THE ECOLOGY OF THE AQUATIC MACROPHYTE MYRIOPHYLLUM SPICATUM L.

by

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ABSTRACT

While aquatic macrophytes appear to play a major role in the ecology of lakes, little is known about the variables that determine the structure of biomass of macrophyte communities in nature. The purpose of this thesis was to quantify variables thought likely to affect the growth of Myriophyllum spicatum L., in order to assess both their variability, and to use the most appropriate variables to predict the in situ growth rate. First, the variance (S^2) around the mean ($\bar{x}$) was determined for each of six variables: growth rates (relative and specific), photosynthetic rate, tissue nutrient content (N&P) and photon flux density. This permitted the determination of the number of samples required to determine statistically significant differences among means (Chapter 1). Second, regression equations were produced that allow the prediction of the expected variance from mean values obtained (Chapter 1). Last, regression models were developed to predict both within season and whole growing season specific growth rates, season maximum biomass and community biomass. This was done using 5 categories of predictors: tissue nutrient content (N,P&K), shoot tip morphology (leaf length, number of whorls), photosynthetic rate, photon flux density and sediment organic matter (Chapter 2). By here quantifying the variability and pattern of growth of one species within one lake, future investigations elsewhere will be in a position to test the generality of these patterns.

RÉSUMÉ

Même si les macrophytes aquatiques semblent jouer un rôle majeur dans l'écologie des lacs, on connaît peu de choses sur les variables qui déterminent la structure de la biomasse des collectivités de macrophytes dans la nature. La présente thèse a pour objectif de quantifier les variables qui affectent probablement la croissance de Myriophyllum spicatum L. afin d'en déterminer la variabilité et de choisir les plus appropriées pour prédire le taux de croissance in situ. En premier lieu, la variance (S^2) autour de la moyenne ($\bar{x}$) a été déterminée pour chacune des six variables: taux de croissance (relatif et spécifique), taux de photosynthèse, teneur tissulaire en nutriments (N&P) et densité du flux de photons. Cette étape a permis de déterminer le nombre d'échantillons requis pour établir les différences d'importance statistique parmi les moyennes (Chapitre 1). En second lieu, les équations de régression ont été élaborées pour permettre la prédiction de la variance attendue à partir des valeurs moyennes obtenues (Chapitre 1). En dernier lieu, des modèles de régression ont été élaborés afin de prédire à la fois au cours de la saison et pour l'ensemble de la saison de croissance, des taux de croissance spécifiques, la biomasse maximum pour la saison et la biomasse de la collectivité. Pour ce faire, on a utilisé cinq catégories d'indices de prédiction: teneur tissulaire en nutriments (N, P&K), morphologie de la pointe des pousses (longueur de la feuille, nombre de circovolutions), taux de photosynthèse, densité du flux de photons et matières organiques dans les sédiments (Chapitre 2). En quantifiant ainsi la variabilité et les schèmes de croissance d'une espèce dans un lac, on pourra, lors des recherches ultérieures en un autre lieu, vérifier la généralité de ces schèmes.

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Chapter 2:

PREFACE

As required by the regulations of the Faculty of Graduate Studies and Research of McGill University, the following statements are made.

This thesis has been prepared in the format of two separate papers, suitable for submission to learned journals, as permitted by Faculty regulations. The first two chapters of the thesis have been submitted for publication co-authored by Dr. Jacob Kalff, who supervised this study.

This thesis constitutes a contribution to original knowledge by showing: 1) that most of the variation in Myriophyllum shoot biomass is described from shoot length (r^2 = 0.77-0.86; 2) the sample size necessary to determine statistically significant differences in Myriophyllum growth rate, photosynthetic rate, tissue nutrient content and photon flux density; 3) that tissue phosphorous is the most important single variable describing (r^2=0.43) specific growth rates of Myriophyllum for the growing season as a whole; 4) that for the growing season as a whole, 65 % of the variation for the specific growth rate of Myriophyllum can be described using the four variables: tissue phosphorus, tissue nitrogen, tissue N:P ratio, and photon flux density; 5) that it is possible to describe most of the variation in specific growth rate during 4 of 5 two week growth periods; 6) that showed season maximum biomass of Myriophyllum, Vallisneria, and all species combined is predictable from sediment organic content; 7) that the number of whorls per stem tip is an excellent predictor (r^2=0.93-0.96) of stem densities in Myriophyllum weedbeds.

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GENERAL INTRODUCTION

The ecology of Myriophyllum spicatum L. has received much attention since its introduction to North America, both because it has become a nuissance growth in many lakes and because its ability to occupy and dominate diverse aquatic habitats has intrigued aquatic ecologists (Grace and Wetzel 1978). Work on this species is, however, but one aspect of studies on the biomass and community composition of the littoral of some lakes (Best 1981, Westlake 1981, Adams and Prentki 1982, Engel and Nichols 1984, Hakanson 1984). Efforts have been made to identify variables that affect plant growth in both laboratory (Aiken and Picard 1980, Barko 1983) and field studies (Adams and McCracken 1974, Nichols and Keeney 1976, Tessenow and Baynes 1978, Carignan and Kalff 1980, Langeland 1982). However, no studies known to me have quantified the temporal and spatial variation of growth influencing variables, with the dual purpose of optimizing sampling effort and selecting statistically significant sample sizes. As a consequence, investigations that do not consider an appropriate sample size will of necessity yield ambiguous results (see Southwood 1966, Cochran 1977, Downing 1979).

Among the variables thought of having an influence on macrophyte growth are: tissue nutrient content (Gerloff 1975, Adams and Prentki 1982), light intensity (Spence 1976, Fair and Meeke 1983, Chambers and Kalff submitted), photosynthetic rate (Simpson et al. 1980, Schmitt and Adams 1981), sediment characteristics (Denny 1972, Bole and Allen 1979, Carignan and

Kalff 1980, Kimbel 1982, Barko and Smart 1983) and wave energy (Keddy 1982). However, these studies provide no insight as to which variables are the most important in Myriophyllum growth in nature.

This thesis is composed of two chapters to describe, and place in perspective, in situ measures of some variables proposed to affect Myriophyllum growth. The first chapter allows the determination of statistically significant sample sizes, by describing the variance (S^2) from mean ($\bar{x}$) values of study variables. In the second chapter models are developed that predict specific growth rate, maximum biomass and community biomass of Myriophyllum weedbeds. Data in both chapters discuss data collected and analysed by two week growth periods and for the 1982 growing season as a whole in Lake Memphremagog, Quebec-Vermont.

Literature Cited

Adams, M.S. and McCracken, M.D., 1974. Seasonal production of the Myriophyllum component of Lake Wingra, Wisconsin. Ecology, 62: 457-467.

Adams, M.S. and Prentki, R.T., 1982. Biology, metabolism and functions of littoral submersed weedbeds of Lake Wingra, Wisconsin, USA: a summary and review. Archiv. f. Hydrobiol. Suppl.-Bd., 62: 333-409.

Aiken, S.G. and Picard, R.R., 1980. The influence of substrate on the growth and morphology of Myriophyllum spicatum and Myriophyllum excalbescens. Can. J. Bot., 58(9): 1111-1118.

Barko, J.W., 1983. The growth of Myriophyllum spicatum L. in relation to selected characteristics of sediment and solution. Aquat. Bot., 15: 91-103.

Barko, J.W. and Smart,R.M., 1983. Effect of organic matter additions to sediment on the growth of aquatic plants. J. Ecol., 71: 161-175.

Best, E.P.H., 1981. A preliminary model of Ceratophyllum demersum L. Verh. Internat. Verin. Limnol., 21: 1484-1491.

Bole, J.B. and Allen, J.R., 1979. Uptake of phosphorus from sediment of aquatic plants Myriophyllum spicatum and Hydrilla verticillatum. Water. Res., 12(5): 353-359.

Carignan, R. and Kalff, J., 1980. Phosphorus sources for aquatic weeds: water or sediments? Science, 207: 987-989.

Chambers, P.A. and Kalff, J., submitted. The influence of sediment and irradiance on the growth and morphology of Myriophyllum spicatum L. Aquat. Bot.

Cochran, W.G., 1977. Sampling techniques. John Wiley and Sons, New York, 428 pp.

Denny, P., 1972. Sites of nutrient absorption in aquatic macrophytes. J. Ecol., 60: 819-829.

Downing, J.A., 1979. Aggregation, transformation, and the design of benthos sampling programs. J. Fish. Res. Board Can., 136: 1454-1463.

Engel, S. and Nichols, S.A., 1984. Lake sediment alteration for macrophyte control. J. Aquat. Plant Manage., 22: 38-41.

Fair, P. and Meeke, L., 1983. Seasonal variations in the pattern of photosynthesis and possible adaptive response to varing light flux regimes in Ceratophyllum demersum L. Aquat. Bot. 15: 81-90.

Hakanson, L., 1984. On the relationship between lake trophic level and lake sediments. Water Res., 18: 303-314.

Gerloff, G.C., 1975. Nutrient ecology of nuisance aquatic plants. Environmental Protection Agency Ecological Research Series. EPA-770/3-75-027. Corvalis, Oregon, USA: USEPA. 78 pp.

Grace, J.B. and Wetzel, R.G., 1978. The production biology of Eurasian watermilfoil (Myriophyllum spicatum L.): a review. J. Aquat. Plant Manage., 16: 1-11.

Keddy, P.A., 1982. Quantifying within lake gradients of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquat. Bot., 14: 41-58.

Kimbel, J.C., 1982. Factors affecting potential intralake colonization by Myriophyllum spicatum L. Aquat. Bot., 14(3): 295-307.

Langeland, K.A., 1982. Relations among hydrosoil, water chemistry, transparency, chlorophyll a, and submersed macrophyte biomass. Ph.D. diss. Univ. of Florida. 143 pp.

Nichols, D.S. and Keeney, D.R., 1976. Nitrogen nutrition of Myriophyllum spicatum: uptake and translocation of N by shoots and roots. Freshwater Biol., 6: 145-154.

Schmitt, M.R. and Adams, M.S., 1981. Dependance of rates of apparent photosynthesis on tissue phosphorus concentrations in Myriophyllum spicatum L. Aquat. Bot., 11: 379-387.

Simpson, P.S., Eaton, J.W., and Hardwick, K., 1980. The influence of environmental factors on apparent photosynthesis and respiration of the submersed macrophyte Elodea canadensis. Plant, Cell and Environ., 3: 415-423.

Southwood, T.R.E., 1966. Ecological methods with particular reference to the study of insect populations. Chapman and Hall, London, 391 pp.

Spence, D.N.H., 1976. Light and plant response in fresh water. In: G.C. Evans, R. Brainbridge and O. Rackman (Editors). Light As An Ecological Factor: II. 16 th Symp. Br. Ecol. Soc. March 26-28, 1974, pp. 93-33.

Tessenow, U. and Baynes, Y., 1978. Redox-chemical effects of Isoetes lacustrus L. in littoral sediments of Lake Feldsee (Black Forest). Archiv. f. Hydrobiol., 82: 20-48.

Westlake, D.F., 1981. The development and structure of aquatic weed populations. In: Proceedings Aquatic Weeds And Their Control 1981, pp. 33-48.

CHAPTER 1

Temporal Variation In *Myriophyllum Spicatum* L.: The Selection Of Sample Size

Abstract

To select the appropriate number of samples, and thus to optimize sampling, the variance (S^2) around the mean ($\bar{x}$) must be known. Here, the variance around mean measures of growth rates (relative and specific), photosynthetic rate, tissue nutrient content (phosphorus, nitrogen and potassium) and photon flux density were determined for a natural population of Myriophyllum spicatum L. growing at 2,6 m in Lake Memphremagog, Quebec-Vermont. The regression equations produced allow the prediction of variance using mean values for all plant attributes, tissue potassium excepted. The required sample size, to estimate 20 % of the mean for a normally distributed population (ie. standard error / mean = 0.2), changed during the growing season but commonly required fewer than 11 replicates for all but growth rate and tissue nitrogen. The required replicates for growth rate were well over 100, whereas, tissue nitrogen required a maximum of 41 samples.

Introduction

Experimental tests of difference between treatments require an estimate of variance because without this the appropriate sample size cannot be selected (Downing 1979, Sokal and Rohlf 1981). Macrophyte beds are notoriously variable in either or both density and species composition with growth reportedly affected by sediment nutrients (Barko 1983), tissue nutrients (Adams et al. 1978, Langeland 1982), light intensity (Barko et al. 1982) and photosynthetic rate (Titus et al. 1975, Best 1981). Light intensity also affects shoot morphology and stem density (Barko et al. 1982, Chambers and Kalff submitted). Yet the freshwater (Aiken and Picard 1980, Schmitt and Adams 1981, Adams and Prentki 1982) and the marine (Nixon and Oviatt 1973, Patrick and DeLaune 1976, Littler and Arnold 1980, Rosenburg and Ramus 1982) literature has not considered the variability in the selection of macrophyte sampling programs or in the interpretation of data.

The purpose of this paper is to assess the in situ variability of 5 plant attributes of Myriophyllum spicatum L. These are: shoot morphology, growth rate, tissue nutrient content (phosphorus, nitrogen and potassium), stem density and maximum biomass. In addition, photon flux density was measured to estimate the photosynthetically active radiation reaching the plant canopy. These plant attributes and light intensity measures were used to determine the relation between their means and variances in order to estimate the optimum sampling effort and sample sizes required.

Methods and Procedures

Thirty adjoining plots (5.0 x 0.5 m) were laid out parallel to the shore at a water depth of 2.6 m in Quinn Bay, Lake Memphremagog, Quebec-Vermont (45° 6' 0" N, 72° 5' 45" W), in May 1982, with each of 6 plots forming a block. One randomly chosen plot in each block was sampled during each of five growth periods. The two week growth periods were started on 5 and 16 June, 2 and 16 July, and 1 August, 1982. At these times a SCUBA diver tagged 7 shoots of Myriophyllum and measured the central and side stem lengths. Two weeks later the tagged shoots were re-measured and the distal 30 cm central stem cut for the analysis of tissue nutrient content and the measurement of photosynthetic rate. Biomass was estimated by measuring stem lengths on 27 June, 7 July and 8 August. The lengths were converted to biomass using linear regression relations developed nearby at a depth of 2.5 m (Table 1). To find the best regressions, data were first transformed using standard statistical procedures (Box and Tidwell 1962, Box and Cox 1964). The relative growth rate ($mg \cdot plant^{-1} \cdot d^{-1}$) was determined by measuring the difference in biomass between the beginning and end of each growth period, while the specific growth rate ($mg \cdot g^{-1} \cdot plant^{-1} \cdot d^{-1}$) was obtained by dividing the relative growth rate by the biomass present at the beginning of a growth period (Evans 1972, Harper 1977).

Table 1. A comparison of Myriophyllum spicatum shoot morphology of central and side stems growing at 2.5 m. Coefficients to predict biomass (g) from stem lengths (cm) use the equation form: $\ln Y = a + b \cdot X^{\alpha}$.

Stem Fraction	Sampling Period	r^2 ($P < 0.001$)	α	Intercept (a)	Slope (b)	C.V. (%)
Central	1	0.80	0.409	-2.60	0.676	19.3
	2	0.77	0.472	-0.42	0.327	18.1
	3	0.78	0.487	-0.68	0.324	23.7
Side	1	0.79	-0.001	3087.	-3094.	13.5
	2	0.79	-0.157	4.39	-11.51	9.6
	3	0.86	-0.091	0.26	- 7.85	11.7

Tissue nutrient concentrations were determined by a wet digestion (Thomas et al. 1967) of the lower 15 cm of the distal 30 cm cut from 7 stems sampled in each plot. Phosphorus (mg $P \cdot g^{-1}$ dry wt) and nitrogen (mg $N \cdot g^{-1}$ dry wt) were measured using the ascorbate method and hydrazine sulphate colour development method, respectively, with a Canlab autoanalyzer; whereas, an atomic absorption spectrophotometer (Perkin-Elmer 403) was used for potassium (mg $K \cdot g^{-1}$ dry wt) (Golterman and Clymo 1969).

