michaelis-Menten V_{max} and Km for photosynthesis versus irradiance, and dark respiration rates correlated with trends observed for these species in community data. _Myriophyllum spicatum_ exhibited a high photosynthetic rate (V_{max}) and high light requirement in both compensation point and higher half-saturation constant (Km), indicative of a high light-adapted species. In contrast, the native species exhibited shade-tolerant characteristics.

INTRODUCTION

The native submersed aquatic vascular plant flora of Lake George is highly diverse, with up to 48 species represented (Madsen et al., 1989). Lake George is geographically divided into a southern and northern basin, with an intervening section known as the Narrows (Figure 1). Although water chemistry values are relatively similar (Eichler and Boylen, 1989), the southern basin has larger areas of shallow embayments (Collins et al., 1987). In general, biomass is significantly higher in the southern basin, and species diversity somewhat lower, when compared to the northern basin (Collins et al., 1987).

Studies comparing a northern basin and southern basin embayment have shown increased productivity and decreased depth distribution of macrophyte species in the southern basin, with little change in the northern basin between 1973 and 1980. These trends are indicative of higher eutrophication rates in the southern basin embayment (Boylen et al., 1981).

Studies comparing native species composition lake-wide in 1972-1973 to 1987 showed little change in the composition of native species lake-wide (RFWI et al., 1988). The only significant change was the dramatic increase in abundance of the invasive exotic species, Eurasian Watermilfoil (*Myriophyllum spicatum* L.). First noted in Lake George in 1985, by 1987 it was the 6th most frequent species in quadrats studied, and the 22nd most common in terms of number of locations in the lake (RFWI et al., 1988). Eurasian Watermilfoil has a significant impact on native vegetation, primarily through shading caused by a dense overhead canopy formed near the water's surface (Madsen et al., 1989).

Native macrophyte species and Eurasian Watermilfoil have a diverse array of morphological and physiological strategies for adapting to their environment. Among these adaptations are photosynthetic characteristics appropriate to their overall strategy. The photosynthesis versus light intensity relationships for Eurasian Watermilfoil and six native species were examined to elucidate differences between the exotic and native species, as well as examining other trends in photosynthetic characteristics.

METHODS

Study Site

Lake George is an oligotrophic lake located in northeastern New York State, on the southeastern edge of the Adirondack Park within the Adirondack Mountains (Figure 1). Lake George has low alkalinity (20-25 mg $CaCO_3$ l^{-1}) and high transparency (Secchi Depth mean = 9.7 m). Lake George has a maximum depth of 58 m, and is 51 km long. All plants utilized in our experiments were taken from Huddle Bay in 2-3 meters of water depth (Figure 1). Huddle Bay is typical of southern basin embayments in Lake George.

Species Studied

The species examined were the native species Elodea canadensis, Potamogeton amplifolius, P. gramineus, P. praelongus, P. robbinsii, and Vallisneria americana; and the exotic invasive species Myriophyllum spicatum. Each of these species are common to dominant in the littoral zone of Huddle Bay. The morphological form and mode of perennation are summarized in Table 1. Vallisneria americana is found from 1 to 5 meters depth, but is most common at the shallow end of this range (Figure 2). Potamogeton gramineus is another shallow species, most common in 1 to 2 meters depth. Potamogeton amplifolius occurs next, with a peak abundance at 2 to 3 meters, followed by P. praelongus which peaks in abundance at 3 to 4 meters. Potamogeton robbinsii is the deepest occuring plant in Huddle Bay, with peak abundance beyond 4 meters; however, it is also found as an understory plant in shallower water. Elodea canadensis is found as an understory plant throughout the 1 to 6 meter depth range, but at lower abundance. The non-native M. spicatum is found from 1 to 5 meters, with peak abundance in 2 to 4 meters depth (RFWI et al., 1988). Maximum reported biomass for these species in Lake George, from unpublished RFWI data, is indicated in Figure 3.

Laboratory Methods

Plants utilized for photosynthesis experiments were maintained in the laboratory at 20 C and supplied with artificial light (200 umol m^{-2} s^{-1}) at the prevalent photoperiod. Photosynthesis was examined using a YSI 5300 Biological Oxygen Monitor to measure short-term oxygen exchange rates (5-30 min.) over a range of eight light intensities from 0 to 1000 umol m^{-2} s^{-1} at 20 C for six to eight replicates. Oxygen exchange rates were converted to carbon exchange using a respiratory coefficient of 1.0, and a photosynthetic coefficient of 1.2. Gross photosynthesis was modeled for light intensity using an iterative Michaelis-Menten equation to derive V_{max} (maximum rate of photosynthesis) and Km (half saturation constant for light). Respiratory rates were utilized to calculate photosynthetic light compensation points from Michaelis-Menten constants.

Data on species occurence in Huddle Bay was taken from Madsen et al. (1989). Percent cover data was used in Principal Components Analysis (PCA) ordinations of both samples and species for transects with (transect 1 = T1) and without (transect 2 = T2) dense stands of M. spicatum.

RESULTS AND DISCUSSION

Net photosynthesis (as oxygen exchange) versus light intensity for the seven species are presented in Figures 4a and 4b. All seven species exhibit some photoinhibition of photosynthesis at higher light intensities.

