

Morphological and Photosynthetic Characteristics of *Potamogeton obtusifolius* from Different Depths

S. C. MABERLY¹

ABSTRACT

Plants rooted between 0.5 m and 3.6 m were collected from Esthwaite Water, UK. Specific leaf area increased and leaf dry weight decreased with depth. Shoot length varied 5-fold over the depth range, largely because of variable mean internode length rather than internode number. Shoots close to the depth limit invested nearly 7-times less biomass in the production of a unit length of shoot than did shoots at 0.5 m. Shoot dry weight varied 14-fold with depth and was least at 3.6 m. Seed heads were not produced on plants rooted at 3.5 or 3.6 m, and side shoots were largely absent from shoots at 3.6 m. This and a very low average dry weight suggest that plants at this the maximum colonized depth are derived from turions produced in shallower water. Analysis of the response of photosynthesis to light at saturating inorganic carbon showed that the saturating rate per unit dry weight declined slightly with depth. The initial slope of photosynthesis to light increased 2.6-fold, the light compensation point decreased 1.4-fold and I_K decreased 3.4-fold with depth. The underwater light climate at any time and depth was modeled from field data in order to assess the relative effects of the measured characteristics on plant production. Calculations suggest that shoot elongation increased production 2.5-fold and superior photosynthesis characteristics increased production 2.8-fold for shoots rooted at 3.5 m. For shoots rooted at 1.5 m, shoot elongation was the major factor allowing increased production. Discrepancies between growth rate calculated from the model and estimated from biomass changes were particularly marked in shallow water and are consistent with carbon-limitation of growth.

Key words: specific leaf area, shoot elongation, light, production model, carbon-limitation.

INTRODUCTION

Differences between the characteristics of freshwater macrophytes from different depths within a lake are usually interpreted as being a response to the quality and, more frequently, the quantity of light to which they are exposed,

although other factors such as different nutrient availability in the sediment (Chambers and Kalff 1987), concentration of inorganic carbon (Maberly 1985b), temperature (Moeller 1980), or the direct effect of pressure (Hutchinson 1975) at great depth could also be involved. Nevertheless, the roughly 10% reduction in above-surface radiation caused by reflection at the air-water interface and the marked attenuation with depth which occurs within the water column mean that all but the most shallow waters are shade environments (Spence 1981). Two types of response to low light are typically recognized. The first includes changed leaf and shoot morphology such as increased shoot length, increased specific leaf area and changes in the content of photosynthetic pigments. The second involves changes in the photosynthetic apparatus which lead to increased rates at low light. However, in very few cases have both types of response been measured (but see Titus and Adams 1979) and so their relative contribution to performance has not been assessed: this is the aim of the present study on the grassy pondweed, *Potamogeton obtusifolius* Mert. and Koch. This species is non-rhizomatous and dies back to overwinter either as turions or potentially as seeds, and so the biomass of a shoot is largely the result of photosynthesis and growth in the current season.

MATERIAL AND METHODS

Collection site. *P. obtusifolius* was collected from the North Bay in Esthwaite Water, English Lake District, toward the end of the growing season between 1 and 14 September 1982. A grab operated from a boat was used to collect whole shoots from five rooting depths: 0.5, 1.5, 2.5, 3.5 and 3.6 m. The last depth was the maximum colonizable by this or any other macrophyte in this site. Attenuation of photosynthetically available radiation (PAR, 400 to 700 nm) was measured with a cosine-corrected submersible quantum sensor (Lambda Q 221-0174).

Morphology. Ten shoots from each depth were scored for shoot length, number of internodes on the main stem, number of branches, number of seed heads and also shoot dry weight after drying at 80°C for 24 hr. From each rooting depth the length and breadth of ten fully expanded leaves (6 for 3.6-m depth) from the apex of the shoots were measured. Leaf area (1-sided) was estimated from a comparison of the weight

¹Institute of Freshwater Ecology, Windermere Laboratory, Far Sawrey, Ambleside, Cumbria, LA22 0LP UK.

of photocopied leaves and graph paper of known area. Leaf weight was measured after drying at 80C for 24 hr.