Photosynthetic carbon fixation rates were obtained by taking the 15 cm tips of 7 central stems, placing one stem from each plot in a 500 ml rectangular glass bottle, adding $NaH^{14}CO_3$ (Adams and McCracken 1974) and incubating the bottles for one hour in a modified Fee incubator (Fee 1973) under saturated light conditions (1000 $\mu E \cdot cm^{-2} \cdot s^{-1}$) (Grace and Wetzel 1978) at the epilimnetic temperature. After incubation the shoots were rinsed sequentially for 30 seconds in each of three solutions: lake water, 0.1 N HCl, and again in lake water, to remove any adhering isotope. Each shoot was then dried at 80° C until constant weight, homogenized and re-dried, subsampled by weighing (10 to 25 mg) into cellophane capsules, combusted in an automated oxidizer (Intertechnique Oximat IM 4101), and the ^{14}C activity determined in a liquid scintillation counter. The photosynthetic rate was expressed as mg $C \cdot g^{-1}$ dry wt $\cdot h^{-1}$ after a 6 % isotope correction factor was applied.

A solarimeter (Yellow Springs, Inc.) located within 1 km of the sample site measured incident solar irradiance (ISI,

$\mu W \cdot cm^{-2} \cdot d^{-1}$). Using ISI and the underwater attenuation coefficients determined with a radiometer (KAHLISCO), the photon flux density ($E \cdot m^{-2} \cdot d^{-1}$) was calculated for the individual plant stem tips at depth, following Chambers and Kalff (submitted).

Stem density was determined at the end of each growth period, but before the cutting of the shoot tips, to give a measure of Myriophyllum abundance. Plants were visually classified, by colour and stem morphology, as either plants that had overwintered (old) or plants of the year (new), and expressed as stems$\cdot m^{-2}$.

A morphological measure of plant adaptation to environmental conditions (Harper 1977) was obtained by measuring both the number of leaf whorls, and the average leaf length (mm) of leaves on the basal whorl of each distal 15 cm central stem. Harvest of macrophyte standing crop between August 15 to 20 provided a measure of the maximum biomass ($g \cdot m^{-2}$). At this time stems were cut at the sediment surface, separated by species, washed free of loose epiphytes, and dried at 80° C to constant weight.

Regression relations were developed to estimate the variance (S^2), using the mean ($\bar{x}$) of sample replicates (i) (Cochran 1977, Downing 1979, Green 1979):

$$(1) \qquad \text{Log}_{10}(S^2_i) = a + b \cdot \text{Log}_{10}(\bar{x}_i)$$

Although variance-mean relations have been comonly criticized for their inability to describe aggregation of organisms (Titmus 1983), the relation remains useful in predicting S^2.

To determine the appropriate sample size (n) for characteristics used, numerical values were substituted into the equation:

$$(2) \qquad n = (S / p \cdot \bar{x})^2$$

with 0.2 chosen as the precision (p), or standard error (SE) size relative to the mean, to represent 20 % of the mean for a population showing a normal distribution (ie. $p = SE / \bar{x} = 0.2$) (Sokal and Rohlf 1981). A precision of 0.2 is commonly used for the selection of sample size (Cochran 1977, Downing 1979). Subsequently, the appropriate sample sizes (n) were calculated using the measured variance (S^2) of the characteristics investigated.

The McGill University computing system and Statistical Analysis Systems (1982) software were used for data analysis. The Duncan's multiple range test was used to identify statistically significant ($P < 0.05$) differences among means (Zar 1974).

Results

Significant ($P < 0.001$) regression equations described the sample variance from the means of the plant attributes and photon flux, tissue potassium content excepted (Table 2). The required sample sizes to determine significant differences (eq. 2) were generally smaller than 11 replicates (Table 3). Two attributes required much larger sample sizes with up to 41 for tissue nitrogen content and well over 100 for growth rate. Significant differences between means were found for all plant attributes and photon flux, tissue nitrogen content excepted, during some growth periods (Table 3). Total stem numbers significantly differed between the first 2 and last 3 growth periods (Fig. 1a), with the new to total stem ratios changing between all but the last two growth periods (Fig. 1b).

Table 2. Linear regression relations predicting variance from mean values, using the model Log (S^2) = a + b·Log ($\bar{x}$), for variables related to Myriophyllum spicatum growth and photosynthesis.

Variable	r^2	Sample Size	Inter-cept (a)	Slope (b)	P > F	Range
a. Specific Growth Rate ($mg \cdot g^{-1} \cdot plant^{-1} \cdot d^{-1}$)	0.57	25	0.34	1.01	0.001	−141 - 279
b. Relative Growth Rate ($mg \cdot plant^{-1} \cdot d^{-1}$)	0.51	25	-0.37	0.87	0.001	-52.0 - 85.1
c.Photo-synthetic Rate ($mg\ C \cdot g^{-1} \cdot h^{-1}$)	0.44	25	-0.37	1.71	0.001	0.11 - 6.79
d. Tissue Phosphorus Content ($mg\ P \cdot g^{-1}$)	0.47	25	-1.49	2.71	0.001	0.20 - 6.40

Table 2. con't.

e. Tissue Nitrogen Content (mg $N \cdot g^{-1}$)	0.81	25	-4.52	5.03	0.001	0.10 - 39.1
f. Tissue Potassium Content (mg $K \cdot g^{-1}$)	-	25	-	-	NS	0.10 - 50.7
e. Photon Flux ($E \cdot m^{-2} \cdot d^{-1}$)	0.84	25	-3.92	4.16	0.001	7.11 - 27.6

Table 3. Variation in growth related variables of Myriophyllum spicatum by growth period during the 1982 growing season in Lake Memphremagog. Means followed by the same letter are insignificantly ($P < 0.05$) different.

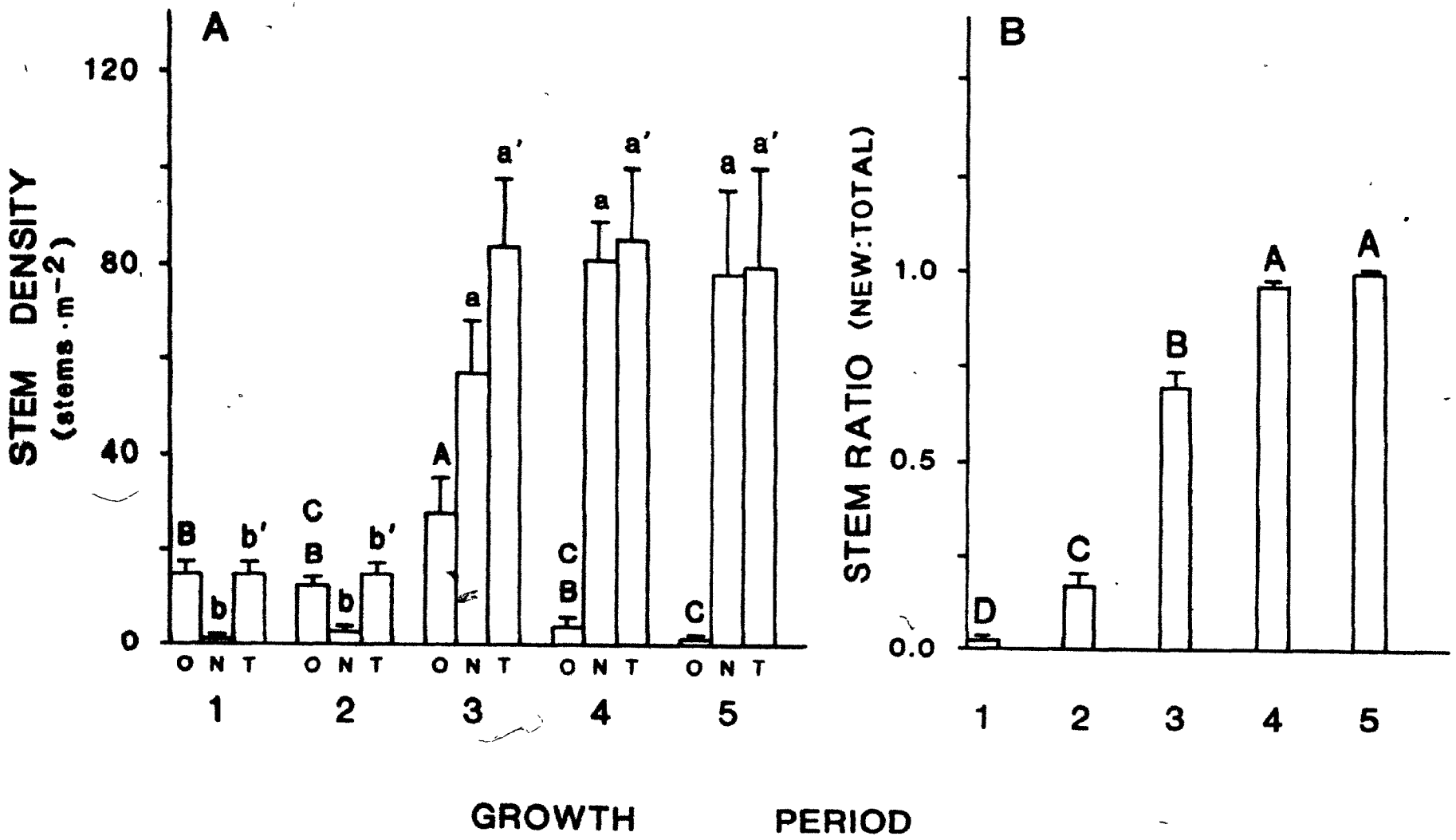
Variable	Growth Period	Actual Sample Size (Stems)	Actual Standard Deviation (S)	Mean ($\bar{x}$)	Calculated Sample Size (n)
a. Specific	1	35	59.72	21.16 AB	199
Growth Rate	2	35	71.50	3.22 B	12327
($mg \cdot g^{-1}$	3	35	83.36	36.44 AB	131
$\cdot plant^{-1} \cdot d^{-1}$)	4	35	70.24	31.86 AB	122
	5	35	85.02	47.61 A	80
b. Relative	1	35	14.37	2.49 B	833
Growth Rate	2	35	23.46	3.23 B	1319
($mg \cdot plant^{-1}$	3	35	23.14	15.16 B	58
$\cdot d^{-1}$)	4	35	13.06	3.98 B	269
	5	35	20.33	5.79 B	308
c. Photo-	1	27	1.18	2.45 B	6
synthetic	2	29	1.04	1.66 C	10
Rate	3	27	1.68	3.06 A	8
($mg\ C \cdot g^{-1} \cdot h^{-1}$)	4	32	0.95	1.63 C	9
	5	31	0.79	1.23 C	10

Table 3. con't.

d. Tissue	1	25	0.93	2.10 BC	5
Phosphorus	2	11	1.17	2.88 A	4
Content	3	25	1.31	2.45 AB	7
(mg $P \cdot g^{-1}$)	4	31	0.49	1.77 C	2
	5	35	0.98	2.18 BC	5
e. Tissue	1	25	32.06	24.91 A	41
Nitrogen	2	11	5.74	17.09 A	3
Content	3	25	8.63	17.53 A	6
(mg $N \cdot g^{-1}$)	4	31	7.47	16.40 A	5
	5	35	13.31	16.97 A	15
f. Tissue	1	24	10,50	22.47 AB	6
Potassium	2	11	7.05	17.63 B	4
Content	3	25	8.98	17.45 B	7
(mg $K \cdot g^{-1}$)	4	31	8.08	20.90 AB	4
	5	35	6.42	25.95 A	2
g. Photon	1	35	1.03	8.03 C	1
Flux	2	35	2.17	9.92 C	2
($E \cdot m^{-2}$	3	35	5.35	16.59 A	3
$\cdot d^{-1}$)	4	35	3.21	14.41 B	2
	5	35	3.41	14.19 B	2

Figure 1

Stem density (A) and stem ratio (B) of Myriophyllum spicatum by growth period in Lake Memphremagog, showing old (O), new (N) and total (T) plant classifications. Means showing the same letter type are not significantly ($P < 0.05$) different, and bars denote 1 standard error.


A
B
STEM DENSITY (stems·m⁻²)
120
80
40
0
STEM RATIO (NEW:TOTAL)
1.0
0.5
0.0
O N T
1
2
3
4
5
GROWTH PERIOD

Discussion

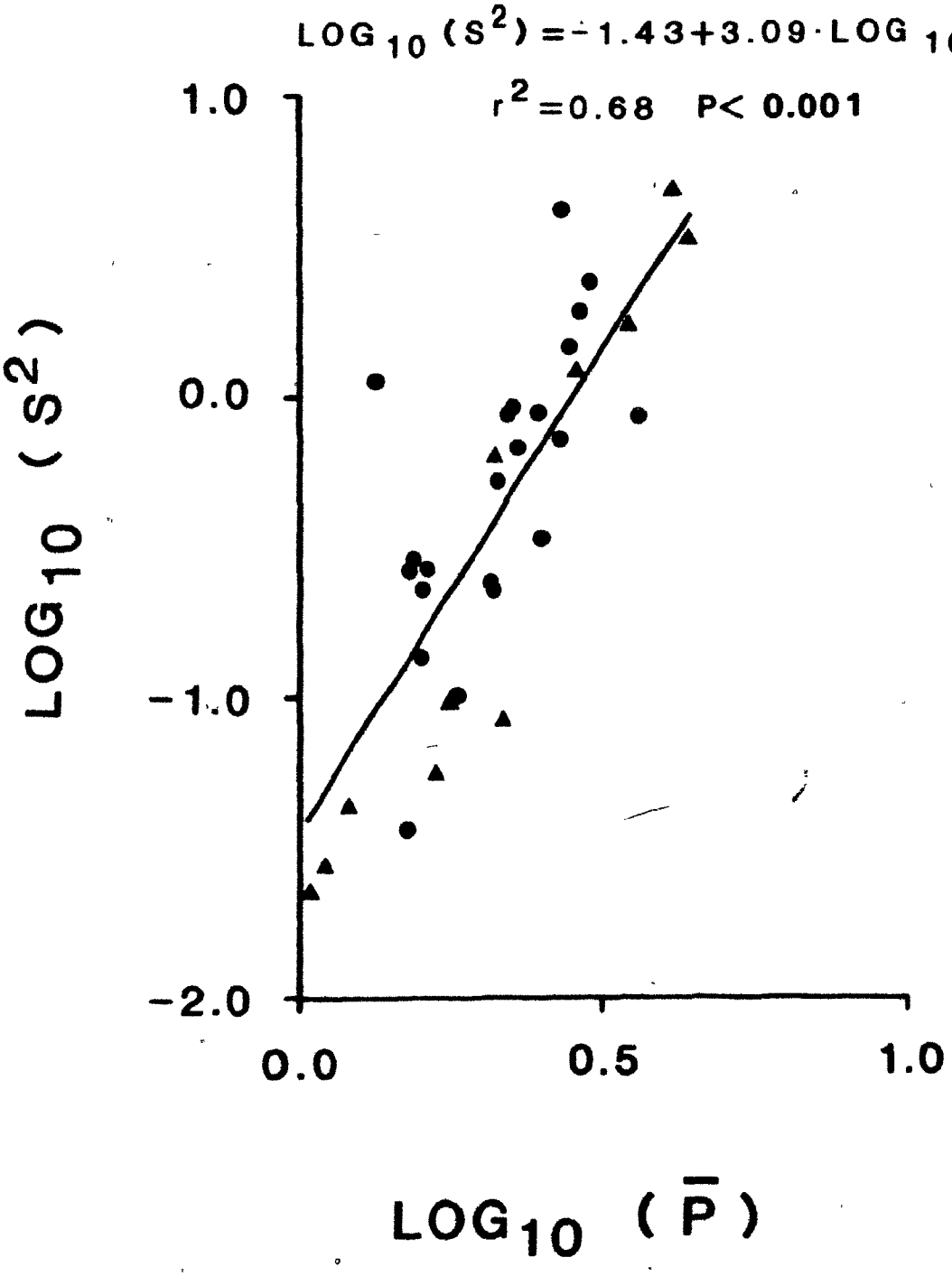
The utility of mathematical transformation of length-weight data to predict Myriophyllum biomass from stem measures is evident in that the proportion of variance (r^2) explained was between 0.77 to 0.86 in our study (Table 1), but only r^2 = 0.35 for an investigation in which plant stems were neither separated into stem fractions nor were transformed (Barko and Smart 1979). The present non-destructive SCUBA sampling technique for growth rate has the added advantage that the sample plants can be sampled at different times during the season rather than only once at the end of the study period.