A comparison of V_{max} versus Km (Figure 5) illustrates three important relationships between M. spicatum and the other aquatic plant species studied. First, M. spicatum has a much higher Km than native plants. Native species tend to be more "shade-tolerant" than the invasive species. This may in part be due to the near-surface monolayer canopy formed by M. spicatum as opposed to the more open, vertical multilayer canopy of native species. Second, M. spicatum exhibits a higher maximum photosynthetic rate than the native species, which may in part account for its greater competitiveness. Last, the native plants are very similar to each other in these two characteristics. However, a possible gradient of depth range may be indicated from higher V_{max} for shallower plants, to the lowest value for the deepest-ranging species, P. robbinsii (Figures 5,6).

A graph of V_{max} versus respiratory rate (Figure 6) indicates a strong inverse relationship between average maximum photosynthetic rate and average respiratory rate. This trend is ecologically significant since plants with higher photosynthetic rates could have an increased metabolic rate, which would result in increasd productivity. Myriophyllum spicatum has the highest V_{max} and respiratory rate while the native species range from deep-habitat P. robbinsii (low productivity) to shallow-habitat P. gramineus (high productivity).

Light compensation point versus Km (Figure 7) possibly indicates the greatest separation of the exotic M. spicatum from native species. Native species are tightly grouped, as "shade-tolerant", while M. spicatum demonstrates a much higher light compensation and half-saturation constant for light, similar to that exhibited by terrestrial "pioneering" species requiring high light intensities (Fitter, 1986; Krebs, 1978).

Ordinations of community percent cover data by samples indicates that dense M. spicatum communities (T1, Figure 8, top) are distinct from areas on the transect without dense M. spicatum. The other transect (T2), without a dense M. spicatum bed, has a heterogeneous composition (Figure 8, bottom). Dense milfoil has a different community species composition than those areas without dense milfoil, possibly reflecting the shading of native plants.

Ordinations of community percent cover by species indicates that M. spicatum is distinct from native species on the transect with the dense bed (T1, Figure 9, top). Potamogeton robbinsii is distinct because it is most commonly found in depths beyond which the other species occur, but it also may be found among the other species at shallower depths. The relationship between species on the transect without dense M. spicatum beds (Figure 9, T2, bottom) indicates a similar relationship between native species as on T1, with the axes expanded to emphasize the differences between them. In this ordination, M. spicatum is not distinct from native vegetation because it does not suppress the growth of other species, but is a minor component in the plant community matrix of species.

The Michaelis-Menten parameters were used, in conjunction with a measured open-water light profile, to calculate the 24-hour carbon balance of each species in relation to depth, given a 14-hour daylength (Figure 10). This simplistic model should be used with caution in that it is based on a single light profile for a clear day, and accounts for leaf photosynthesis only, and does not incorporate stem and root respiration. Although actual 24-hour carbon balance limits will be significantly less than those presented here, these values are useful for comparative purposes. This simplistic model does indicate that on a daily basis, the exotic Eurasian Watermilfoil has a significantly higher carbon balance in 0 to 4 meters of water depth than native species, with a greater decrease in carbon gain with increasing depth. It is the first species to encounter a negative balance, at the relatively shallow depth of 10 meters (by this model). The relationships between native species in this model are less representative of what was observed in community data. For instance, P. amplifolius and P. praelongus must maintain a significant biomass of nonphotosynthetic rhizomes and stems, which would reduce the observed depth limits. Potamogeton robbinsii, with little root biomass to maintain, would have a more favorable whole-plant carbon balance than other Potamogeton species. Elodea canadensis is representative in this model, having a deeper depth limit relative to other native species, except P. robbinsii.

When this carbon balance model is applied using a measured light intensity profile in a dense M. spicatum bed, significant observations on expected performance can be made (Figure 11). Eurasian Watermilfoil leaf positive carbon balance will only occur in the upper 1 meter of the canopy, an indication of potential self-shading. Therefore, Eurasian Watermilfoil is intolerant of its own shade. Native plants all show positive carbon balance at 1 meter depth, but only P. amplifolius and E. canadensis exhibit positive carbon balance at 2 meters below the surface. Since water depth is over 3.5 meters in this profile, no low-growing native plants could sustain positive daily carbon balance and only the uppermost leaves of P.

praelongus could survive under natural growth conditions, given a plant height of 2 meters. This model would predict that native plants would not tolerate the shade of *M. spicatum*, and that *M. spicatum* leaves below 1 meter of the canopy top would senesce due to self-shading.

In conclusion, photosynthesis patterns indicate that native species are much more shade tolerant than the invasive exotic *M. spicatum*, having lower maximum photosynthetic rates. Relationships in photosynthetic characteristics between species are further reflected in ordinations of community data. The higher light saturation and compensation points of *M. spicatum* may be due to its formation of a surface monolayer canopy.

ACKNOWLEDGMENTS

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Table 1. Macrophyte species examined for photosynthetic rates, with their morphological form and mode of perennation.