Photosynthesis and respiration. Net photosynthesis and respiration were measured on healthy 5-cm apical shoots with duplicate measurements for each depth studied: 0.5, 1.5 and 3.5 m. Changes in O₂ concentration were measured under well-stirred conditions in a KHCO₃ solution of 0.4 mequiv l⁻¹, which is similar to the alkalinity of the site (Sutcliffe *et al.* 1982), using a Clark-type electrode (Radiometer E5046) in a perspex chamber at 14C, the ambient temperature at the time of collection. A pH value of 6.0, maintained by automatic injection of CO₂-enriched KHCO₃ solution controlled by a pH-stat system, produced a CO₂ concentration of 1.04 mmol l⁻¹ which was probably at or close to saturating. The chamber was illuminated from above by a 1000-W tungsten-halogen lamp whose light was filtered through a 16-cm-deep running water bath. Different photon irradiances, produced by interposing neutral-density filters between the lamp and the chamber, were measured with the sensor used in the field studies, placed in the position of the chamber. A dark respiration rate was measured at the end of the exposure to light. Full details of the equipment and procedure are given in Maberly (1985a). A non-linear regression was used to obtain estimates of the maximum gross rate of photosynthesis (P_{max}^{gross}) and the initial

slope of photosynthesis versus photon irradiance (α_p) using the equations of Smith (1936) as a model. The rate of dark respiration (R) was calculated from the mean of two measurements.

RESULTS AND DISCUSSION

Leaves. There was a progressive decline in average leaf dry weight with depth, and leaves at 0.5 m were nearly 1.5 times heavier than leaves at 3.6 m (Figure 1). Average leaf area was greatest between 1.5 and 3.5 m with slightly smaller leaves at the two extreme depths, but area only varied 1.13-fold. The average 1-sided specific leaf area (SLA) derived from these two measures followed the converse pattern to that for dry weight with leaves from 0.5 m having a low SLA of 0.72 cm² mg⁻¹ increasing 1.51-fold to 1.09 cm² mg⁻¹ at 3.5 m (Figure 1). The increase in SLA with depth is in broad agreement with the results of Spence and Chrystal (1970), Spence *et al.* (1973) and Spence and Dale (1978) for this and other species of *Potamogeton*. Average leaf length varied in a similar way to leaf area since the mean breadth at the different depths varied by only 0.15 mm. A linear regression between leaf length/mm (y) as a function of 1-sided area/cm² (x) yielded $y = 30.5 + 22.1*x$. The adjusted variance