The principal finding was that it is possible, with the exception for tissue potassium, to predict the variance from the mean values for plant attributes and photon flux (Table 2). The predictive relations support, what Taylor (1961) first recognized for animal populations, that the variance commonly increases with the mean (Southwood 1966). That the present variance-mean relations have generality beyond the lake for which they were derived was shown by the relation for tissue phosphorus (Fig. 2), which did not significantly differ from the intercepts or slopes obtained individually for lakes Memphremagog, Quebec-Vermont, and Lake Wingra, Wisconsin (Carpenter and Adams 1976); nor did the slopes and intercepts differ when the two lakes were compared separately.

A third finding was the great differences in both mean growth rate between the individual growth periods (Table 3) and the high variance in all the Myriophyllum dominated macrophyte

Figure 2

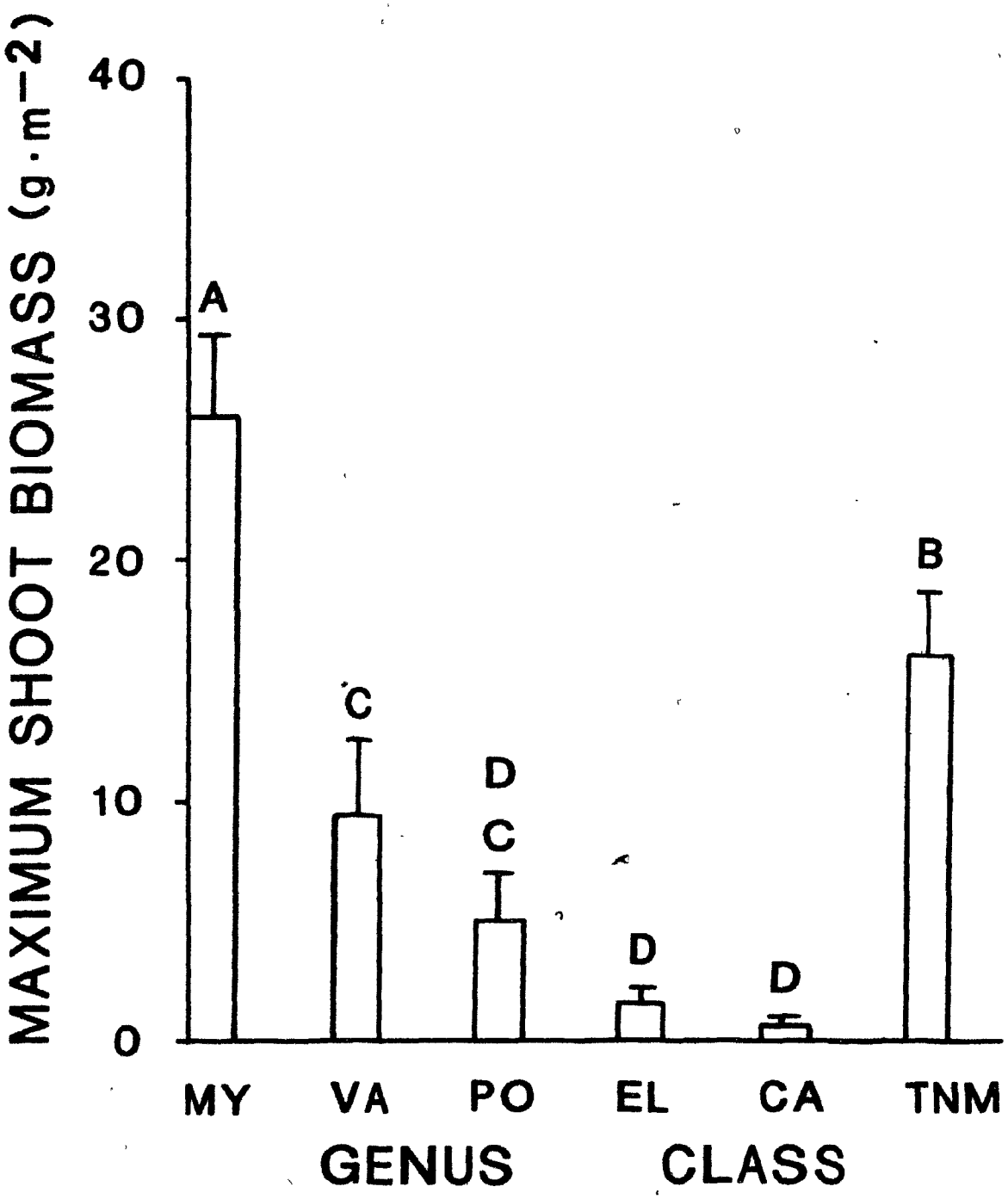
Linear regression relations predicting variance using mean values for tissue phosphorus in Myriophyllum spicatum, for data from lakes Wingra (▲) (Carpenter and Adams 1976) and Memphremagog (●).


$LOG_{10}(S^2) = -1.43 + 3.09 \cdot LOG_{10}(\bar{P})$
$r^2 = 0.68$ $P < 0.001$
1.0
0.0
−1.0
−2.0
0.0
0.5
1.0
$LOG_{10}(S^2)$
$LOG_{10}(\bar{P})$

community (Fig. 3), requiring sample sizes well in excess of those commonly collected by macrophyte ecologists (Adams and Prentki 1982, Langeland 1982). The source of the observed variation among plants is unclear. We suspected this variation to be correlated with the stem density, which significantly differed between the first two and last three growth periods (Fig. 1a), and with the proportion of new stems (plants of the year) to total stems, which significantly differed for all but growth periods 4 and 5 (Fig. 1b). Unfortunately, none of the variables measured correlated significantly with the stem ratio or total stem number (Chapter 2). Although the reasons for the variability observed remains unclear, the similarity in the variance-mean relations for tissue phosphorus content in two lakes (Fig. 2) indicates, until shown otherwise, that these variance-mean relations (Table 2) are useful in determining the optimal sample size for aquatic macrophytes in other lakes (see Downing 1979). The determination of appropriate sample size is an essential first step in drawing statistically supported conclusions on all aspects of the dynamics of aquatic macrophytes in nature.

Figure 3

Maximum biomass by genus within study plots at 2.6 m in Lake Memphremagog: *Myriophyllum* (MY), *Vallisneria* (VA), *Potamogeton* (PO), *Elodea* (EL), *Cabomba* (CA) and total non-*Myriophyllum* species (TNM).


MAXIMUM SHOOT BIOMASS (g·m−2)
40
30
20
10
0
A
C
D
C
D
D
B
MY
VA
PO
EL
CA
TNM
GENUS
CLASS

Literature Cited

Adams, M.S. and McCracken, M.D., 1974. Seasonal production of the Myriophyllum component of Lake Wingra, Wisconsin. J. Ecol., 62: 457-467.

Adams, M.S., Guilizzoni, P. and Adams, S., 1978. Relationship of dissolved inorganic carbon to macrophyte photosynthesis in some Italian Lakes. Limnol. Oceanogr., 23: 912-919.

Adams, M.S. and Prentki, R.T., 1982. Biology, metabolism and functions of littoral submersed weedbeds of Lake Wingra, Wisconsin, USA : A summary and review. Archiv. f. Hydrobiol. Suppl.-Bd., 62: 333-409.

Aiken, S.G. and Picard, R.R., 1980. The influence of substrate on the growth and morphology of Myriophyllum spicatum and Myriophyllum excalbescens. Can. J. Bot., 58(9): 1111-1118.

Barko, J.W., 1983. The growth of Myriophyllum spicatum L. in relation to selected characteristics of sediment and solution. Aquat. Bot., 15: 91-103.

Barko, J.W. and Smart, R.M., 1979. The role of Myriophyllum spicatum in the mobilization of sediment phosphorus. In: J.E. Breck, R.T. Prentki and O.L. Loucks (Editors). Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting. Conf. Proc. Inst. Environ. Stud. February 14-16, Univ. of Wisconsin, Madison, pp. 177-190.

Barko, J.W., Hardin, D.G. and Matthews, M.S., 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. Can. J. Bot., 60: 877-887.

Best, E.P.H., 1981. A preliminary model for growth of Ceratophyllum demersum L. Verh. Inter. Verin. Limnol., 21: 1484-1491.

Box, G.E.P. and Tidwell, P.W., 1962. Transformations of the independant variables. Technometrics, 4: 531-550.

Box, G.E.P. and Cox, D.R., 1964. An analysis of transformations. J.R. Statist. Soc. Ser. B., 26: 211-243.

Carpenter, S.R. and Adams, M.S., 1977. The macrophyte tissue nutrient pool of a hardwater eutrophic lake: implications for macrophyte harvesting. Aquat. Bot., 3: 229-235.

Chambers, P.A. and Kalff, J., submitted. The influence of sediment and irradiance on the growth and morphology of Myriophyllum spicatum L. Aquat. Bot.

Cochran, W.G., 1977. Sampling techniques. John Wiley and Sons, New York, 428 pp.

Downing, J.A., 1979. Aggregation, transformation, and the design of benthos sampling programs. J. Fish. Res. Board Can., 36: 1454-1463.

Evans, G.C., 1972. The quantitative analysis of plant growth. Univ. of California Press, Berkeley, 734 pp.

Fee, E.J., 1973. A numerical model for determining integral primary production and its application to Lake Michigan. J. Fish. Res. Board Can., 30: 1447-1468.

Golterman, H.L. and R.S. Clymo [ed.]. 1969. Methods for chemical analysis of fresh waters. IBP Handbook No. 8. Blackwell Scientific Publishers, Edinburigh, 166 pp.

Grace, J.B. and Wetzel, R.G., 1978. The productive biology of Eurasian watermilfoil (Myriophyllum spicatum L.): a review. J. Aquat. Plant Manage., 16: 1-11.

Green, R.H., 1979. Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York, 245 pp.

Harper, J.L., 1977. Population biology of plants. Academic Press, London, England, 892 pp.

Langeland, K.A., 1982. Relations among hydrosoil, water chemistry, chlorophyll a, and submersed macrophyte biomass. Ph.D. diss. Univ. of Florida. 143 pp.

Littler, M.M. and Arnold, K.E., 1980. Sources of variability in macroalgal primary productivity: sampling and interpretive problems. Mar. Biol., 8: 141-156.

Nixon, S.W. and Oviatt, C.A., 1973. Analysis of local variation in standing crop of Spartina alterniflora. Botanica Marina, 16: 103-109.

Patrick, W.H. Jr. and DeLaune, R.D., 1976. Nitrogen and phosphorus utilization by Spartina alterniflora in a salt marsh in Barataria Bay, Louisiana. Estuarine and Costal Marine Science, 4: 59-64.

Rosenburg, G. and Ramus, J., 1982. Ecological growth strategies in the seaweeds Gracilaria foliifera (Rhodophyceae) and Ulva sp. (Chlorophyceae): soluable nitrogen and reserve carbohydrates.

Schmitt, M.R. and Adams, M.S., 1981. Dependance of rates of apparent photosynthesis on tissue phosphorus concentrations in Myriophyllum spicatum L. Aquat. Bot., 11: 379-387.

Sokal, R.R. and Rohlf, F.J., 1981. Biometry: principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco, 859 pp.

Southwood, T.R.E., 1966. Ecological methods with particular reference to the study of insect populations. Chapman and Hall, London, 391 pp.

Statistical Analysis Systems, 1982. SAS user's guide: statistics (1982 ed.). SAS Institute, Inc., Cary, N.C., 584 pp.

Taylor, L.R., 1961. Aggregation, variance, and the mean. Nature (Lond.), 189: 732-735.

Thomas, R.L., Sheard, R.W. and Moyer, J.R., 1967. Comparison of conventional and automated procedures for nitrogen, phosphorus and potassium analysis of plant material using a single digestion. Agron. J., 59: 240-243.

Titmus, G., 1983. Are animal populations really aggregated? Oikos, 40: 64-68.

Titus, J.E., Goldstein, R.A., Adams, M.S., Mankin, J.B., O'Neill, R.V., Weiler, P.R. Jr., Shugart, H.H. and Booth, R.S., 1975. A production model for Myriophyllum spicatum L. Ecology, 56: 1129-1138.

Zar, J.H., 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J., 620 pp.

CHAPTER 2

Models Predicting *In Situ* Growth and Biomass of the Aquatic Macrophyte *Myriophyllum Spicatum* L.

Abstract

Regression relations were developed predicting Myriophyllum spicatum L. growth rate, season maximum biomass, and community biomass, in Lake Memphremagog, Quebec-Vermont. Five categories of predictors were investigated: tissue nutrient content (nitrogen, phosphorus and potassium), shoot tip morphology (leaf length, number of leaf whorls), photosynthetic rate, photon flux density, and sediment organic content. Most of the variation in growth rates was explained during 4 of the 5 two week growth periods as well as for the study period as a whole. The growth rate became negative between 1.0 to 1.4 mg $P \cdot g^{-1}$ dry wt (0.10 to 0.14 % P) (95 % CI). The number of leaf whorls on Myriophyllum shoot tips were highly correlated with stem densities ($r^2 = 0.96$, $P < 0.004$). A high sediment organic content was correlated with a low maximum biomass of Myriophyllum ($r^2 = 0.33$, $P < 0.003$), Vallisneria americana L. ($r^2 = 0.85$, $P < 0.025$), and all species combined ($r^2 = 0.51$, $P < 0.001$). Nutrient (nitrogen, phosphorus and potassium) additions to in situ sediments yielded significantly greater maximum biomass only for Vallisneria americana.

Introduction

Aquatic macrophytes play a significant role in the ecology of lakes by affecting the water chemistry through primary production and excretion (Wetzel and Allen 1970), by serving as substrate for algae, herbivores and decomposers (Cattaneo and Kalff 1979, Eminson and Moss 1980), and by acting as both a source and sink in the nutrient cycles of lakes (Best and Mantai 1978, Carpenter and Adams 1979, Best 1981).

In contrast to the phytoplankton where biomass (Kalff and Knoechel 1978), production (Smith 1979, 1982) and to some extent community structure (Kalff and Knoechel 1978, Tilman 1982, Smith 1983) are now roughly predictable, no equivalent prediction are as yet possible for the submergent freshwater macrophytes. Work to date suggests that such macrophyte predictions may well be more difficult to obtain than for the phytoplankton. Most aquatic macrophytes are rooted and obtain virtually all of their phosphorus (Carignan and Kalff 1980) and probably much of their other nutrients from the sediments. Both the positive and negative correlations reported between sediment organic matter and macrophyte abundance (Sand-Jensen and Sondergaard 1979, Barko and Smart 1983) do not resolve the importance of sediment characteristics as a determinant of macrophyte abundance. Yet sediment characteristics in the littoral are highly variable, among others apparently affected by currents and wave action (Pearsall 1920, Spence 1967, Aiken and Gillet 1974, Nicholson et al. 1975), with the distribution of macrophytes at least partially controled by wave action

(Keddy 1982, 1983). Consequently, models describing macrophyte abundance and distribution will almost certainly have to be considered for a larger number of environmental variables than those for the phytoplankton. Which specific variables need be considered for weed models remains unclear, although it is evident that some measure of irradiance, turbulence, sediment characteristics and nutrient status need to be incorporated into models to make a first prediction possible.

The present paper is an early attempt to relate Myriophyllum spicatum L. growth and biomass, measured in situ, to a number of environmental factors to discover which of these might be considered for incorporation in more general future models. The variables considered were tissue nitrogen (N), tissue phosphorus (P), tissue potassium (K), shoot tip morphology (leaf length (LL) and number of leaf whorls (NW)), photosynthetic rate (PR), photon flux (PF), and sediment organic matter (OM).