Species	Morphological Form	Mode of Perennation
Elodea canadensis	Recumbent	Evergreen, Hibernaculae
Myriophyllum spicatum	Caulescent	Evergreen, Root crown
Potamogeton amplifolius	Caulescent	Rhizome
Potamogeton gramineus	Caulescent	Rhizome
Potamogeton praelongus	Caulescent	Rhizome
Potamogeton robbinsii	Recumbent	Evergreen, Turion
Vallisneria americana	Rosette	Tuber

Figure 1. Map showing the location of Lake George in New York State (inset), and the location of the sampling site, Huddle Bay, in Lake George.

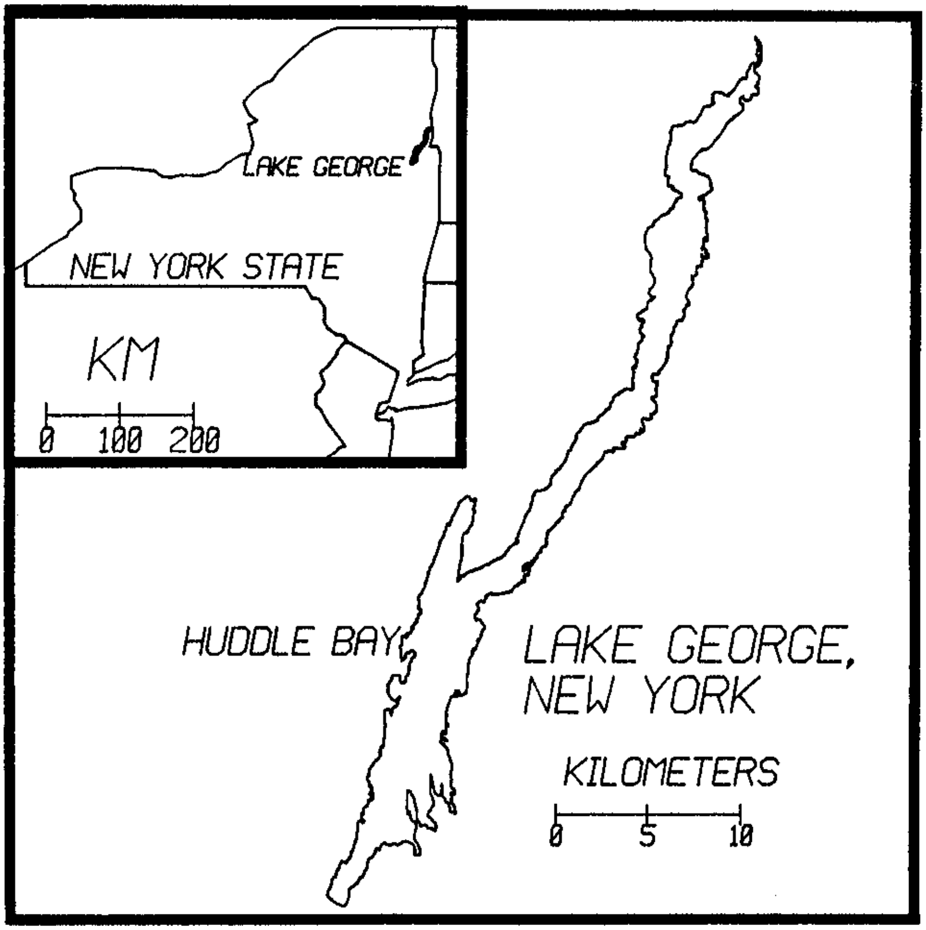


Figure 2. Depth distribution of the seven macrophyte species examined in Lake George. EC, *E. canadensis*; MS, *M. spicatum*; PA, *P. amplifolius*; PG, *P. gramineus*; PP, *P. praelongus*; PR, *P. robbinsii*; VA, *V. americana*.