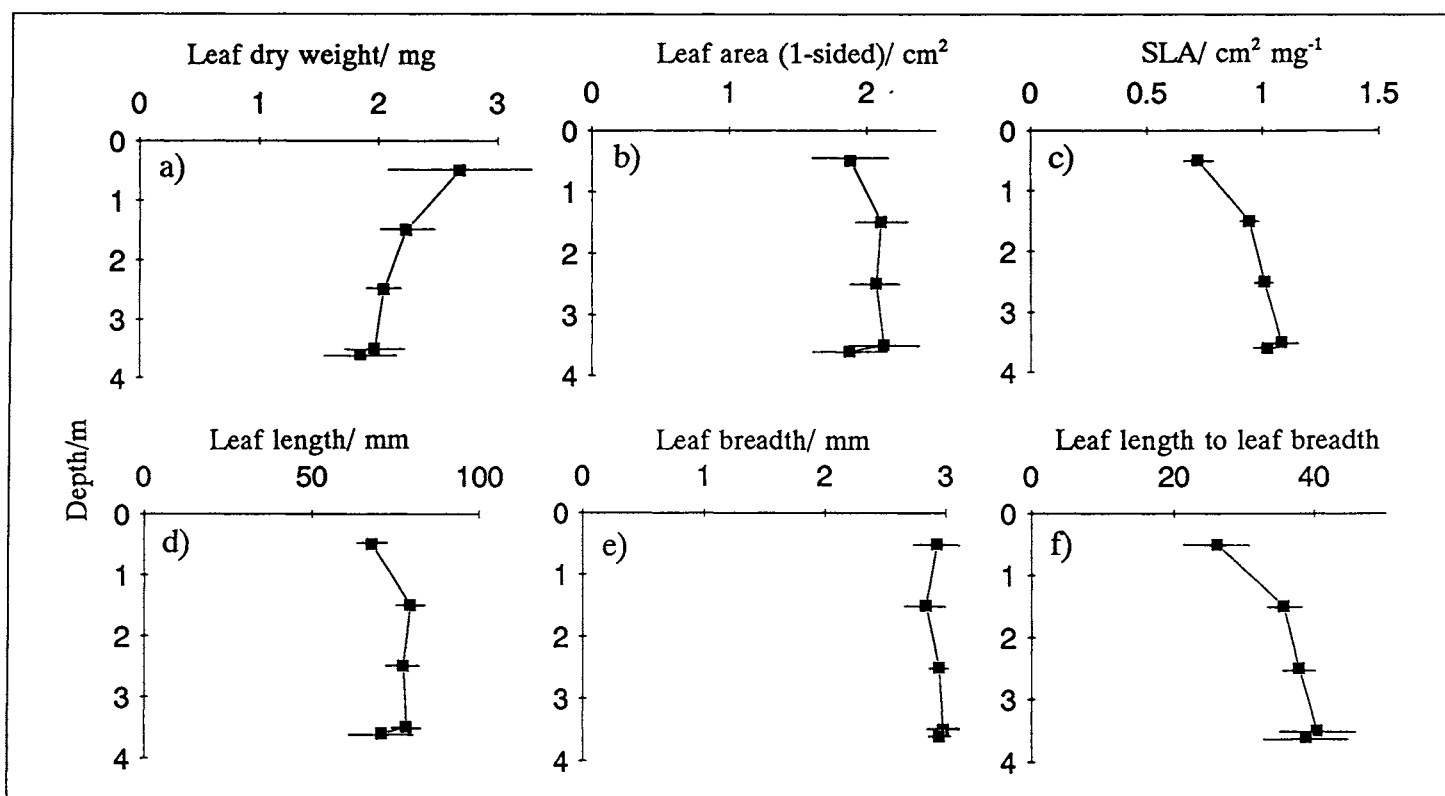


Figure 1. Average leaf characteristics at different depths; a) dry weight, b) 1-sided area, c) 1-sided SLA, d) length, e) breadth, f) length-to-breadth ratio. Error bars represent one standard deviation.

accounted for, r^2 , was 0.60 and an analysis of variance showed this to be statistically significant with $p < 0.001$. The average ratio of length to breadth varied 1.2-fold and was least at 0.5 m, but showed little trend unlike *P. richardsonii* where the length-to-breadth ratio increased at low light (Spence and Dale 1978).

Shoots. Average shoot dry weight varied 14.5-fold from a maximum of 591 mg at 1.5 m and a minimum of 41 mg at 3.6 m (Figure 2). Shoot length varied 5.16-fold and was greatest at 2.5 m and least at 0.5 m. The variation in shoot length with depth was mainly a result of the mean internode length (MIL) which varied 3.92-fold, while the number of internodes on the main stem varied only 1.76-fold (Figure 2). A similar increase in shoot length and internode length at low light has been found in a laboratory study with *P. crispus* (Tobiessen and Snow 1984). In *P. obtusifolius*, shoot length per unit dry weight increased monotonically with depth, so that shoots close to the depth limit invested nearly 7-times less biomass in the production of a unit length of shoot than did shoots at 0.5 m (Figure 2). This was achieved by plants at a depth of 3.6 m nearly eliminating side branches and producing leaves of low weight at each node. The average MIL of these plants, however, was only 2 cm which is less than that at all depths except in the shallowest water and plants at 2.5 m produced internodes with an average length of nearly 4 cm. The major morphological responses to growth at depth noted here, namely increased SLA, increased shoot length and increased MIL, are likely to be caused in large part by the reduced light level at depth, although other factors such as

temperature (Spence and Dale 1978; Barko *et al.* 1981) may also be involved.