Methods and Procedures

The research was done between June and September 1982 in Quinn Bay (45° 6′ 0" N, 72° 15′ 45" W) of Lake Memphremagog, Quebec-Vermont, at a site dominated by Myriophyllum spicatum. A randomized block design was used to distribute 15 pairs of plots among the 5 blocks that formed a continuous rectangle parallel to the shore. Only 5 of 6 plots in each block were sampled during the two week growth periods beginning on 5 and 16 June, 2 and 16 July, and August 1, 1982. At the beginning of the July 2 growth period, the remaining plot in each block was fertilized using slow release Jobes Ltd., nutrient sticks (9 sticks per plot, 0.5 m spacing, total plot dosages; 63.7 g $N \cdot m^{-2}$, 32.0 g $P \cdot m^{-2}$, and 42.5 g $K \cdot m^{-2}$). The five fertilized and twenty-five unfertilized plots were harvested between August 15 to 20 for a measure of the maximum community biomass. Previous sampling of the unfertilized plots had at most removed 1 % of the final biomass.

Methods for the measurement of maximum biomass, specific growth rate ($mg \cdot g^{-1} \cdot plant^{-1} \cdot d^{-1}$), tissue nutrient content (mg $P \cdot g^{-1}$, mg $N \cdot g^{-1}$ and mg $K \cdot g^{-1}$), photosynthetic rate (mg $C \cdot g^{-1} \cdot h^{-1}$), photon flux density ($E \cdot m^{-2} \cdot d^{-1}$), shoot tip morphology (leaf length (cm) and number of leaf whorls), and stem density ($stems \cdot m^{-2}$), are described elsewhere (Rivard and Kalff submitted). Sediment organic content was measured using 4 random samples taken from each plot. The upper 10 cm of each sediment core was passed through a 5 mm mesh screen, homogenized, dried at 110° C for 48 hours, and combusted at

content as loss-on-ignition was expressed as a percent of the dry weight (Sand-Jensen and Søndergaard 1979).

The McGill University computer system and Statistical Analysis Systems (1982) software were used for data analysis. Selection of variables in the regression analysis and model building followed Montgomery and Peck (1982). Specific growth rates in the regression analysis were weighted with the variance (S^2) associated with estimates of the whole shoot biomass. The positive effect of this is to give greater weight to growth rates with low variance (Draper and Smith 1981). A minor but visually disturbing disadvantage of the weighting is that the resulting line of best fit often does not pass through the center of the data (eg. Fig. 1). The Duncans' multiple range test was used to identify statistically significant ($P < 0.05$) differences among means (Zar 1974).

Results

Tissue phosphorus was the single best predictor of specific growth rate (r^2 = 0.43, $P < 0.001$) over the growing season as a whole (Table 1, Fig. 1). The stepwise multiple linear regression procedure selected tissue P and the tissue N:P ratio as the most powerful predictors in a bivariate model, increasing the R^2 to 0.54 ($P < 0.001$). Adding the photon flux received at the stem tip (PF) as a third variable raised the portion of the variance explained to 0.61 ($P < 0.001$). Tissue N alone explained only a few additional percent in a four variable model. Photosynthetic rate (PR), tissue potassium content (K), number of shoot tip whorls (NW), leaf length (LL) and sediment organic matter (OM), did not contribute significantly to this model.

When the data were examined by growth period a different pattern emerged. During the first two weeks the photosynthetic rate of shoot tips alone explained 52 percent (r^2 = 0.52, $P < 0.001$) of the variance in growth (Table 2). While the coefficient of determination (r^2 or R^2) rose modestly by also including the photon flux density and the N:P ratio, the rise was not statistically significant. The second growth period was exceptional both for the high proportion of the variance (r^2 = 0.80, $P < 0.001$) of the growth rate explained by one variable, (P), and the total variance explained (R^2 = 0.97, $P < 0.001$) using P, PR and PF. In growth period 3, not only did the amount of variation explained decline sharply with PF emerging as the most important predictor (r^2 = 0.58, $P < 0.001$), but only here

Table 1. Models describing specific growth rate of Myriophyllum spicatum selected by stepwise regression analysis, using tissue phosphorus (P), tissue nitrogen (N), tissue potassium (K), leaf length (LL), number of whorls (NW), photosynthetic rate (PR), photon flux density (PF), and sediment organic matter (OM), for all data from all growth periods combined (n = 121 stems). Specific growth rate was weighted with the variance (S^2) associated with estimating whole stem biomass. Variables not shown in the table did not contribute significantly ($P < 0.001$) to the models. The proportion of variation explained was presented for both simple linear (r^2) and multiple linear (R^2) regression relations.

Model No.	Variables Selected	r^2 or R^2	Intercept (a)	Slope (b)	P(b)>F
I	P	0.43	-60.71	49.57	0.001
II	P	0.54	-104.10	60.59	0.001
	N:P			1.77	0.001
III	P	0.61	4.51	50.78	0.001
	N:P			1.46	0.001
	PF			-1.06	0.001
IV	P	0.65	44.80	51.96	0.001
	N:P			1.89	0.001
	PF			-5.84	0.001
	N			-2.37	0.001

Figure 1

Specific growth rate was estimated using Myriophyllum spicatum tissue phosphorus ($Y = -60.71 + 49.57\ X$). The 95 % confidence interval for the line shows growth to be negative between 1.0 to 1.4 mg $P \cdot g^{-1}$. Specific growth rates were weighted with the variance (S^2) associated with estimating whole stem biomass (see methods).

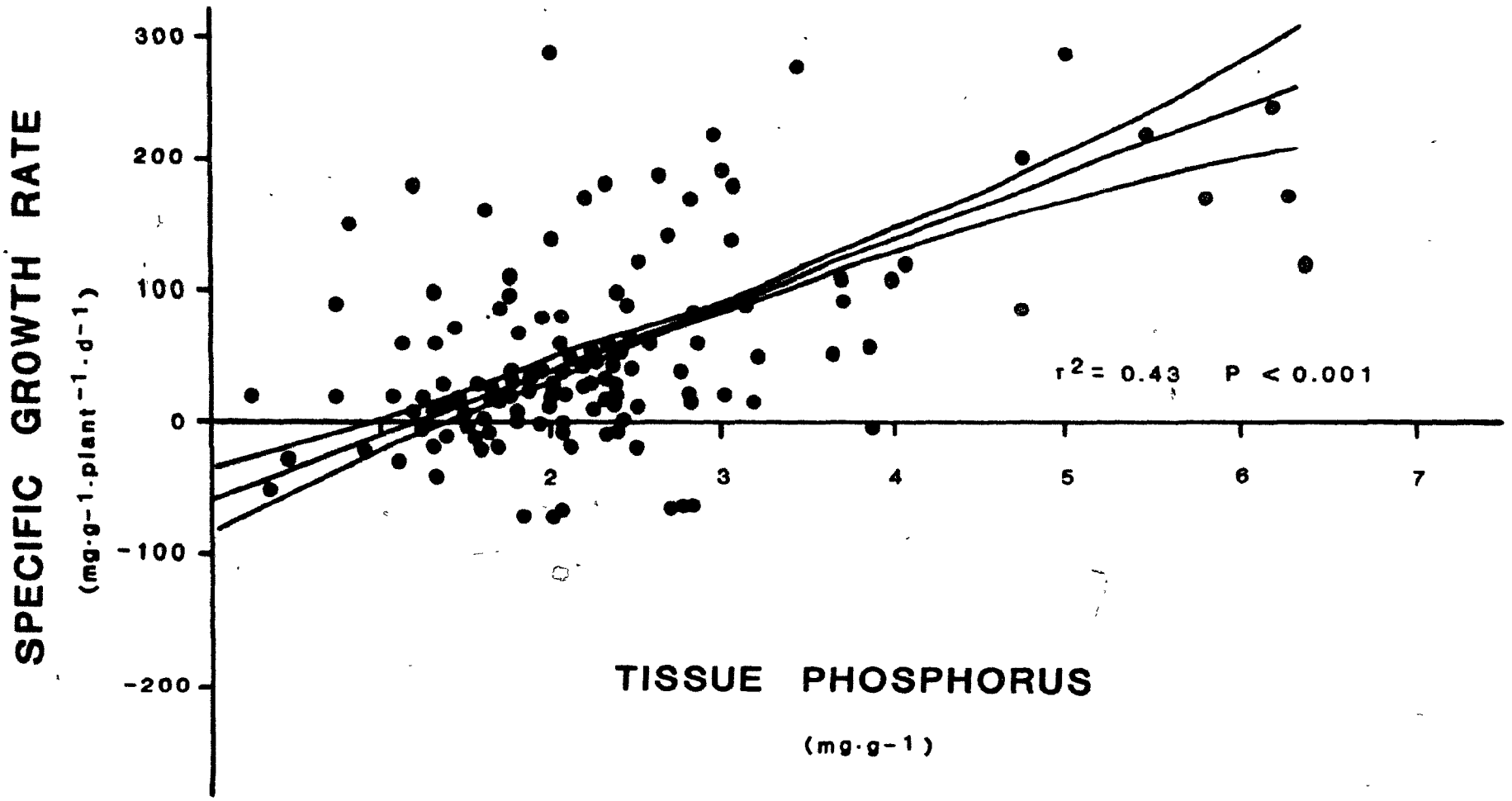

SPECIFIC GROWTH RATE
(mg·g-1·plant-1·d-1)
300
200
100
0
-100
-200
2
3
4
5
6
7
r2 = 0.43 P < 0.001
TISSUE PHOSPHORUS
(mg·g-1)

Table 2. Models describing specific growth rate of Myriophyllum spicatum using all regressor variables investigated (see Table 1) for data separated by growth period. Specific growth rate was weighted with the variance (S^2) associated with estimating whole stem biomass.

Growth Period	Model No.	Variable Selected	r^2 or R^2	Stem No. (n)	Intercept (a)	Slope (b)	P(b)>F
1	I	PR	0.52	24	-48.65	34.13	0.001
	II	PR	0.58	24	183.90	30.84	0.001
		PF				-25.89	0.092
	III	PR	0.63	24	165.60	34.77	0.001
		PF				-27.16	0.072
		N:P				1.66	0.156
2	I	P	0.80	11	-134.90	79.22	0.001
	II	P	0.92	11	-71.21	96.49	0.001
		PR				-64.47	0.001
	III	P	0.97	11	-264.40	127.78	0.001
		PR				-55.21	0.002
		N:P				10.87	0.014

Table 2. con't

3	I	PF	0.58	24	211.00	-8.36	0.001
	II	PF	0.67	24	61.00	-9.15	0.001
		LL				5.33	0.030
	III	PF	0.76	24	-3.70	-8.04	0.001
		LL				5.81	0.009
		N				2.14	0.011
4	I	PF	0.10	31	79.11	-3.81	0.092
	II	PF	0.25	31	191.60	-7.07	0.007
		P				-35.12	0.022
	III	PF	0.29	31	207.10	-9.08	0.005
		P				-34.13	0.025
		NW				1.89	0.244
5	I	PF	0.30	31	284.10	-15.91	0.001
	II	PF	0.51	31	251.30	-19.95	0.001
		P				48.45	0.002
	III	PF	0.58	31	185.60	-17.85	0.001
		P				47.46	0.001
		PR				30.08	0.037

did leaf length, a measure of leaf surface area, add modestly to the predictive power. The fourth growth period revealed how little the attributes measured explained growth rates. PF and P together explained only 22 % of the variation. During the last period PF and P together explained much more (51 %) of the variation in growth, with photosynthetic rate once again playing a minor but significant role by raising the variation explained to 58 % . Although the specific growth rate correlated in a seasonally changing fashion with environmental and plant attributes (Table 2) the growth rates themselves differed significantly only between 2 of the 5 periods (Table 3).

While the above results identify variables investigated that correlate with growth, the maximum biomass measurements allow an examination of how yield, rather than growth rate, is related to the same environmental and plant characteristics. Sediment organic matter was a predictor of the maximum biomass of Myriophyllum (r^2 = 0.33), Vallisneria americana L. (r^2 = 0.85) and all species combined (r^2 = 0.51), and in all cases maximum biomass declined as sediment organic matter levels increased (Table 4). None of the other variables were correlated with maximum biomass.

Table 3. Specific growth rate ($mg \cdot g^{-1} \cdot plant^{-1} \cdot d^{-1}$) by growth period for Myriophyllum spicatum in Lake Memphremagog. Means followed by the same letter are insignificantly ($P < 0.05$) different.

Growth Period	Stem No. (n)	Mean ($\bar{x}$)		Standard Error (SE)
1	35	21.16	AB	11.04
2	35	3.22	B	12.08
3	35	36.44	AB	13.04
4	35	31.86	AB	11.97
5	35	47.61	A	13.17
1-5 Combined	175	28.06	-	5.54

Table 4. Models describing season maximum biomass in Lake Memphremagog using sediment organic content (OM). Regression equations were weighted with the variance (S^2) associated with replicate (n = 5 plots·block^{-1}) measures.

Species	Variable Selected	r^2	Intercept (a)	Slope (b)	P(b)>F
Myriophyllum spicatum	OM	0.33	59.91	-2.411	0.003
Vallisneria americana	OM	0.85	42.62	-2.458	0.001
All Species Combined	OM	0.51	102.30	-4.247	0.001

Discussion

For the growing season as a whole, tissue phosphorus was the best predictor of the specific growth rate of Myriophyllum with the N:P ratio and PF added as significant variables in the bivariate and trivariate models (Table 1). Nitrogen alone contributed a small amount to the four variable model but added to the bivariate model through the inclusion of the N:P ratio in the multiple linear regression models. Models containing either or both N and P are acceptable if all the variables added are, as they were here, individually significant ($P(b) < F$) (Montgomery and Peck 1982; Smith 1982, 1983). The absence of a significant linear relation between tissue N and P (data not shown) indicated that the uptake or retention of these two nutrients is independent of the other.

While Gerloff (1975) was the first to estimate the tissue nutrient levels at which growth becomes limiting, his short - term (6 wk) laboratory studies, using small and floating plants, may not reflect the situation in nature. Field data were collected by Adams and Prentki (1982) who concluded that tissue P levels in Myriophyllum were less than optimal for growth below 4.5 mg $P \cdot g^{-1}$ dry wt, whereas, Gerloff (1975) had suggested a critical P level of 0.7 mg $P \cdot g^{-1}$ dry wt. The present regression relations shows that growth declines as the tissue P levels decrease from a high of at least 6.4 $mg \cdot g^{-1}$, showing that growth is affected over a much wider range of nutrient levels (Fig. 1). In addition, the 95 % confidence interval, where the line intercepts the ordinate, indicates

negative growth below 1.0 to 1.4 mg $P \cdot g^{-1}$.

Todate, measures of macrophyte dynamics in nature have been exclusively based on photosynthetic measures made on plant tips (Titus et al. 1975, Ondok and Gloser 1978 a, b), rather than on other in situ measures of variables thought to affect growth. Such measures obtained here, by measuring tagged plants, show that measures of photosynthesis (^{14}C uptake) are a totally inappropriate measure of growth rate in nature for the growing season as a whole (Table 1). While photosynthetic rates were coupled to growth during the early growing season (Table 2) the absence of the relation for the season as a whole shows the only very modest impact of photosynthetic rate measurements on growth.

Over the entire season, tissue P was the single best predictor of growth (Table 1), which was attributable to growing conditions during periods 2, 4 and 5 (Table 2). In contrast to P, nitrogen alone explained only a very modest portion of the variation and then only during growth period 3. This suggests that the supply of P is the more important determinant to growth. The amount of light reaching the plant tips (PF) was most important as a predictor during the third period. That the PF-growth relations had a negative slope was surprising but indicates that shorter plants grow more rapidly than taller ones.