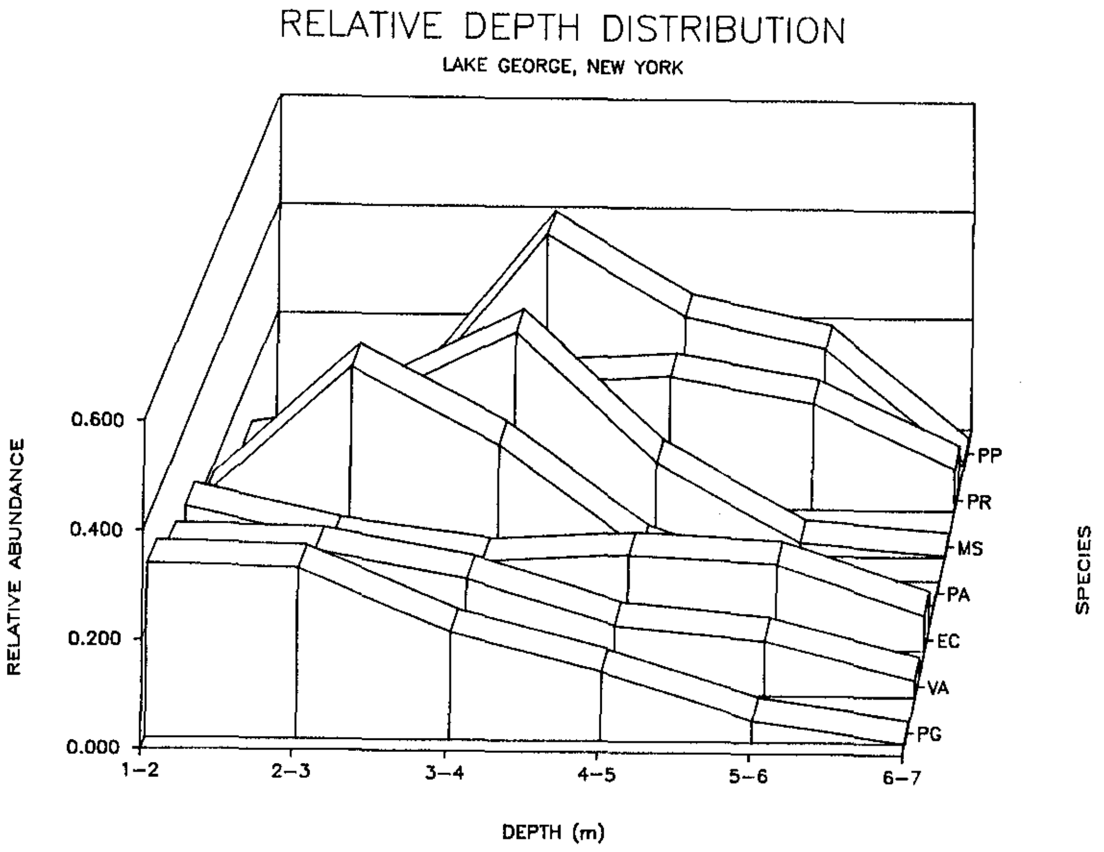


Figure 3. Maximum biomass (g dry wt. m^{-2}) reported for the seven macrophyte species examined in Lake George. Data from RFWI, unpubl. EC, *E. canadensis*; MS, *M. spicatum*; PA, *P. amplifolius*; PG, *P. gramineus*; PP, *P. praelongus*; PR, *P. robbinsii*; VA, *V. americana*.

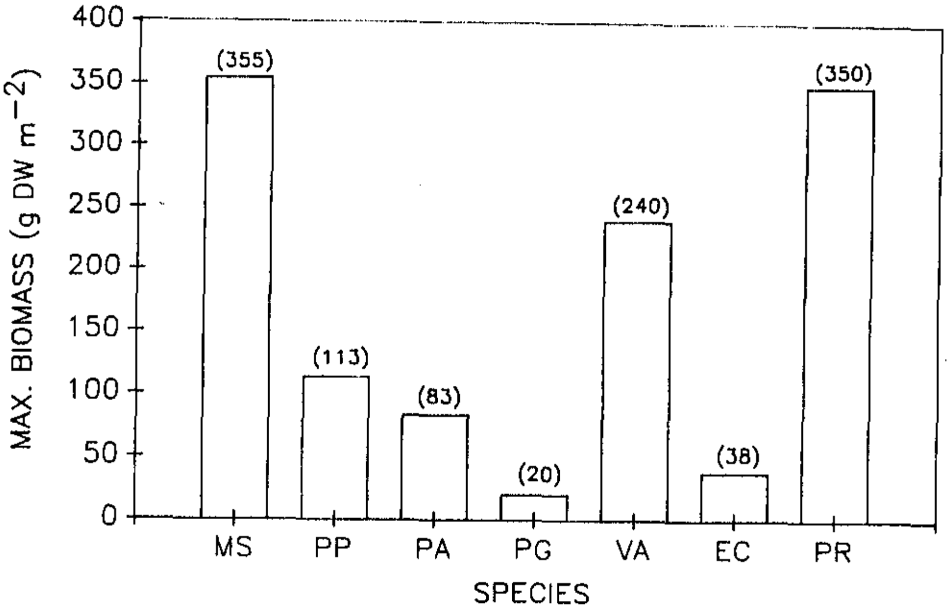


Figure 4a. Net photosynthesis versus light intensity for the seven macrophyte species examined.