Reproduction. Since *P. obtusifolius* is neither rhizomatous nor evergreen, next year's plants will derive either from seeds or from turions which, in this species, are starch-filled axial shoots with unextended internodes. A measure of the ability of plants from each rooting depth to contribute to next year's population was estimated from the number of seed heads and the number of side branches, which will determine the upper limit to the number of turions which can be produced. The number of seed heads produced per shoot at each depth was very variable, with a maximum of 7 for one plant at 1.5 m, the depth with the maximum average seed-head production and where 8 of the 10 shoots examined had flowered (Figure 2). Plants at 3.5 and 3.6 m failed to produce seed heads and only two of the plants at 0.5 m produced seed heads. A linear regression on all the data between number of seed heads per shoot (y) and shoot dry weight/mg (x) yielded: $y = -0.435 + 0.0041*x$; $r^2 = 0.56$, $p < 0.001$. The number of side branches, providing sites for turion production, in addition to the apex, was greatest on shoots at 1.5 and 2.5 m. At 3.6 m, only 1 of the 10 shoots had a side branch (Figure 2). A linear regression on all the data, except for three with high numbers of branches, between number of side branches per shoot (y) and shoot dry weight/mg (x) yielded: $y = 1.66 + 0.0289*x$; $r^2 = 0.62$, $p < 0.001$. The slope of this regression indicates that on average one side branch is produced for every 34.6 mg dry weight. This value is nearly identical to the average reported turion dry weight in this species of 33.8 mg (Webster 1975,

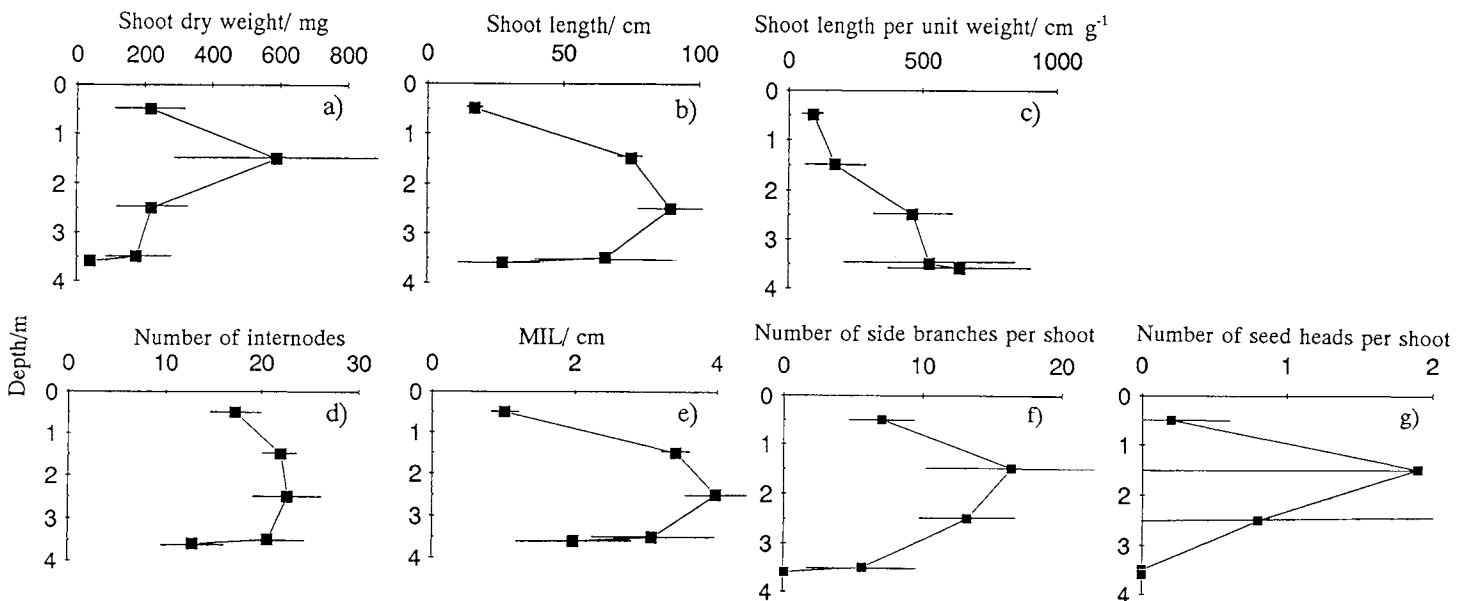


Figure 2. Average shoot characteristics at different depths; a) dry weight, b) length, c) length per unit dry weight, d) number of internodes on the main stem, e) MIL, f) number of side branches, g) number of seed heads. Error bars represent one standard deviation.