The smallest fraction of the specific growth rate was described during growth period 4 (Table 2). It may be, as was noted in Lake Wingra (Titus and Adams 1979), that Nemphremagog root biomass too increased disproportionately between mid-July

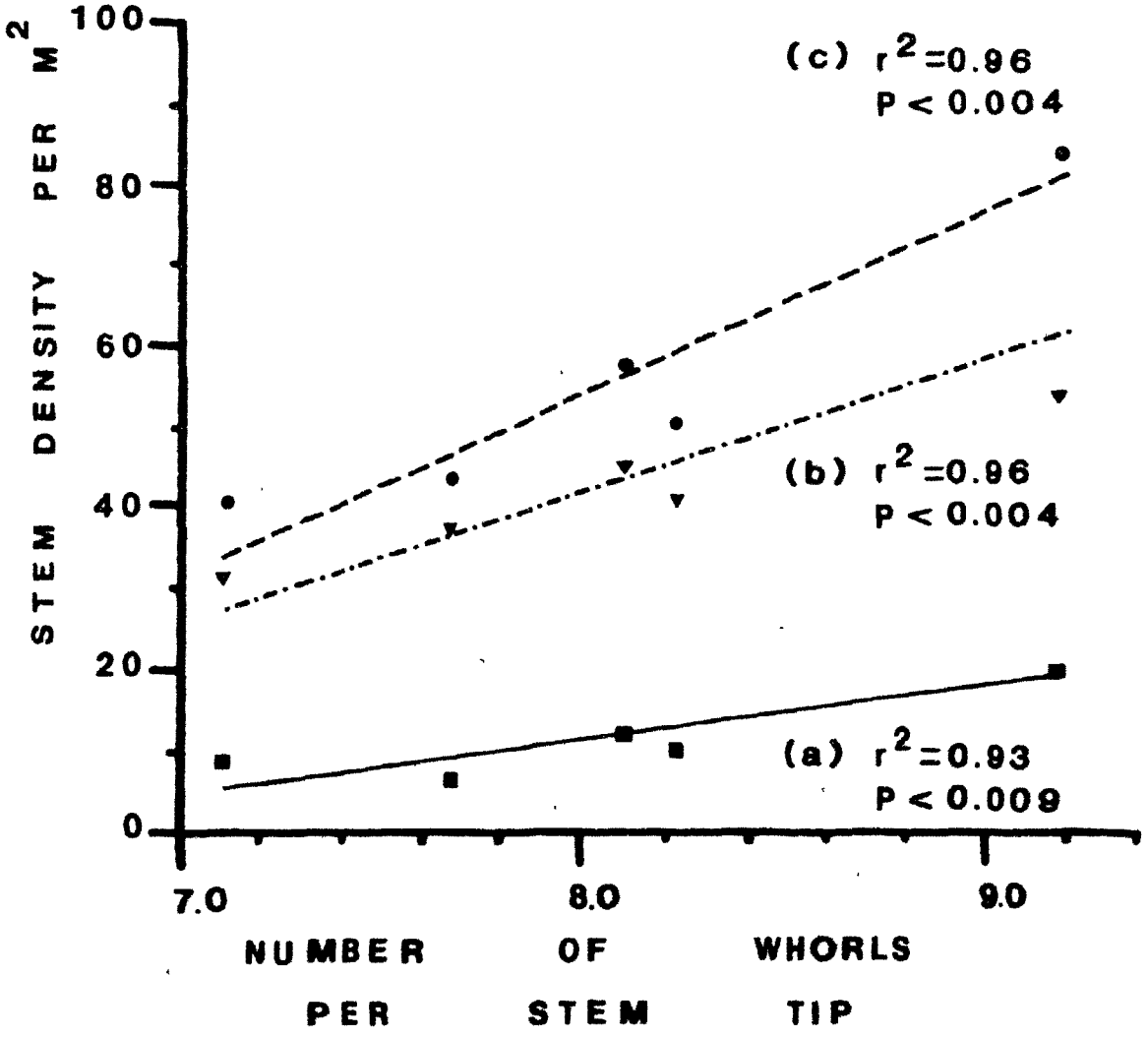
and mid-August, thereby reducing the importance of the relation between shoot growth and the attributes studied.

A very high variation in growth rates of individual stems was noted and initially this was attributed both to the appearance of new stems during the growing season and the dieback of the overwintered old stems. However, none of the variables measured correlated significantly with the ratio of new to total stems, or stem numbers (Chapter 1). In addition, we showed there that the new to total stem ratio did not significantly differ during the last two growth periods and that the absolute number of stems per area significantly changed only between the first 2 and final 3 periods. Consequently, the reason for the very high variation in growth rates of individual stems noted during all growth periods remains obscure. However, the number of whorls (NW) on the shoot tips was highly correlated with stem density (Fig. 2), with the number of whorls in the upper 15 cm of the shoots increasing as Myriophyllum density increased. This correlation suggests that the enumeration of whorls is an efficient method for determining density and biomass, and a simpler one than the transect count method, using SCUBA, proposed by Sheldon and Boylen (1978).

While in situ growth rate of Myriophyllum was highly correlated with tissue P for both the season as a whole and for some of the individual growth periods (Table 2), the maximum biomass attained as a result of this growth was correlated with neither tissue P or the direct measurements of growth rate. Two

Figure 2

Stem density of Myriophyllum spicatum predicted from the number of whorls on the distal 15 cm of the central stem. Regression equations were weighted with the variance (S^2) associated with replicate (n = 5 plots·block^{-1}) measures. Separate relations are shown for (a) old (Y = −36.12 + 6.00 X), (b) new (Y = −84.17 + 15.86 X) and (c) total stems (Y = −125.5 + 22.42 X) counted within study plots.


STEM DENSITY PER M 2
100
80
60
40
20
0
(c) r 2 =0.96
P < 0.004
(b) r 2 =0.96
P < 0.004
(a) r 2 =0.93
P < 0.009
7.0
8.0
9.0
NUMBER OF WHORLS PER STEM TIP

possible explainations present themselves. The first such explaination was that abcission of branches was sufficiently large to eliminate the relation between growth rate and final biomass. This is, however, unlikely because few floating stem fragments were noted within the dense and well protected macrophyte bed, which showed no sign of breakdown at the time of sampling. Fragments settling to the sediments would have in any case been collected at the time of harvesting. A more plausible second explaination was related to the growth behaviour of Myriophyllum and our sampling. As shown by the relation between growth rate and photon flux density, growth slows down as the measured stems approach the surface (Table 2). However, unmeasured but faster growing young shoots continue to add to the season maximum biomass, removing the relation between the growth rate measured and biomass.

With plant phosphorus almost exclusively obtained from the sediments (Carignan and Kalff 1980) and tissue P correlated with growth rate (Tables 1, 2; Fig. 1) an increase in sediment nutrients upon fertilization should have resulted in a significantly greater final biomass for Myriophyllum in the fertilized plots. That we did not find this (Table 5) may again be the result of a decreased lengthening rate of the tall stems in the fertilized plots and a catching-up of biomass in the unfertilized plots at the time of sampling. However, the high variability in stem growth rates and the small number of plots fertilized, mitigated against being able to conclude that the 37 % greater growth in the fertilized plots was significant (Table 5). High variability and insufficient sample size are

Table 5. Maximum biomass ($g \cdot m^{-2}$) by species growing on fertilized (N,P&K additions) (n = 5 plots) and unfertilized (n = 25 plots) sediments in Myriophyllum spicatum dominated weedbeds in Lake Memphremagog. Only Vallisneria biomass was significantly ($P < 0.05$) greater in fertilized than unfertilized sediments.

Species	Fertilized Mean ($\bar{x} \pm SE$)	Unfertilized Mean ($\bar{x} \pm SE$)	Difference Between Fertilized and Unfertilized Means (%)
Myriophyllum spicatum	35.5 ± 6.74	25.9 ± 3.40	37
Vallisneria americana	19.9 ± 3.60	8.4 ± 2.05	137
Elodea canadensis	3.5 ± 2.92	1.6 ± 0.49	119
Potamogeton robbinsii	5.5 ± 3.57	5.1 ± 1.77	7
Potamogeton crispus	0.7 ± 0.45	0.8 ± 0.20	-1
Potamogeton natans	0.4 ± 0.37	0.1 ± 0.07	414
Cabomba spp.	0.5 ± 0.31	0.6 ± 0.19	-19

Table 5. con't.

Non-*Myriophyllum* Combined	20.5 ± 7.07	16.6 ± 2.68	24
All Species Combined	66.0 ± 8.06	42.4 ± 4.86	56

responsible for much of the ambiguity in the macrophyte literature.

The inverse relation between sediment organic matter and maximum biomass in the unfertilized plots (Table 4) shows this biomass to be primarly a function of sediment characteristics. It is these same characteristics that are responsible for the high variability in observed shoot growth.

Although photosynthesis and shoot growth were correlated early in the season, they were not correlated for most of the individual growth periods, nor were they correlated for the season as a whole. Consequently, the literatures' emphasis on the measurement of photosynthetic rates as a surrogate for growth rate is unwarranted. Thus, the photosynthetic rate, the growth rate and the maximum biomass are shown to be less directly linked, and thus, less equitable than assumed by aquatic ecologists. However, the results provide support for the view, first expressed by Pearsall (1920, 1921), that sediment characteristics are of the greatest significance in determining the macrophyte biomass of lakes.

If the prediction of community biomass and growth is to become a reality, the relevant environmental factors which can be used to predict macrophyte growth and biomass must be identified and incorporated into predictive models. The present study identifies some such predictors of Myriophyllum shoot growth in Lake Memphremagog. Unfortunately, above ground growth responds in a seasonally changing fashion to its environment, requiring a seasonally changing set of predictors if growth is to be well described.

Literature Cited

Adams, M.S. and Prentki, R.T., 1982. Biology, metabolism and functions of littoral submersed weedbeds of Lake Wingra Wisconsin, USA : A summary and review. Archiv. f. Hydrobiol. Suppl.-Bd., 62: 333-409.

Aiken, S.G. and Gillet, J.M., 1974. The distribution of aquatic plants in selected lakes in Gatineau Park, Quebec. Can. Field-Naturalist., 88: 437-448.

Barko, J.W. and Smart, J.M., 1983. Effects of organic matter additions to sediment on the growth of aquatic plants., J. Ecol. 71: 161-175.

Best, E.P.H., 1981. A preliminary model for growth of Ceratophyllum demersum L. Verh. Inter. Verin. Limnol., 21: 1484-1491.

Best, M.D. and Mantai, K.E., 1978. Growth of Myriophyllum: sediment or lake water as the source of nitrogen or phosphorus. Ecology, 58: 1075-1080.

Carignan, R. and Kalff, J., 1980. Phosphorus sources for aquatic weeds: water or sediments? Science, 207: 987-989.

Carpenter, S.R. and Adams, M.S., 1979. Effects of nutrients and temperature on decomposition of Myriophyllum spicatum L. in a hardwater eutrophic lake. Limnol. Oceanogr., 24: 520-528.

Cattaneo, A. and Kalff, J., 1979. Primary production of algae growing on natural and artificial aquatic plants: a study of interactions between ephiphytes and their substrate. Limnol. Oceanogr., 24: 1031-1037.

Draper, N.R. and Smith, H., 1981. Applied regression analysis. 2 nd ed. John Wiley and Sons, Inc., N.Y., 709 pp.

Eminson, D. and Moss, B., 1980. The composition and ecology of periphyton communities in freshwaters. I. The influence of host type and external environment on community composition. Br. Phycol. J., 15: 429-446.

Fair, P. and Meeke, L., 1983. Seasonal variations in the pattern of photosynthesis and possible adaptive response to varing light flux regimes in Ceratophyllum demersum L., Aquat. Bot., 15: 81-90.

Gerloff, G.C., 1975. Nutritional ecology of nuisance aquatic plants. U.S.E.P.A. Ecological Research Series No. 660/3-75-027. Environm. Prot. Ag., Corvallis, Oregon., 79 pp.

Kalff, J. and Knoechel, R., 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. Annv. Rev. Ecol. Syst., 9: 475-495.

Keddy, P.A., 1982. Quantifying within lake gradients of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquat. Bot., 14: 41-58.

Keddy, P.A., 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. Ecology , 64(2): 331-344.

Montgomery, D.C. and Peck, E.A., 1982. Introduction to linear regression analysis. John Wiley and Sons,Inc., N.Y., 504 pp.

Nicholson, S.A., Levey, R.A.,and Clute, P.R., 1975. Macrophyte-sediment relationships in Chautauqua Lake. Verh. Inter. Verin. Limnol., 19: 2758-2764.

Ondok, J.P. and Gloser, J., 1978 a. Net photosynthesis and dark respiration in a stand of Phragmites communis Trin. calculated by means of a model. I. Description by means of a model. Photosynthetica, 12: 328-336.

Ondok, J.P. and Gloser, J., 1978 b. Net photosynthesis and dark respiration in a stand of Phragmites communis Trin. calculated by means of a model. II. Results. Photosynthetica, 12: 337-343.

Pearsall, W.H., 1920. The aquatic vegetation of the English Lakes. J. Ecol., 8: 163-201.

Pearsall, W.H., 1921. The development of vegetation in the English Lakes, considered in relation to the general evolution of glacial lakes and rock basins. Proc. R. Soc. B., 92: 259-284.

Sand-Jensen, K. and Søndergaard, M., 1979. Distribution and quantitative development of aquatic macrophytes in relation to sediment characteristics in oligotrophic Lake Kalgaard, Denmark. Freshwater Biol., 9: 1-11.

Sheldon, R.B. and Boylen, C.W., 1978. An underwater survey method for estimating submerged macrophyte population density and biomass. Aquat. Bot., 4: 65-72.

Smith, V.H., 1979. Nutrient dependance of primary productivity in lakes. Limnol. Oceanogr., 24: 1051-1064.

Smith, V.H., 1982. The nitrogen and phosphorus dependance of algal biomass in lakes: an empirical and theoretical analysis. Limnol. Oceanogr., 27: 1101-1112.

Smith, V.H., 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science, 221: 669-671.

Spence, D.N.H., 1967. Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. J. Ecol., 55: 147-170.

Statistical Analysis Systems, 1982. SAS user's guide: statistics (1982 ed.). SAS Institute, Inc., Cary, N.C., 584 pp.

Tilman, D., 1982. Resource competition and community structure. Princeton Monogr. Pop. Biol., 17.

Titus, J.E. and Adams, M.S., 1979. Comparitive carbohydrate storage and utilization patterns in the submersed macrophytes Myriophyllum spicatum and Vallisneria americana. Amer. Midl. Natur., 102: 263-272.

Titus, J.E., Goldstein, R.A., Adams, M.S.,Mankin, J.B., O'Neill, R.V., Weiler, P.R. Jr., Shugart, H.H., and Booth, R.S., 1975. A production model for Myriophyllum spicatum L. Ecology, 56: 1129-1138.

Wetzel, R.G. and Allen, H.L., 1970. Functions and interactions of dissolved organic matter and the littoral zone in lake metabolism and eutrophication. In: Z. Kajak and A. Hillbricht-Ilkowska (Editors), Productivity Problems of Freshwaters. Warsaw, PNW Polish Scientific Publishers. pp. 333-347.

Zar, J.H., 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J., 620 pp.

RECAPITULATION AND CONCLUSIONS

The purpose of this study was to quantify the variability in, and the most important variables describing, the growth and maximum biomass of the aquatic macrophyte Myriophyllum spicatum L. in nature.

The first chapter of this study identified patterns in variance (S^2) and mean ($\bar{x}$) values of growth rates, tissue nutrient content, photosynthetic rate and photon flux density. Such patterns are in themselves interesting because they imply relations which may later be correlated with macrophyte growth. Variance-mean correlations determined for these measures can be used to calculate the necessary number of samples to collect. Collecting the appropriate number of samples is a major first step towards answering major questions about the dynamics of macrophytes in nature.

Chapter two identified regression model relations describing macrophyte growth. Regressor variables studied significantly ($P < 0.001$) described the majority of variation in Myriophyllum growth rates for data in 4 of 5 growth periods, and for all data combined, with tissue P the most important single variable for the season as a whole. The number of whorls on the shoot tips of Myriophyllum were shown to be accurate estimators of both Myriophyllum stem densities and season maximum biomass of non-Myriophyllum species combined. High organic content in sediments was associated with low maximum biomass for Myriophyllum, Vallisneria americana L. and all species combined. In addition, nutrient (N,P&K) additions to in

situ sediments yielded significantly ($P < 0.05$) larger maximum biomass for only *Vallisneria* compared to plants grown on unfertilized sediments. No significant ($P < 0.05$) difference in biomass was shown for *Myriophyllum* maximum biomass compared between fertilized and unfertilized sediments, even though biomass on fertilized sediments was 37 % greater.