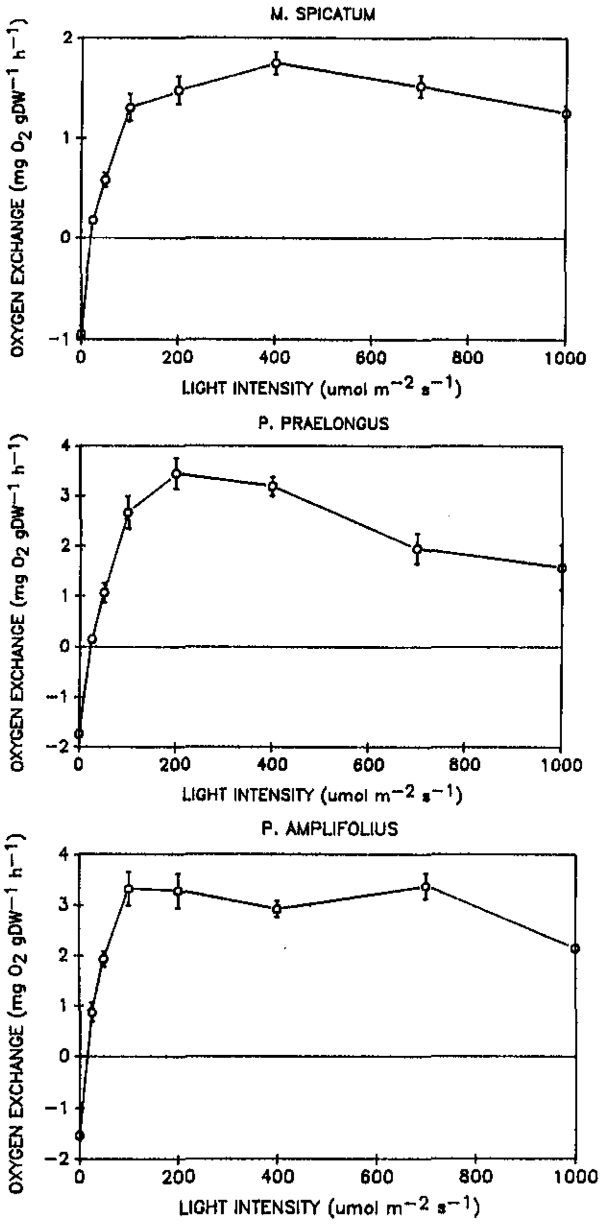


Figure 4b. Net photosynthesis versus light intensity for the seven macrophyte species examined.

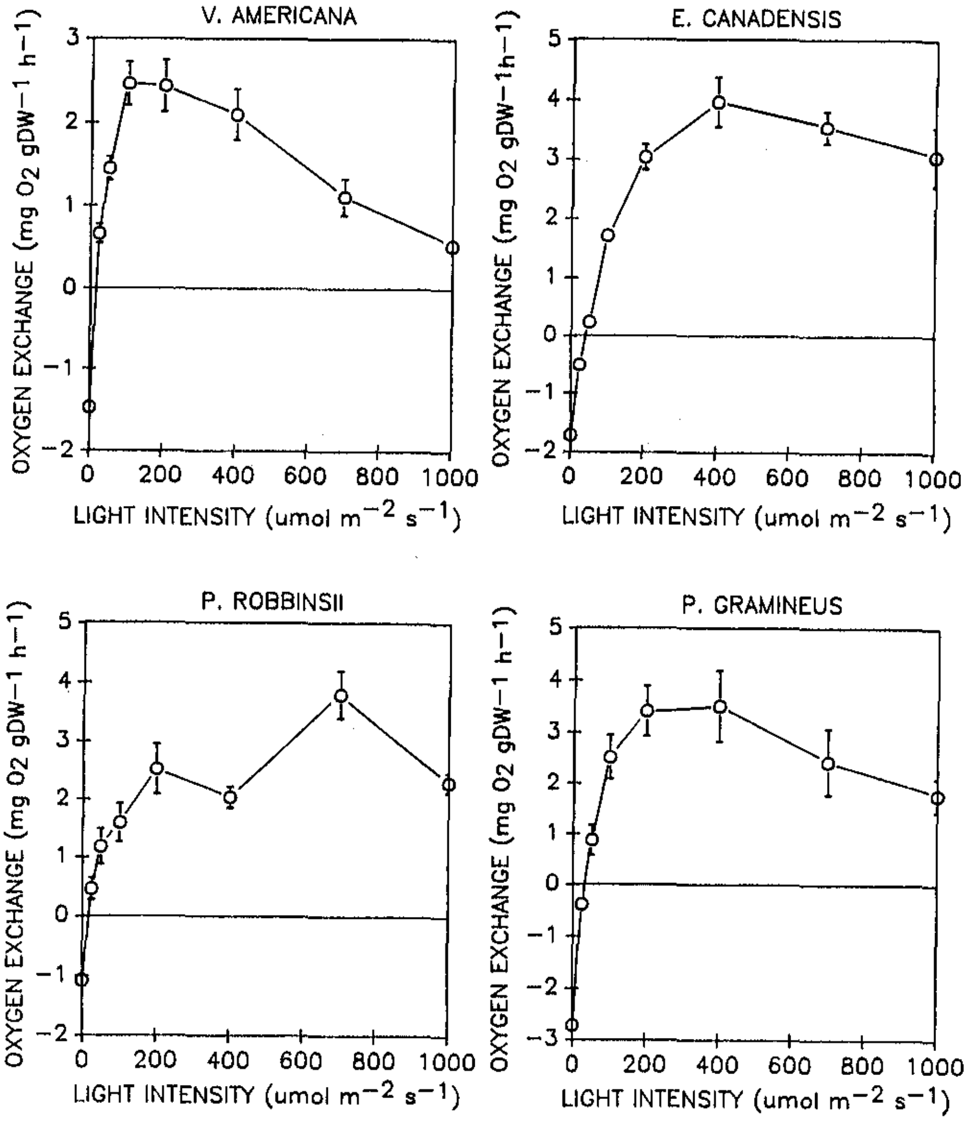


Figure 5. Michaelis-Menten maximum photosynthetic rate (V_{max}) versus the half-saturation constant for light intensity (Km). EC, *E. canadensis*; MS, *M. spicatum*; PA, *P. amplifolius*; PG, *P. gramineus*; PP, *P. praelongus*; PR, *P. robbinsii*; VA, *V. americana*.