unpublished Ph.D. thesis, St. Andrews University, U.K.), which indicates that side branches are produced in relation to the capacity of the shoot to support turions. Shoots at the depth-limit of 3.6 m at the time of collection near the end of the growing season had no seed heads, and their average dry weight of 41 mg suggests that on average only 1 turion will be produced per plant, indicating no net population growth. If possible losses are taken into account then plants at this depth are probably maintained by transport of turions from shallower water.

Photosynthesis. The Smith (1936) model of the effect of light on rate of photosynthesis provided an adequate description of the data with the adjusted percentage variance accounted for varying between 87 and 99% (Table 1). The gross rate of photosynthesis at light- and CO₂-saturation was higher for plants rooted at 0.5 m than for those at the two other depths, but only varied 1.4-fold. If these rates are divided by the average specific leaf area (Figure 1) for each depth to estimate rates on an area basis, there is a 2-fold range with calculated rates of 2.52, 1.37 and 1.25 μmol O₂ m⁻² s⁻¹ (both sides) for shoots rooted at 0.5, 1.5 and 3.5 m, respectively. Surprisingly, the rate of dark respiration was greatest at 3.5 m (Table 1). The reason for this is unclear, although a similar effect has been described for *Hydrilla verticillata* (Barko and Smart 1981). The effect of the higher rate of dark respiration on rates of net photosynthesis at low light is largely offset by the high value of α₁ which was about 2.6-fold higher at 3.5 m than at 0.5 m. As a result, the calculated light compensation point (I_c) for shoots from 3.5 m was 1.4-fold lower than for shoots from 0.5 and 1.5 m. The calculated value I_K, which expresses the onset of light saturation, varied 3.4-fold and decreased with rooting depth (Table 1).

Modeled production. In order to assess the relative effect of the various morphological and physiological responses to growth at depth outlined above, a model was constructed to predict rates of photosynthesis using the photosynthetic responses in Table 1, and calculations of underwater photon irradiance following the approach in Maberly (1985b). The

photon irradiance at a given depth and time, I_z^t, (μmol m⁻² s⁻¹) was estimated from

$$I_z^t = \left\{ \text{antilog}_e \left[\log_e (0.9I_0^\Sigma) - (Kz) \right] / \lambda \right\} \left[1 + \cos \left(\frac{2\pi}{\lambda t} \right) \right] * 10^6 \quad (1)$$

where I₀^Σ is the daily photon irradiance (PAR) at the surface (mol m⁻²), K is the attenuation coefficient for PAR (log_e m⁻¹), z is the depth below the water surface (m), λ is the day length (s), and t is the time (s) from noon. Production over 24 hr was calculated for the weekly average values of I₀^Σ, K, z and λ for 15 wk between the end of April and the end of September 1982 where data were available. As will be discussed later, no account was taken of the effects of temperature and concentration of CO₂ on rates of photosynthesis.

The light climate and photosynthesis characteristics allowed shoot apices at 0.33 m to be 3.8-fold more productive than shoot apices at 2.84 m although the average daily photon irradiance was 6.1-fold higher (Table 2A). Shoot elongation was responsible for a small increase in light availability and productivity to plants rooted at 0.5 m. Shoots rooted at 1.5 m received 1.7-fold more light as a result of shoot elongation, causing a commensurate gain in production. Shoots rooted at 3.5 m received 1.55 times more light as a result of elongation, and this allowed production to increase by 2.5-fold (Table 2A).

The photosynthetic characteristics of shoots rooted at 3.5 m gave greater modeled production at all depths because of the high α₁ value. However, differences between the different photosynthesis characteristics were relatively minor at the surface whereas at 2.84 m, the depth of the 3.5-m apices, there was a 2.8-fold and 1.4-fold greater production for the photosynthesis characteristics of shoots rooted at 3.5 m compared to 0.5 m and 1.5 m, respectively (Table 2B).