The search for pattern in Lake Memphremagog is but a first step in the search for pattern in the ecology of submersed aquatic macrophytes elsewhere.

APPENDIX A

This appendix gives the raw data for the stem length (mm) and weight (g) of Myriophyllum spicatum L. at 2.5 m depth in Lake Memphremagog and was used to identify regression relations (Chapter 1, Table 1). The first column gives the sample period (SP; 1 = 27 June, 2 = 7 July, 3 = 8 August) during 1982; the second column specifies the stem fraction (SF) class (C = central, S = side); the third column indicates the length (L) of each stem fraction; and column four presents the weight (W) of each stem fraction measured.

SP	SF	L	W
1	C	73.8	0.4296
1	C	108.0	0.6243
1	C	100.0	0.4791
1	C	41.0	0.1186
1	C	81.0	0.2647
1	C	90.0	0.3854
1	C	51.2	0.0986
1	C	75.4	0.4012
1	C	109.0	0.3954
1	C	90.4	0.3493
1	C	82.5	0.2752
1	C	82.2	0.2651
1	C	85.2	0.3924
1	C	98.2	0.4261
1	C	67.6	0.1677
1	C	96.0	0.3467
1	C	89.3	0.2883
1	C	95.5	0.4602
1	C	92.4	0.2070
1	C	42.5	0.1201
1	C	47.2	0.0967
1	C	47.0	0.1511
1	C	110.2	0.5628
1	C	53.4	0.1786
1	C	46.0	0.1483

1	S	6.2	0.0247
1	S	38.6	0.1550
1	S	4.5	0.0139
1	S	6.5	0.0430
1	S	6.3	0.0112
1	S	12.5	0.0441
1	S	110.5	0.4641
1	S	22.5	0.0827
1	S	18.5	0.0545
1	S	7.8	0.0325
1	S	5.5	0.0269
1	S	10.0	0.0415
1	S	6.5	0.0113
1	S	12.0	0.0471
1	S	14.0	0.0329
1	S	13.0	0.0222
1	S	18.0	0.0524
1	S	14.0	0.0390
1	S	17.8	0.0757
1	S	21.7	0.0576
1	S	17.5	0.0471
1	S	25.0	0.0529
1	S	6.0	0.0176
1	S	16.0	0.1034
1	S	38.5	0.1643
1	S	7.8	0.0174
1	S	6.4	0.0206
1	S	29.0	0.0694

1	S	24.3	0.0968
1	S	11.7	0.0554
1	S	18.6	0.0468
1	S	9.6	0.0144
1	S	51.6	0.1270
1	S	12.1	0.0900
1	S	11.8	0.0273
1	S	25.0	0.0929
1	S	74.8	0.2640
1	S	6.7	0.0100
1	S	13.5	0.0231
1	S	11.5	0.0236
1	S	24.1	0.0943
1	S	29.8	0.1266
1	S	12.1	0.0321
1	S	31.2	0.0675
1	S	11.7	0.0194
1	S	13.9	0.0371
1	S	9.3	0.0164
1	S	8.9	0.0437
1	S	67.0	0.2477
1	S	54.7	0.2699
1	S	1.9	0.0853
1	S	18.3	0.0408
2	C	77.0	0.1791
2	C	39.5	0.0916
2	C	105.0	0.3947

2	C	65.5	0.2497
2	C	37.0	0.0776
2	C	166.0	0.6928
2	C	103.0	0.3067
2	C	90.5	0.2019
2	C	69.0	0.1486
2	C	76.0	0.1683
2	S	7.0	0.0134
2	S	38.0	0.1135
2	S	9.0	0.0162
2	S	9.0	0.0181
2	S	15.0	0.0397
2	S	19.0	0.0494
2	S	12.0	0.0380
2	S	12.0	0.0399
2	S	6.5	0.0214
2	S	20.5	0.0930
2	S	16.5	0.0519
2	S	6.0	0.0126
2	S	6.5	0.0198
2	S	13.5	0.0411
2	S	5.5	0.0153
2	S	7.0	0.0230
2	S	15.5	0.0458
2	S	20.0	0.0663
2	S	22.0	0.0663
2	S	24.0	0.0814
2	S	17.4	0.0583

2	S	11.0	0.0340
2	S	8.0	0.0242
2	S	6.5	0.0131
2	S	7.0	0.0170
2	S	9.5	0.0281
2	S	23.5	0.0854
2	S	9.0	0.0271
2	S	7.0	0.0196
2	S	16.0	0.0471
2	S	22.5	0.1097
2	S	10.0	0.0518
2	S	6.0	0.0220
2	S	5.5	0.0171
2	S	6.0	0.0169
2	S	17.5	0.0566
2	S	17.0	0.0481
2	S	17.0	0.0796
2	S	18.0	0.0544
2	S	25.0	0.0726
2	S	6.5	0.0144
2	S	7.0	0.0143
2	S	5.5	0.0123
2	S	5.0	0.0167
2	S	10.5	0.0192
2	S	12.0	0.0560
2	S	22.0	0.1019
2	S	6.0	0.0233
2	S	7.0	0.0097

2	S	10.0	0.0152
2	S	10.0	0.0169
2	S	6.0	0.0093
2	S	6.5	0.0091
2	S	9.5	0.0124
2	S	9.5	0.0198
2	S	31.5	0.0533
2	S	16.0	0.0205
2	S	19.0	0.0448
2	S	5.5	0.0081
2	S	6.5	0.0099
2	S	7.0	0.0112
3	C	103.5	0.1881
3	C	85.5	0.1314
3	C	100.5	0.1111
3	C	152.0	0.4326
3	C	161.5	0.4543
3	C	198.0	0.9253
3	C	170.5	0.5211
3	C	166.0	0.2994
3	C	46.5	0.0565
3	C	143.5	0.3576
3	C	101.5	0.1812
3	C	156.5	0.5076
3	C	116.5	0.3774
3	C	181.0	0.5617
3	C	155.5	0.2889

3	C	75.0	0.1825
3	C	77.5	0.2000
3	C	102.0	0.1429
3	C	103.5	0.2413
3	C	74.5	0.1258
3	C	157.0	0.3919
3	C	138.0	0.5278
3	C	78.5	0.2160
3	C	160.0	0.2664
3	C	156.5	0.4568
3	S	96.0	0.1497
3	S	17.0	0.0482
3	S	7.0	0.0122
3	S	19.0	0.0233
3	S	64.0	0.2685
3	S	8.5	0.0358
3	S	7.5	0.0132
3	S	6.0	0.0159
3	S	8.0	0.0180
3	S	10.5	0.0273
3	S	11.0	0.0342
3	S	21.0	0.0681
3	S	7.0	0.0230
3	S	5.0	0.0174
3	S	5.0	0.0167
3	S	56.0	0.1690
3	S	126.0	0.3616
3	S	12.0	0.0281

3	S	13.0	0.0307
3	S	25.0	0.0648
3	S	20.5	0.0696
3	S	11.0	0.0325
3	S	10.0	0.0309
3	S	20.5	0.0644
3	S	17.5	0.0613
3	S	5.0	0.0195
3	S	14.5	0.0665
3	S	19.5	0.1280
3	S	83.0	0.1422
3	S	8.5	0.0210
3	S	6.0	0.0120
3	S	11.5	0.0431
3	S	35.5	0.1632
3	S	13.0	0.0753
3	S	10.0	0.0394
3	S	1.5	0.0016
3	S	188.0	0.4673
3	S	7.5	0.0138
3	S	11.5	0.0319
3	S	10.5	0.0297
3	S	4.0	0.0050
3	S	9.0	0.0216
3	S	14.5	0.0356
3	S	34.0	0.1169
3	S	12.5	0.0321

3	S	7.5	0.0150
3	S	29.0	0.0471
3	S	25.0	0.0522
3	S	32.0	0.0805
3	S	13.5	0.0261
3	S	28.5	0.0926
3	S	10.0	0.0393
3	S	97.5	0.2450
3	S	6.0	0.0121
3	S	8.0	0.0161
3	S	7.0	0.0163
3	S	15.0	0.0474
3	S	13.0	0.0279
3	S	12.0	0.0270
3	S	17.5	0.0500
3	S	5.0	0.0135
3	S	14.0	0.0485
3	S	14.5	0.0478
3	S	6.0	0.0219
3	S	7.5	0.0322
3	S	3.0	0.0078
3	S	5.0	0.0118
3	S	5.0	0.0100
3	S	5.0	0.0113
3	S	13.5	0.0262
3	S	22.5	0.0457
3	S	9.0	0.0207
3	S	36.0	0.0576

3	S	9.5	0.0280
3	S	236.5	0.6165
3	S	12.0	0.0134
3	S	13.0	0.0220
3	S	153.0	0.2928
3	S	26.0	0.0266
3	S	8.5	0.0109
3	S	17.0	0.0471
3	S	20.0	0.0568
3	S	6.5	0.0235
3	S	6.5	0.0472
3	S	13.0	0.0405
3	S	13.5	0.0470
3	S	14.5	0.0394
3	S	11.0	0.0228
3	S	6.0	0.0093
3	S	10.0	0.0205
3	S	7.0	0.0141
3	S	103.0	0.1654
3	S	166.0	0.4387
3	S	32.0	0.0377
3	S	6.5	0.0254

APPENDIX B

This appendix gives the raw data of measures for variables thought likely to be correlated with Myriophyllum spicatum growth during 1982 in Lake Memphremagog. These variables appear by block class (BC), growth period (GP) and plant number (PN) classifications in the following table as: N = tissue nitrogen (g $N \cdot g^{-1}$), P = tissue phosphorus (g $P \cdot g^{-1}$), K = tissue potassium (g $K \cdot g^{-1}$), NW = number of whorls on the distal 15 cm of a central stem, LL = average length (cm) of leaves on the basal whorl of the distal 15 cm of a central stem, PF = photon flux density ($E \cdot m^{-2} \cdot d^{-1}$), SGR = specific growth rate ($mg \cdot g^{-1} \cdot plant^{-1} \cdot d^{-1}$), S^2 of SGR = variance associated with estimating specific growth rates using lenght-weight relations, RGR = relative growth rate ($g \cdot plant^{-1} \cdot d^{-1}$) and S^2 of RGR = variance associated with estimating relative growth rates using length-weight relations.

BC	GP	PN	N	P	K	NW	LL	PF	SGR	S^2 of SGR	RGR	S^2 of RGR	PR
A	1	1	11.67	1.98	21.38	3	33	9.15	7.67	0.412	2.89	0.0066	1.99
A	1	2	75.46	1.66	50.68	8	30	8.94	-15.14	0.341	-4.96	0.0304	1.40
A	1	3	7.92	1.17	21.35	14	38	9.20	-12.42	0.359	-4.34	0.0159	2.00
A	1	4	.	.	.	.	.	10.19	-71.54	0.069	-40.37	0.3456	.
A	1	5	12.26	1.86	17.03	11	18	7.28	39.58	0.055	3.36	0.0105	3.32
A	1	6	.	.	.	.	.	7.62	-71.34	0.368	-14.45	0.1841	.
A	1	7	12.26	1.26	33.92	4	28	9.20	-12.42	0.359	-4.34	0.0159	2.00
B	1	1	.	.	.	.	.	8.69	-71.54	0.451	-17.96	0.2255	.
B	1	2	.	.	.	.	.	9.09	-4.59	0.327	-1.39	0.0076	.
B	1	3	.	.	.	7	24	8.11	17.82	0.154	3.56	0.0229	2.12
B	1	4	14.42	2.36	31.23	8	29	7.24	22.49	0.229	4.25	0.0292	1.80
B	1	5	11.40	2.79	32.32	3	34	7.58	22.25	0.131	3.11	0.0514	2.06

B	1	6	14.04	1.10	23.62	6	15	7.32	-26.14	0.056	-2.30	0.0092	1.02
B	1	7	95.91	2.39	.	6	20	7.12	-9.58	0.041	-0.79	0.0055	2.36
C	1	1	24.18	3.09	40.79	10	28	8.02	138.30	0.412	21.02	0.3006	4.54
C	1	2	.	.	.	.	.	8.40	-71.55	0.367	-17.38	0.1834	.
C	1	3	5.94	3.98	5.18	9	17	7.49	108.86	0.278	17.63	0.1676	3.34
C	1	4	.	.	.	.	.	9.80	-5.84	0.607	-2.51	0.0277	.
C	1	5	18.24	2.34	5.70	10	24	8.69	16.73	0.220	3.43	0.0066	1.94
C	1	6	10.04	2.11	10.19	4	37	7.37	-15.62	0.054	-1.42	0.0044	1.57
C	1	7	32.15	1.19	20.71	2	30	7.67	182.39	0.423	24.25	0.3455	1.90
D	1	1	20.14	2.49	23.13	9	35	8.73	124.22	2.148	41.99	1.8359	4.66
D	1	2	9.79	1.38	13.87	4	26	8.64	31.78	0.375	11.19	0.0721	1.70
D	1	3	9.80	4.76	18.02	13	28	7.20	79.79	0.149	10.29	0.0758	2.98
D	1	4	15.97	2.47	25.57	10	37	7.28	93.15	0.114	9.04	0.0671	5.81
D	1	5	.	.	.	12	30	8.21	15.36	0.144	2.46	0.0103	2.43
D	1	6	142.30	3.01	15.05	16	16	7.12	20.94	0.039	1.53	0.0035	2.18
D	1	7	.	.	.	.	.	8.84	44.36	0.444	12.82	0.1355	.
E	1	1	10.27	2.09	11.75	9	35	8.21	18.93	0.899	6.66	0.2871	4.02

E	1	2	16.55	1.34	27.49	3	13	8.45	-21.37	0.199	-4.81	0.0174	1.10
E	1	3	14.87	1.42	23.01	10	35	7.20	66.27	0.066	5.24	0.0263	2.14
E	1	4	13.68	0.92	20.83	13	33	9.36	-20.78	1.761	-14.11	0.6917	1.52
E	1	5	.	.	.	.	.	7.28	62.40	0.775	7.55	0.0389	.
E	1	6	12.11	2.32	19.45	5	33	8.21	-12.17	0.202	-3.01	0.0324	1.66
E	1	7	11.48	1.14	26.96	13	30	8.89	61.19	0.774	26.44	0.3860	3.16
A	2	1	.	.	.	2	32	10.94	-5.29	0.534	-1.71	0.0059	1.62
A	2	2	.	.	.	8	35	17.18	12.75	11.931	18.17	1.3909	2.62
A	2	3	.	.	.	9	37	12.45	7.90	2.267	5.84	0.2390	3.85
A	2	4	.	.	.	2	35	13.40	-22.40	2.515	-16.26	0.2195	0.50
A	2	5	.	.	.	.	.	11.06	-71.37	1.565	-32.90	0.7824	.
A	2	6	.	.	.	7	27	9.99	24.33	0.339	6.64	0.0464	1.17
A	2	7	.	.	.	19	25	12.67	-47.66	2.102	-25.07	0.6226	1.26
B	2	1	.	.	.	.	.	10.05	-71.19	0.718	-23.85	0.3591	.
B	2	2	.	.	.	16	15	10.27	-1.46	0.379	-0.52	0.0092	0.97
B	2	3	.	.	.	6	30	9.33	11.78	0.212	2.72	0.0316	0.80
B	2	4	.	.	.	6	27	11.06	-18.39	2.240	-8.70	0.0774	0.59