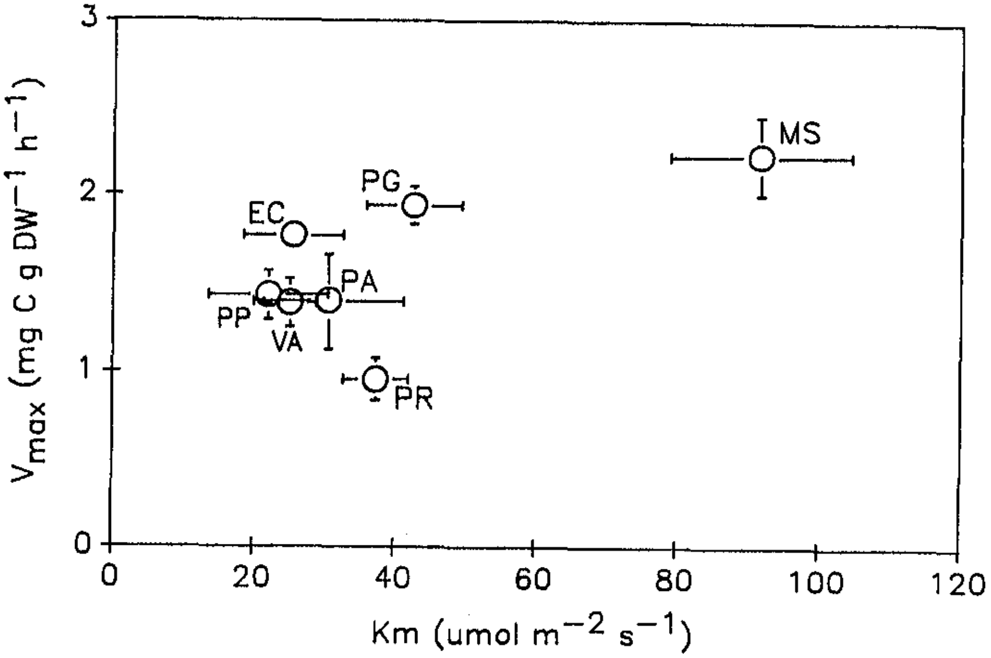


Figure 6. Michaelis-Menten maximum photosynthetic rate (V_{max}) versus respiration rate. EC, _E_. _canadensis_; MS, _M_. _spicatum_; PA, _P_. _amplifolius_; PG, _P_. _gramineus_; PP, _P_. _praelongus_; PR, _P_. _robbinsii_; VA, _V_. _americana_.

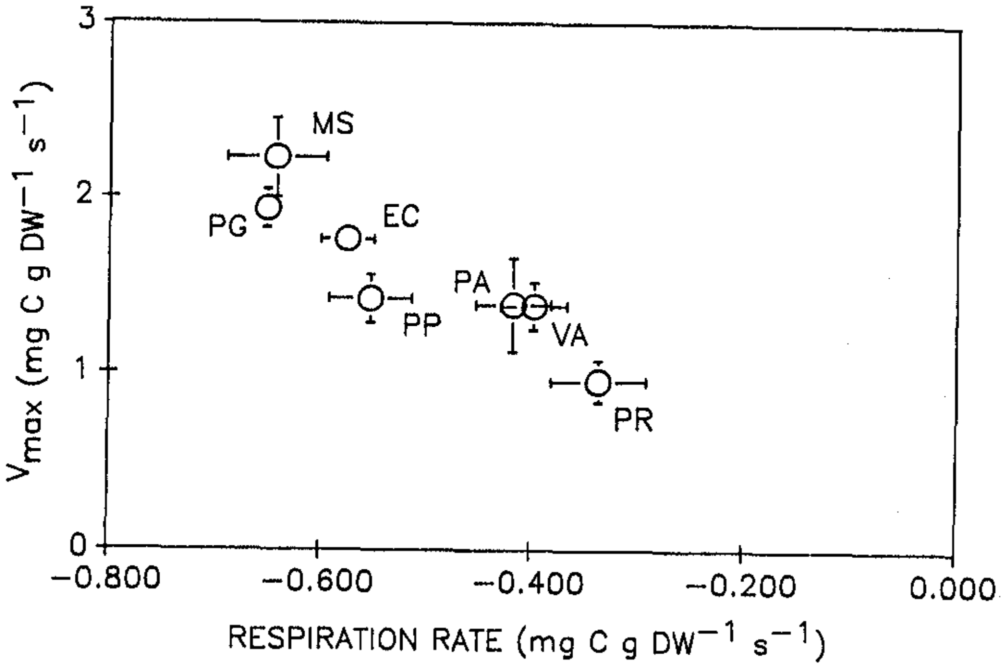


Figure 7. Light compensation point versus Michaelis-Menten half-saturation constant for light intensity (Km). EC, *E. canadensis*; MS, *M. spicatum*; PA, *P. amplifolius*; PG, *P. gramineus*; PP, *P. praelongus*; PR, *P. robbinsii*; VA, *V. americana*.