TABLE 1. CHARACTERISTICS OF THE RESPONSE OF PHOTOSYNTHESIS TO LIGHT AT 0.4 mmol HCO₃⁻¹, SATURATING CONCENTRATION OF 1.0 mmol CO₂ l⁻¹, AND 14C. R DETERMINED AS THE MEAN OF TWO VALUES, P_{max}^{gross} AND α₁ DETERMINED BY NONLINEAR REGRESSION, SEE TEXT. STANDARD DEVIATIONS GIVEN IN PARENTHESES.

Rooting depth (m)	P _{max} ^{gross}	R	α ₁ ⁻¹ (μmol O ₂ g ⁻¹ DW h ⁻¹ / μmol photon m ⁻² s ⁻¹)	I _c	I _K	r ²
	(μmol O ₂ g ⁻¹ DW h ⁻¹)			(μmol photon m ⁻² s ⁻¹)		
0.5	1304 (66)	-39.9 (5.3)	3.08 (0.22)	12.9	423	0.97
1.5	933 (75)	-32.9 (1.2)	3.35 (0.49)	9.8	278	0.87
3.5	972 (16)	-74.5 (1.2)	7.89 (0.33)	9.5	123	0.99

TABLE 2. COMPARISONS OF MODELED AVERAGE PRODUCTION OVER 24 HR ($\text{mmol O}_2 \text{ g}^{-1} \text{ DW d}^{-1}$) AND AVERAGE DAILY PHOTON IRRADIANCE AT DEPTH ($\text{mol m}^{-2} \text{ d}^{-1}$) FOR DIFFERENT STATED CONDITIONS IN RESPONSE TO A. SHOOT ELONGATION, B. PHOTOSYNTHESIS CHARACTERISTICS, AND C. THE RELATIVE EFFECT OF SHOOT ELONGATION AND PHOTOSYNTHETIC CHARACTERISTICS

A. Effect of shoot elongation from the rooting depth								
Depth (m)		Average I_z^{Σ}		24-hr production		Top/bottom		
Bottom	Top	Bottom	Top	Bottom	Top	Average I_z^{Σ}	24-hr production	
0.5	0.33	10.73	12.27	6.42	7.15	1.14	1.11	
1.5	0.75	5.07	8.84	3.71	5.46	1.74	1.47	
3.5	2.84	1.29	2.00	0.77	1.90	1.55	2.47	

B. Effect of photosynthesis characteristics of named rooting depths					
Depth of shoot top (m)	24-hr production			24-hr production stated depth/0.5 m	
	0.5 m	1.5 m	3.5 m	1.5 m	3.5 m
0.33	7.15	6.86	8.65	0.96	1.21
0.75	5.41	5.46	7.55	1.01	1.40
2.84	0.68	0.94	1.90	1.38	2.79

C. The relative effect of shoot elongation and photosynthesis characteristics								
Rooting depth (m)	Features characteristic of named rooting depths				24-hr production		% contribution to increased production	
	Unadapted		Adapted		Unadapted	Adapted	Length	P vs I
	Length	P vs I	Length	P vs I				
1.5	0.5	0.5	1.5	1.5	3.46	5.46	88.5	11.5
1.5	0.5	0.5	1.5	3.5	3.46	7.55	48.1	51.9
3.5	0.5	0.5	3.5	3.5	0.22	1.90	36.1	63.9

The relative contribution of shoot elongation and photosynthetic characteristics to the greater modeled production at depth by the shoots rooted at 1.5 m and 3.5 m compared to those at 0.5 m was assessed by modeling production when only one of these two variables was optimal. The results suggest (Table 2C) that for shoots rooted at 3.5 m, 64% of the increased production is a result of "shade" photosynthesis characteristics. For shoots rooted at 1.5 m, shoot elongation was responsible for 89% of the increased production. If these shoots had the photosynthesis characteristics of the 3.5-m shoots, however, then production would have increased by 1.4-fold and shoot elongation and "shade" photosynthesis characteristics would have had approximately equal influence in allowing increased production. The production data in Table 2 can be used to calculate relative growth rates using the assumptions that 1 mol O_2 produced is equivalent to 1 mol