B	2	5	.	.	.	2	32	8.97	-48.32	0.170	-7.83	0.0547	0.71
B	2	6	.	.	.	.	.	8.39	-71.69	0.153	-9.75	0.0766	.
B	2	7	.	.	.	8	16	8.01	-58.46	0.170	-8.24	0.0761	1.53
C	2	1	.	.	.	.	.	9.44	-71.31	0.418	-16.43	0.2090	.
C	2	2	16.12	2.18	9.98	9	20	10.69	26.85	1.137	13.69	0.4897	1.51
C	2	3	.	.	.	9	22	7.92	26.80	0.158	4.53	0.0904	2.79
C	2	4	.	.	.	5	30	8.58	-9.84	0.077	-1.12	0.0030	0.58
C	2	5	.	.	.	4	20	12.04	-32.43	1.421	-19.23	0.2704	0.67
C	2	6	.	.	.	11	22	8.67	71.43	0.167	9.71	0.0821	1.60
C	2	7	.	.	.	10	32	13.94	58.84	8.146	58.49	4.8059	1.51
D	2	1	12.58	2.26	19.39	5	25	10.33	25.42	0.807	12.10	0.1967	1.44
D	2	2	24.44	5.19	6.60	8	33	10.33	48.50	3.106	25.71	2.3596	3.50
D	2	3	7.23	2.38	13.95	6	22	9.13	12.35	0.161	2.46	0.0079	1.81
D	2	4	22.81	4.06	25.47	8	27	8.43	20.59	0.150	23.64	0.0304	2.02
D	2	5	15.77	1.95	15.32	3	35	11.90	0.53	2.984	0.40	1.2121	1.09
D	2	6	.	.	.	.	.	9.93	-71.55	0.517	-17.17	0.2586	.
D	2	7	.	.	.	2	20	8.20	-34.98	0.062	-3.08	0.0148	0.43

E	2	1	25.73	3.20	17.73	6	24	11.06	10.27	0.757	3.73	0.1745	2.91
E	2	2	10.57	4.99	11.02	8	20	9.77	278.97	15.790	85.09	15.5196	2.18
E	2	3	19.36	3.86	23.80	7	35	9.18	49.09	0.822	14.63	0.5874	2.81
E	2	4	17.09	0.73	21.36	4	39	9.66	91.25	1.356	40.24	0.9171	0.00
E	2	5	.	.	.	7	14	7.70	3.76	0.038	1.12	0.0030	1.94
E	2	6	.	.	.	.	.	9.13	-141.84	0.672	-25.96	0.3359	.
E	2	7	16.25	2.84	29.34	8	22	9.39	9.71	0.241	2.46	0.0360	3.85
A	3	1	12.08	1.97	16.22	12	34	22.43	18.92	8.299	29.24	5.2687	2.64
A	3	2	18.55	0.22	0.10	11	21	11.02	20.86	0.022	2.11	0.0081	1.15
A	3	3	.	.	.	.	.	13.78	39.30	0.441	15.05	0.2029	.
A	3	4	14.73	2.13	15.34	3	34	17.15	19.09	2.544	16.53	1.0542	1.16
A	3	5	11.99	2.28	19.72	11	21	14.25	10.52	0.232	4.65	0.0937	4.13
A	3	6	.	.	.	.	.	11.46	-73.93	0.066	-7.39	0.0559	.
A	3	7	25.67	0.20	14.33	15	33	15.41	140.20	3.999	84.12	3.4764	3.11
B	3	1	.	.	.	.	.	12.89	-73.72	0.144	-11.28	0.1229	.
B	3	2	29.17	4.73	7.58	9	35	13.63	197.17	2.025	42.79	1.9884	2.84
B	3	3	.	.	.	10	28	12.74	20.41	0.101	4.02	0.0493	5.46

B	3	4	15.78	2.77	30.25	10	31	24.33	43.47	1.579	39.95	1.1924	.
B	3	5	21.91	3.68	27.96	9	30	13.25	94.61	1.491	28.19	1.3099	5.97
B	3	6	.	.	.	.	.	11.72	-72.60	0.249	-14.16	0.1515	.
B	3	7	.	.	.	.	.	11.32	-73.69	0.061	-7.22	0.0512	.
C	3	1	18.70	1.98	18.00	16	29	18.75	27.45	4.753	21.63	3.7005	3.90
C	3	2	.	.	.	.	.	10.65	167.74	0.087	10.06	0.0816	.
C	3	3	.	.	.	17	33	17.44	4.99	2.467	4.11	1.4349	1.17
C	3	4	14.73	1.29	19.67	9	25	14.91	104.34	1.377	44.66	1.0942	3.44
C	3	5	5.48	2.53	14.74	21	30	14.91	64.58	14.558	17.44	14.5034	3.70
C	3	6	11.89	1.54	26.34	14	30	27.44	-20.74	0.645	-19.01	0.3446	0.75
C	3	7	30.91	3.88	33.65	13	35	17.34	46.32	0.489	23.11	0.0392	5.39
D	3	1	19.56	3.06	9.65	5	36	12.32	178.61	0.537	30.36	0.5091	3.19
D	3	2	0.10	1.34	17.65	3	31	15.41	-38.01	0.178	-11.59	0.0976	1.52
D	3	3	16.62	2.71	1.85	2	31	13.10	-73.46	0.159	-11.90	0.1362	0.60
D	3	4	29.49	3.01	27.08	7	25	10.83	183.69	0.149	16.43	0.1398	5.27
D	3	5	14.05	2.76	27.15	7	26	11.58	-73.67	0.072	-7.74	0.0607	6.79
D	3	6	19.21	2.68	24.06	10	24	13.18	65.31	1.922	34.61	1.2425	3.61

D	3	7	17.61	2.62	15.30	7	35	11.65	189.83	1.780	56.00	1.6837	3.10
E	3	1	16.84	2.47	17.45	14	26	22.59	4.00	5.889	6.60	3.2978	2.64
E	3	2	.	.	.	4	28	14.74	85.97	0.599	26.05	0.5035	3.25
E	3	3	39.07	6.40	23.60	11	26	17.44	95.92	1.618	45.18	1.4376	3.37
E	3	4	17.27	1.73	18.10	5	32	25.37	24.66	1.620	26.14	1.1710	1.55
E	3	5	12.39	1.52	0.67	14	34	27.60	-1.74	1.161	-1.67	0.1201	1.63
E	3	6	.	.	.	.	.	11.08	-73.79	0.049	-5.61	0.0420	.
E	3	7	4.57	1.89	10.84	7	33	26.69	-0.34	11.640	-0.80	5.3826	1.38
A	4	1	15.29	2.48	28.48	3	33	12.91	-20.58	0.741	-10.23	0.2006	1.30
A	4	2	12.98	1.75	20.55	7	22	13.46	18.85	0.258	3.60	0.0392	1.78
A	4	3	.	.	.	.	.	13.53	-71.46	0.468	-15.15	0.2341	.
A	4	4	17.19	1.81	20.58	13	23	20.04	15.29	2.811	10.87	0.9312	2.48
A	4	5	16.97	2.80	24.17	9	25	10.45	166.59	0.216	15.49	0.1667	2.34
A	4	6	14.64	1.55	15.74	7	32	17.25	33.90	2.412	28.27	1.0981	1.36
A	4	7	12.87	1.79	34.38	11	28	16.38	14.58	2.533	10.09	1.1541	1.68
B	4	1	12.45	1.04	12.04	4	32	15.39	19.40	3.078	13.31	1.8251	0.77
B	4	2	18.30	2.17	6.81	7	22	10.29	165.12	0.124	9.91	0.0883	2.51

B	4	3	18.00	1.93	23.58	9	31	16.13	36.41	3.904	33.17	1.7703	1.99
B	4	4	10.68	0.99	15.14	18	24	21.89	-0.18	7.137	-0.29	2.2172	1.03
B	4	5	.	.	.	.	.	12.91	-36.46	0.477	-18.19	0.2386	.
B	4	6	16.16	1.79	27.34	4	30	17.43	2.91	2.657	2.01	1.1381	1.21
B	4	7	33.01	1.69	28.48	4	28	13.59	20.02	1.229	7.49	0.7747	1.41
C	4	1	14.24	2.07	22.24	9	24	13.53	-71.59	0.445	-12.74	0.2225	1.42
C	4	2	11.12	1.30	29.60	5	36	19.43	12.43	2.304	11.06	0.3494	1.08
C	4	3	16.10	2.02	19.74	7	25	12.14	136.42	0.293	19.37	0.1711	1.67
C	4	4	5.76	2.06	15.19	12	27	15.08	-3.82	1.682	-2.46	0.6644	1.97
C	4	5	16.20	2.29	14.21	6	26	10.66	179.76	0.255	12.94	0.2071	1.32
C	4	6	15.65	1.92	23.59	10	28	13.18	84.76	0.394	17.21	0.1899	0.92
C	4	7	17.82	2.93	10.06	5	28	15.24	-71.48	1.823	-33.16	0.9117	2.18
D	4	1	9.79	0.80	25.42	10	18	11.00	149.74	0.279	12.28	0.2190	0.51
D	4	2	.	.	.	.	.	12.85	-71.51	0.344	-12.80	0.1718	.
D	4	3	14.17	1.74	21.16	5	20	10.83	42.49	0.076	3.27	0.0228	1.69
D	4	4	22.32	1.34	21.50	12	21	11.83	61.84	0.163	7.24	0.0641	1.12
D	4	5	29.94	2.09	6.87	5	25	9.97	41.11	0.081	4.19	0.0235	0.54

D	4	6	13.15	2.22	24.34	11	24	13.18	2.62	0.276	0.58	0.0608	1.88
D	4	7	44.55	1.64	35.30	3	40	14.47	-7.52	0.724	-3.52	0.0251	5.93
E	4	1	11.18	1.68	19.34	8	23	12.01	89.03	0.192	10.25	0.0842	1.70
E	4	2	17.44	1.41	23.78	12	26	14.92	18.27	0.630	8.00	0.1089	1.19
E	4	3	11.64	1.63	30.15	7	20	9.87	158.16	0.090	7.75	0.0646	1.72
E	4	4	11.81	1.22	0.15	15	23	12.01	-5.98	0.166	-1.03	0.0191	2.20
E	4	5	11.98	1.59	24.74	3	34	16.55	-5.54	0.680	-1.89	0.0116	0.65
E	4	6	.	.	.	10	24	14.62	-9.23	1.192	-6.06	0.5116	1.50
E	4	7	14.85	1.28	23.29	6	34	16.55	20.60	0.780	8.71	0.0514	1.05
A	5	1	14.65	1.76	26.31	7	22	16.40	96.74	1.688	32.21	1.0053	1.30
A	5	2	10.99	1.83	21.89	6	32	16.03	65.38	1.165	33.34	0.4373	1.33
A	5	3	22.02	3.43	30.03	7	32	11.98	268.02	1.144	46.64	0.9859	2.31
A	5	4	12.61	1.38	24.38	11	25	19.29	5.15	2.214	3.91	0.4596	2.93
A	5	5	16.35	2.09	26.08	2	34	19.18	60.68	2.613	32.89	1.1894	0.43
A	5	6	4.78	3.87	19.03	9	24	21.82	-13.78	3.988	-15.67	0.1697	0.62
A	5	7	17.00	1.80	29.15	7	37	18.13	-71.45	3.962	-52.01	1.9809	0.62
B	5	1	5.83	3.65	20.55	11	22	10.71	50.34	0.406	12.54	0.2106	.

B	5	2	34.09	1.40	33.65	7	24	16.03	-5.64	3.980	-4.98	2.0502	0.65
B	5	3	18.15	1.59	33.03	4	23	12.89	-16.31	1.109	-6.44	0.4836	0.65
B	5	4	79.34	2.69	49.47	7	21	10.07	137.88	0.192	9.51	0.1458	0.01
B	5	5	29.34	1.74	32.92	5	27	12.32	112.62	0.506	22.75	0.3039	.
B	5	6	4.76	2.96	21.78	8	23	11.20	223.82	0.967	42.75	0.8453	2.66
B	5	7	33.75	2.35	32.78	12	24	11.46	26.36	0.125	2.98	0.0195	1.87
C	5	1	10.14	2.51	17.35	7	28	17.15	7.48	0.959	4.02	0.0011	0.36
C	5	2	8.70	0.75	20.32	6	24	13.40	21.82	0.279	4.36	0.0251	0.53
C	5	3	16.07	1.52	31.04	9	23	13.78	14.32	0.291	2.79	0.0029	0.84
C	5	4	14.08	1.16	27.15	10	24	14.74	5.95	0.410	1.39	0.0056	1.29
C	5	5	13.53	1.33	21.52	16	26	16.77	-20.31	0.817	-7.01	0.0561	2.26
C	5	6	4.31	1.60	29.30	5	24	13.86	-10.11	0.392	-3.70	0.0227	0.59
C	5	7	11.74	1.60	29.30	8	18	15.94	4.96	0.690	2.11	0.0168	1.16
D	5	1	31.19	2.34	25.15	6	22	11.72	15.35	0.128	1.86	0.0091	2.47
D	5	2	7.33	5.83	24.93	.	.	11.39	169.30	0.643	24.38	0.5283	.
D	5	3	15.22	2.01	26.21	11	27	10.71	276.24	0.163	24.59	0.5436	1.32
D	5	4	21.39	3.67	22.95	6	16	11.59	112.88	0.317	13.21	0.2045	1.74

D	5	5	17.04	2.86	14.93	3	29	11.46	61.25	0.140	6.92	0.0354	1.73
D	5	6	17.51	2.01	20.87	3	32	16.96	-71.43	2.461	144.57	1.2306	0.82
D	5	7	15.63	2.05	31.91	8	25	16.12	-5.44	0.632	-1.58	0.0070	1.21
E	5	1	13.43	1.59	21.98	10	24	16.49	4.57	0.845	1.96	0.0161	0.01
E	5	2	13.52	1.48	18.08	4	24	14.33	-8.11	0.360	-1.92	0.0052	0.67
E	5	3	14.93	2.05	21.34	10	19	12.39	82.65	0.288	12.89	0.1219	2.09
E	5	4	4.37	1.71	22.78	.	.	12.60	-24.04	0.950	-11.64	0.3033	.
E	5	5	16.84	2.36	24.51	5	28	13.18	97.73	0.452	16.91	0.2194	0.94
E	5	6	11.13	1.93	24.98	7	23	16.58	3.50	1.876	2.66	0.2754	2.00
E	5	7	11.24	1.48	30.73	6	40	15.42	-11.78	2.013	-7.35	0.4176	0.69

APPENDIX C

This appendix gives the raw data of maximum biomass ($g \cdot m^{-2}$) measures by species located within study plots, for both unfertilized (U) and nutrient addition (NA) fertilized (F) sediments in Lake Memphremagog, presented by block class (BC) and growth period (GP). The symbols on the following table heading represent the aquatic macrophyte species: Myriophyllum spicatum (MY), Vallisneria americana (VA), Potomegeton robbinsii (PR), Potomegeton crispus (PC), Potomegeton natans (PN), Elodea spp. (EL), Cabomba spp. (CA), total non-Myriophyllum (TNMY) species , and the biomass of all species combined (BTOT). In addition, stems that had overwintered (SO = old stems$\cdot m^{-2}$), stems of the year (SN = new stems$\cdot m^{-2}$) and the organic content of sediments within plots as loss-on-ignition (ASH = ash weight in percent of sediment dry wt) are presented for each plot.