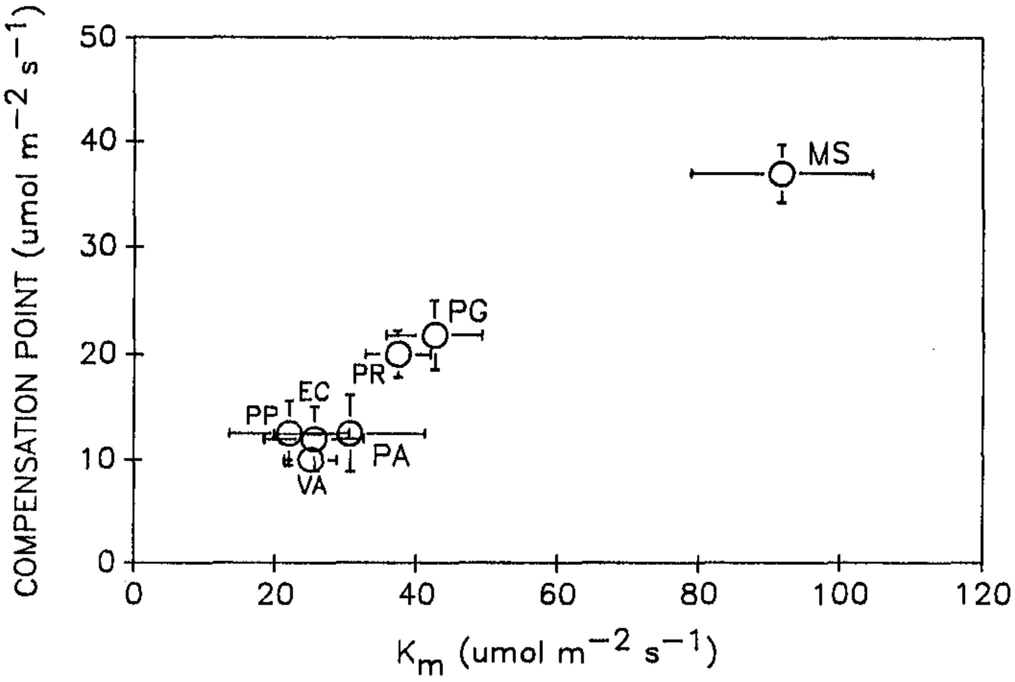
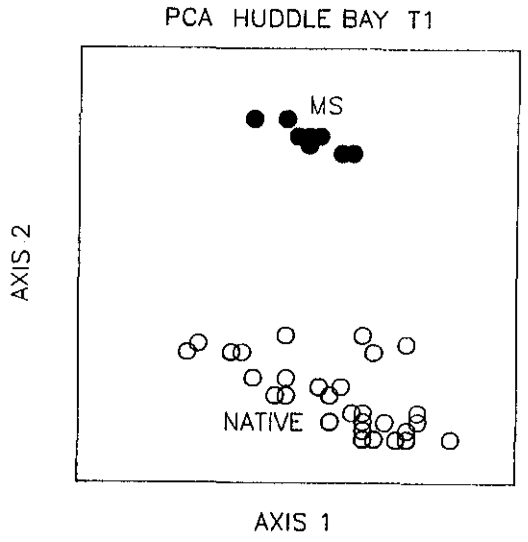


Figure 8. Principal Components Analysis (PCA) ordinations of percent cover quadrats by species for samples on a transect with a dense <u>M. spicatum</u> bed (T1, top) and a transect without a dense <u>M. spicatum</u> bed (T2, bottom).



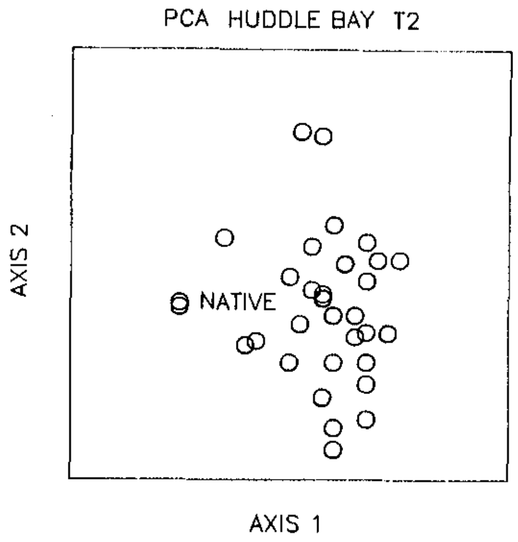
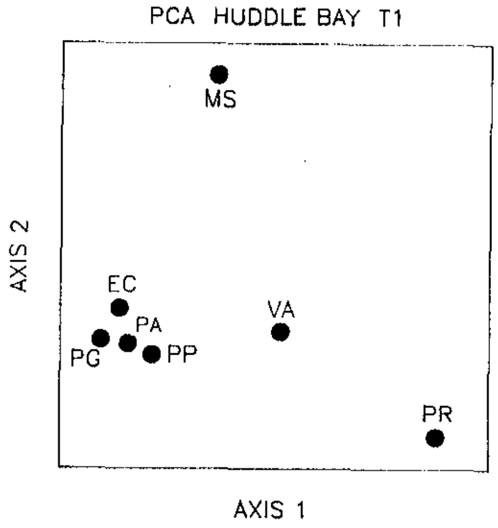


Figure 9. Principal Components Analysis (PCA) ordinations of species by percent cover quadrats for samples on a transect with a dense _M_. _spicatum_ bed (T1, top) and a transect without a dense _M_. _spicatum_ bed (T2, bottom). EC, _E_. _canadensis_; MS, _M_. _spicatum_; PA, _P_. _amplifolius_; PG, _P_. _gramineus_; PP, _P_. _praelongus_; PR, _P_. _robbinsii_; VA, _V_. _americana_.