CO_2 fixed, and that carbon forms 0.45 g of each gram dry weight. These calculations yield average relative growth rates of 0.167, 0.111 and 0.024 $\log_e \text{ d}^{-1}$ for shoots rooted at 0.5, 1.5 and 3.5 m, respectively. Biomass-based growth rates were calculated from the measured average shoot biomass, an assumed initial turion biomass of 35 mg dry weight and an assumed growing season of 130 days. These growth rates were lower than those predicted by the model at 0.014, 0.022 and 0.012 $\log_e \text{ d}^{-1}$, by 11.9, 5.1 and 2.0-fold for 0.5, 1.5 and 3.5 m, respectively. The generally lower growth rates based on biomass changes could be caused by several factors such as loss of dry weight during the growing season and a shorter growing season than assumed. However, the fact that the difference between modeled and biomass based growth rates decreases with depth strongly suggests that a major cause of the difference is likely to be limitation of rates of photosynthesis

by availability of inorganic carbon. Depth profiles of CO₂ concentration made during the season show increased concentration at depth (see for example Maberly 1985b, Figures 1 and 2), which is in accord with the suggestion that carbon-limitation is involved.

ACKNOWLEDGMENTS

I thank Margaret Hurley for performing the statistical calculations. This work was supported by the N.E.R.C.

LITERATURE CITED

- Barko, J. W., D. G. Hardin and M. S. Matthews. 1981. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. *Can. J. Bot.* 60:877-887.
- Barko, J. W. and R. M. Smart. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. *Ecol. Monogr.* 51:219-235.
- Chambers, P. A. and J. Kalf. 1987. Light and nutrients in the control of aquatic plant community structure. I. *In situ* experiments. *J. Ecol.* 75: 611-619.
- Hutchinson, G. E. 1975. *A Treatise on Limnology*, Vol. III Limnological Botany. John Wiley & Sons, NY. 660 pp.
- Maberly, S. C. 1985a. Photosynthesis by *Fontinalis antipyretica*. I. Interaction between photon irradiance, concentration of carbon dioxide and temperature. *New Phytol.* 100:127-140.
- Maberly, S. C. 1985b. Photosynthesis by *Fontinalis antipyretica*. II. Assessment of environmental factors limiting photosynthesis and production. *New Phytol.* 100:141-155.
- Moeller, R. E. 1980. The temperature-determined growing season of a submerged hydrophyte: tissue chemistry and biomass turnover of *Utricularia purpurea*. *Freshwat. Biol.* 6:137-144.
- Smith, E. L. 1936. Photosynthesis in relation to light and carbon dioxide. *Proc. Natl. Acad. Sci.* 22:504-511.
- Spence, D. H. N. 1981. Light quality and plant response underwater. *In: Plants and the Daylight Spectrum* Ed. H. Smith. pp. 245-275. Academic Press, London.
- Spence, D.H.N., R.M. Campbell and J. Chrystal. 1973. Specific leaf areas and zonation of freshwater macrophytes. *J. Ecol.* 61:317-328.
- Spence, D.H.N. and J. Chrystal. 1970. Photosynthesis and zonation of freshwater macrophytes. II. Adaptability of species of deep and shallow water. *New Phytol.* 69:217-227.
- Spence, D.H.N. and H.M. Dale. 1978. Variations in the shallow water form of *Potamogeton richardsonii* induced by some environmental factors. *Freshwat. Biol.* 8:251-268.
- Sutcliffe, D.W., T.R. Carrick, J. Heron, E. Rigg, J.F. Talling, C.W. Woof and J.W.G. Lund. 1982. Long-term and seasonal changes in the chemical composition of precipitation and surface waters of lakes and tarns in the English Lake District. *Freshwat. Biol.* 12: 451-506.
- Titus, J.E. and M.S. Adams. 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. *Oecologia* 40:273-286.
- Tobiessen, P. and P.D. Snow. 1984. Temperature and light effects on the growth of *Potamogeton crispus* in Collins Lake, New York State. *Can. J. Bot.* 62:2822-2826.