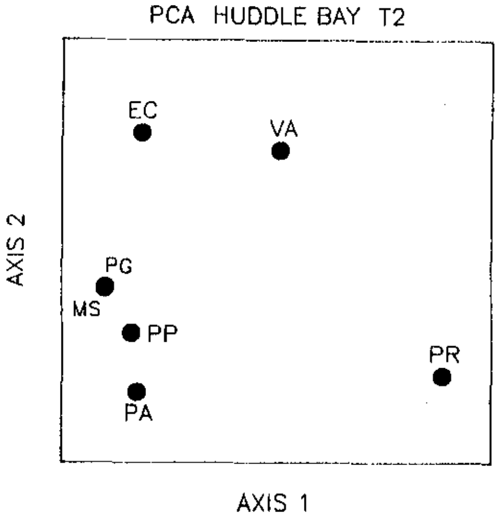
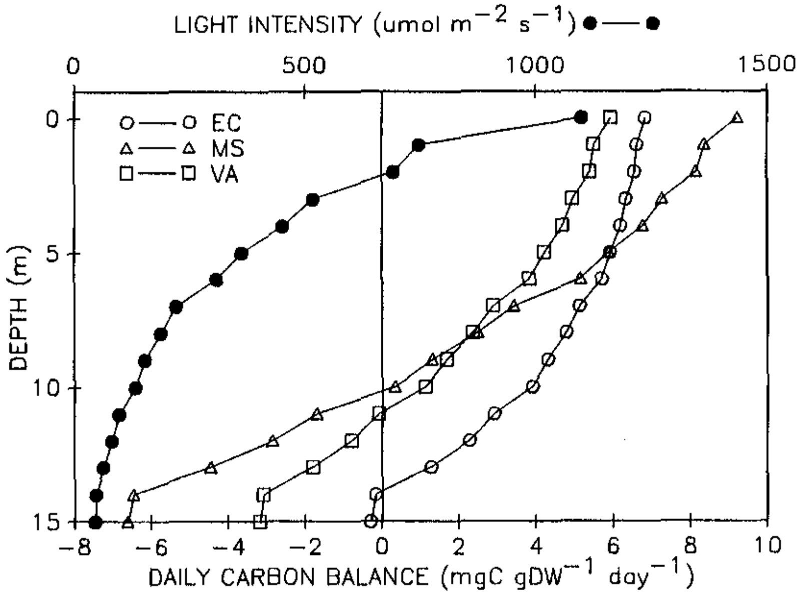


Figure 10. Light intensity profile (solid) used to model the 24-hour carbon balance of the seven species examined (open) utilizing the Michaelis-Menten parameters and measured respiration rates. EC, *E. canadensis*; MS, *M. spicatum*; PA, *P. amplifolius*; PG, *P. gramineus*; PP, *P. praelongus*; PR, *P. robbinsii*; VA, *V. americana*.



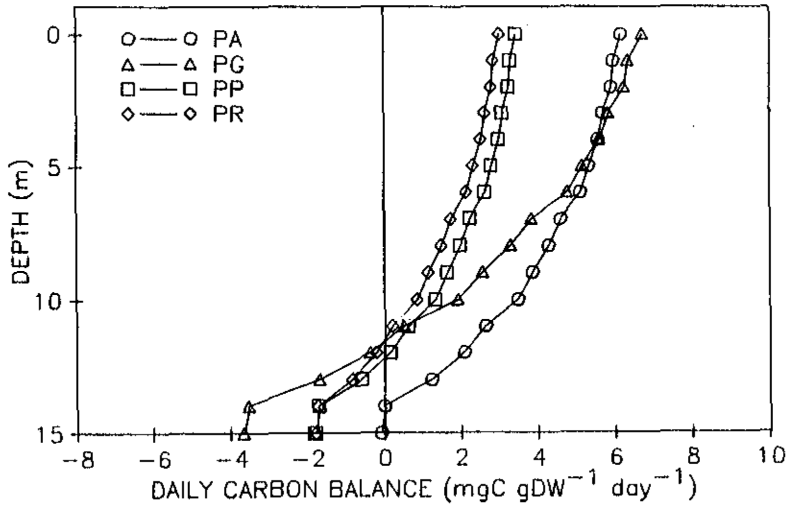


Figure 11. Light intensity profile (solid) through a *M. spicatum* canopy used to model the 24-hour carbon balance of the seven species examined (open) utilizing the Michaelis-Menten parameters and measured respiration rates. EC, *E. canadensis*; MS, *M. spicatum*; PA, *P. amplifolius*; PG, *P. gramineus*; PP, *P. praelongus*; PR, *P. robbinsii*; VA, *V. americana*.