NA	BC	GP	MY	VA	EL	PR	PC	PN	CA	TNMY	BTOT	SO	SN	ASH
U	A	1	32.95	0.98	0.66	20.31	0.12	0.00	0.73	22.79	55.74	17.2	0.0	**15.24**
U	B	1	11.71	3.22	0.00	3.59	0.22	0.00	0.00	7.04	18.75	10.0	0.4	**18.83**
U	C	1	24.52	4.63	0.00	0.07	1.06	0.00	0.00	5.75	30.30	23.2	0.0	**18.37**
U	D	1	68.71	12.08	0.20	0.85	0.84	1.63	0.00	15.06	84.31	9.6	0.0	**8.89**
U	E	1	27.17	18.13	2.30	2.24	0.00	0.00	0.32	23.00	50.17	12.8	1.2	**9.54**
U	A	2	46.93	6.51	1.22	26.80	0.00	0.00	0.55	35.08	82.02	12.0	1.6	**16.76**
U	B	2	4.00	2.23	0.00	0.13	0.31	0.00	0.12	2.80	6.79	4.8	0.8	**17.14**
U	C	2	41.90	11.14	0.61	0.32	1.39	0.00	0.17	13.63	55.54	16.4	2.4	**12.25**
U	D	2	22.02	24.93	1.81	1.04	0.16	0.00	0.00	27.94	49.96	10.0	4.0	**11.43**
U	E	2	10.68	3.20	0.00	0.06	3.38	0.00	0.62	7.25	17.93	18.4	3.6	**15.78**
U	A	3	26.07	0.08	0.00	1.46	0.00	0.00	0.00	1.46	27.54	22.0	51.2	**15.37**
U	B	3	14.61	0.92	0.16	2.03	0.41	0.00	0.39	3.92	18.53	14.8	74.8	**19.58**
U	C	3	47.30	4.35	0.11	0.33	0.05	0.00	0.00	4.84	52.14	57.2	83.2	**16.21**
U	D	3	24.90	2.87	6.88	32.04	0.93	0.00	0.30	43.01	67.91	22.8	46.4	**9.79**
U	E	3	33.01	6.40	0.16	0.23	2.05	0.00	0.69	9.52	41.54	16.0	28.8	**10.65**

F	A	3	30.92	16.69	15.18	19.21	2.61	1.38	0.00	55.07	85.46	10.4	47.6	.
F	B	3	23.98	16.50	0.00	0.00	0.24	0.00	0.00	16.74	40.72	6.0	35.2	.
F	C	3	35.09	18.38	0.00	5.52	0.00	0.00	0.00	23.89	58.96	20.4	74.0	.
F	D	3	61.44	13.88	1.23	2.15	0.56	0.00	1.83	19.64	81.08	18.0	41.6	.
F	E	3	26.69	34.02	1.26	0.42	0.31	1.16	0.00	37.17	63.86	20.0	54.4	.
U	A	4	19.44	0.00	5.23	5.87	2.08	0.00	4.03	17.06	37.05	2.0	69.2	15.41
U	B	4	1.64	0.64	0.22	4.36	0.00	0.00	0.00	5.23	6.87	2.0	82.0	21.75
U	C	4	34.52	2.96	0.23	3.05	0.00	0.00	0.04	6.27	40.80	2.4	80.8	12.04
U	D	4	12.75	6.67	1.63	16.51	0.00	0.00	0.32	25.13	37.88	1.2	60.8	13.11
U	E	4	57.57	35.35	5.88	0.86	2.42	0.00	1.67	46.16	101.33	11.6	109.2	6.49
U	A	5	20.44	0.25	8.58	4.38	2.37	0.00	2.80	18.37	38.81	0.4	78.4	17.24
U	B	5	2.80	0.64	0.06	0.03	0.00	0.00	0.65	1.38	4.18	0.8	28.4	19.34
U	C	5	31.19	9.45	0.96	0.13	0.44	0.00	0.57	11.56	42.75	0.0	153.2	9.02
U	D	5	8.21	34.74	2.55	1.19	0.47	0.00	0.69	39.65	47.86	0.4	46.0	12.33
U	E	5	24.29	17.24	0.41	0.00	0.14	0.00	1.14	18.92	43.21	1.6	83.2	9.85

APPENDIX D

This appendix gives the summary, methods , results and data of a preliminary investigation to assess the affect of increasing sediment organic content on *Myriophyllum spicatum* photosynthetic and growth rates, *in vitro*.

Summary

Growth of the aquatic macrophyte Myriophyllum spicatum L. was investigated using proportions (0, 25, 50, 75 and 100 %) of organic pond sediment diluted with pure silica sand. Analysis of covariance (ANCOVA) models identified substrate type as effecting photosynthetic and growth rates in culture by showing optimum rates for plants on medium (50 %) proportions compared to low (0 %) and high (100 %) proportions of pond sediment substrate. Photosynthetic rate ANCOVA models significantly ($P < 0.001$) explained 63 % of the total variation using three variables: the proportion of pond sediment, shoot tissue phosphorus and shoot tip biomass. Relative growth rate ANCOVA models significantly ($P < 0.001$) identified 67 % of the total variation using three variables: the proportion of pond sediment, initial plant biomass and shoot tissue phosphorus. Although root iron content increased as the proportion of pond sediment increased, Fe did not contribute significantly ($P < 0.05$) to ANCOVA models describing photosynthetic or growth rates.

Methods and Procedure

Sediment types consisting of 0, 25, 50, 75 and 100 % of a natural organic pond sediment were prepared by diluting the sediment with washed quartz sand (dia. ca. 0.5 mm) obtained from Indusmin, Ltd. A volume of 200 ml for each of these five substrate types was placed in twenty 250 ml pyrex beakers and covered with a 20 ml layer of quartz sand followed by 20 ml of coarse (dia. ca. 5 mm) quartz pebbles. The top two layers insured against loss of prepared sediments from the beakers when they were later placed in the experimental flowtank.

To induce rootlet production, one hundred 15 cm long shoots of M. spicatum were planted for one week in pure washed silica. Following an inspection for sucessful rootlet production, the plants were washed free of silica, blotted dry and weighted, and then replanted in the prepared substrates. The planted shoots were arranged in a randomized pattern of 5 rows and 20 columns on the bottom of a 5000 L Coldstream, Ltd., flowtank. The water flow rate through the tank was 7 $cm \cdot s^{-1}$, yielding a water replacement rate of 83 hours. Tank water had a pH range of 7.5 to 8.0 and varied in temperature between 20 to 22° C. A 14 hour photoperiod was provided by 12 General Electric overhead floodlights (500 watts, 115 volts). Photosynthetically active radiation (PAR) was measured with the underwater cell of a KAHLSICO irradiance meter ($\mu W \cdot cm^{-2}$) at water depths of 1 cm and 50 cm, and converted to the photon flux density of 1000 $\mu E \cdot cm^{-2} \cdot s^{-1}$ and 400 $\mu E \cdot cm^{-2} \cdot s^{-1}$ (Wetzel 1975), respectively.

Plants were harvested after 25 days when the majority of the shoots had reached the surface of the 70 cm deep flowtank. The plants were then washed free of debris and sectioned into 3 segments: upper 15 cm shoot tips, remaining lower shoots, and roots. The latter two segments were quick-frozen, oven dried to constant weight at 80° C, and ground in a Whiley mill to pass through a 40 mesh stainless steel screen.

Photosynthetic rate was measured using the upper 15 cm shoot tips at the end of the growing period. These shoots were placed in 500 ml flat-sided culture bottles filled with flowtank water. The bottles were inoculated with 10 ml of a 12600 x 10^6 dpm·ml^{-1} $NaH^{14}CO_3$ solution, and incubated at 1000 $\mu E \cdot cm^{-2} \cdot s^{-1}$ PAR for one hour in the flowtank. These plants were subsequently placed on 0.1 N HCl for 15 seconds to remove any adhering ^{14}C, and then rinced with flowtank water. Immediately after rincing, the shoot tips were frozen and later dried and ground using the same techniques employed for lower shoot and root segments. A subsample (10-25 mg) of the re-dried shoot tip homogenate was combusted in an automated oxidizer (Intertechnique Oxymat IM 4101) to determine ^{14}C activity, and the photosynthetic rate was expressed as mg $C \cdot g^{-1} \cdot h^{-1}$.

Plant tissues were digested using a sulphuric acid - hydrogen peroxide solution following Thomas et al. (1967). Shoot tip phosphorus (mg $P \cdot g^{-1}$ dry wt) was measured with the ascorbate method (Golterman and Clymo 1970) using a Bausch and Lomb Spectronic - 100 spectrophotometer. Root iron (mg $Fe \cdot g^{-1}$ dry wt) was determined with a Perkins-Elmer Atomic Absorption Spectrophotometer - 403.

In this study, the relative growth rate ($mg \cdot plant^{-1} \cdot d^{-1}$) was calculated by determining the difference in plant biomass, as the whole plant final biomass minus the initial biomass, during the growth period. The specific growth rate ($mg \cdot g^{-1} \cdot plant^{-1} \cdot d^{-1}$) was derived by dividing this difference in plant biomass during the growth period with the initial plant biomass (cf. Evans 1972, Harper 1977).

Sediment organic matter was defined as the percent loss-on-ignition of dry weight after ashing the sediments at 550° C for 6 hours (Sand-Jensen and Søndergaard 1979). The measured organic content was 0, 0.85, 2.33, 7.65 and 19.0 % dry wt for the 0, 25, 50, 75 and 100 % proportions of pond sediment (PPS) in the substrate, respectively. The sediment bulk density was determined as 1.43, 1.12, 0.82, 0.37 and 0.20 g dry $wt \cdot ml^{-1}$ for the 0, 25, 50, 75 and 100 % PPS.

Data were analysed with the McGill University computer systems using Statistical Analysis Systems (1982) software. Duncan's multiple range test (Zar 1974) was used to identify statistically significant ($P < 0.05$) differences among mean values. Any linearization of independant (x) variables used the Box and Tidwell (1962) method to improve the proportion of variation explained during linear regression. Analysis of covariance (ANCOVA) models used least square means (LSM) to test for significant ($P < 0.05$) differences among characteristics of plants grown on prepared substrate types, when covariance of these variables investigated biased analysis of variance (ANOVA). So that the mean plant weights were not

significantly different among substrate types at planting time, 5 of 20 replicates in the 25 % pond sediment were removed from the final statistical analysis.

Results

Photosynthetic rates increased from plants grown on low proportions of pond sediment (PPS) substrate (0 and 25 % PPS), to those grown on medium (50 % PPS) and high (75 and 100 % PPS) proportions, where no significant ($P < 0.05$) difference in upper photosynthetic rates were maintained (Table 1). In contrast, the mean relative growth rates did not significantly differ among the 0, 25, 50 and 75 % PPS treatments, but significantly decreased on 100 % PPS (Table 2a). Specific growth rates differed insignificantly among all substrate types (Table 2b).

Final whole plant biomass (Table 3a) and final shoot biomass (Table 3b) were highest for treatments of 25, 50 and 75 % PPS, and significantly different from biomass grown on 100 % PPS. The distal 15 cm shoot biomass (Table 3c) was highest for 0 and 25 % PPS and significantly different than those for 50, 75 and 100 % PPS. Root final biomass (Table 3d) peaked on 50 % PPS, and was significantly different from all other substrate proportions. Although there existed a considerable range in root to shoot ratios (R:S) (Table 3e), the R:S on 50 % PPS were significantly different from those plants on 0, 25, 75 and 100 % PPS.

The shoot tip phosphorus content peaked on 75 % PPS but was significantly different only from the 0 and 100 % PPS treatments (Table 4a). The root iron content consistantly increased on substrates of increasing % PPS and was significantly different, except between the lowest two

proportions of 0 and 25 % PPS (Table 4b).

Significant ($P < 0.001$) linear regression relations were identified describing photosynthetic rate using shoot tip biomass ($r^2=0.46$), shoot phosphorus content ($r^2=0.54$), and only marginaly, root iron content ($r^2=0.17$) (Table 5a-c). To linearize the relation describing photosynthetic rate using shoot tip biomass (Table 5a), the transformation of $X^{-0.65}$ was performed on shoot tip biomass increasing r^2 to 0.51 (Table 5d) and stabilizing the residuals about the predicted line. In contrast, relative growth rates were correlated with whole plant biomass ($r^2=0.50$) at the beginning of the experiment (Table 5e), even though no significant differences had existed among the initial fresh weights of the whole plants. Additionally, shoot phosphorus content was significantly correlated with the distal 15 cm shoot biomass ($r^2=0.50$) (Table 5f).

To test the effect of only substrate type on photosynthetic and growth rates, the individual portions of variation explained by characteristics of the plant were sought. Hence, the analysis of covariance (ANCOVA) was used to explain the variation not attributable to the effect of sediment type (for details of ANCOVA see: Cochran 1957, Legendre and Legendre 1983) and test if differences in photosynthesis and growth rates occured due to the treatments of sediment type alone. The majority of variation ($R^2=0.63$, $P < 0.001$) in photosynthetic rate was described with ANCOVA using PPS, shoot phosphorus content, and transformed shoot tip biomass (Table 6). Here, the least square means (LSM)

calculated for photosynthetic rate used the class variable PPS to show significant ($P < 0.05$) differences between the peak value on 50 % PPS, and the lower values at 0 and 100 % PPS. For relative growth rates, the ANCOVA model accounted for R^2=0.67 ($P < 0.001$) of the variation using PPS, initial plant biomass, and shoot phosphorus content (Table 7). This relative growth rate model showed the two highest values for 25 and 50 % PPS were significantly different from the two lowest growth rates on 0 and 100 % PPS. Root iron was not identified as a significant contributor to either ANCOVA models.

Table 1. Photosynthetic rate (mg $C \cdot g^{-1} \cdot h^{-1}$) means of Myriophyllum spicatum shoot tips (15 cm) presented by the proportion of organic pond sediment in the substrate. Means with the same letter do not significantly ($P < 0.05$) differ.

	Proportion of Pond Sediment (%)				
	0	25	50	75	100
Photo-synthetic Rate	2.016 B	2.317 B	3.283 A	2.969 A	3.010 A
n	16	15	16	16	16
SE	0.176	0.153	0.247	0.238	0.305

Table 2. Relative ($mg \cdot plant^{-1} \cdot d^{-1}$) and specific ($mg \cdot g^{-1} \cdot plant^{-1} \cdot d^{-1}$) growth rate means of *Myriophyllum spicatum* presented by the proportion of organic pond sediment in the substrate. Means with the same letter do not significantly ($P < 0.05$) differ.

	Proportion of Pond Sediment (%)				
	0	25	50	75	100
a. Relative Growth Rate	20.58 AB	26.94 A	24.44 A	26.47 A	16.71 B
n	20	15	20	20	20
SE	1.69	3.31	1.73	2.23	1.65
b. Specific Growth Rate	199.7 A	221.9 A	216.2 A	214.7 A	182.3 A
n	20	20	20	20	20
SE	39.1	19.7	11.0	12.1	9.5

Table 3. Biomass (g) allocation of *Myriophyllum spicatum* listed by whole plant , shoot, distal 15 cm shoot, root and the root to shoot (R:S) ratio, and presented by the proportion of organic pond sediment in the substrate. Means with the same letter do not significantly ($P < 0.05$) differ.

	Proportion of Pond Sediment (%)				
	0	25	50	75	100
a. Whole	0.640	0.789	0.725	0.785	0.508
	AB	A	A	A	B
n	20	15	20	20	20
SE	0.005	0.090	0.048	0.061	0.049
b. Shoot	0.582	0.707	0.611	0.694	0.447
	AB	A	A	A	B
n	20	15	20	20	20
SE	0.048	0.084	0.043	0.055	0.043
c. Distal	0.294	0.277	0.196	0.173	0.161
Shoot Tip	A	A	B	B	B
n	18	15	18	18	18
SE	0.020	0.015	0.010	0.011	0.010

Table 3. con't.

d. Root	0.055	0.081	0.114	0.089	0.061
	C	B	A	B	C
n	20	15	20	20	20
SE	0.005	0.008	0.009	0.006	0.006
e. R:S	0.113	0.130	0.195	0.132	0.137
Ratio	B	B	A	B	B
n	20	15	20	20	20
SE	0.019	0.014	0.012	0.006	0.006

Table 4. Tissue content of Myriophyllum spicatum shoot phosphorus (mg $P \cdot g^{-1}$) and root iron (mg $Fe \cdot g^{-1}$) presented by the proportion of organic pond sediment in the substrate. Means with the same letter do not significantly ($P < 0.05$) differ.

	Proportion of Pond Sediment (%)				
	0	25	50	75	100
a. Shoot P	1.417	1.477	1.737	1.854	1.654
	B	AB	AB	A	B
n	20	15	20	20	20
SE	0.085	0.056	0.079	0.122	0.086
b. Root Fe	0.681	0.750	1.441	2.002	2.725
	D	D	C	B	A
n	20	15	20	20	20
SE	0.148	0.183	0.079	0.173	0.206

Table 5. Linear regression relations describing photosynthetic rate (mg $C \cdot g^{-1} \cdot h^{-1}$), relative growth rate (mg $\cdot plant^{-1} \cdot d^{-1}$), and shoot tissue phosphorus (mg $P \cdot g^{-1}$) for Myriophyllum spicatum grown in culture.

	r^2	n	Intercept (a)	Slope (b)	P > F
			Photosynthetic Rate		
a. Distal 15 cm Shoot Biomass (g)	0.46	79	4.638	-8.585	0.001
b. Shoot P (mg $P \cdot g^{-1}$)	0.54	79	-0.401	1.851	0.001
c. Root Fe (mg $Fe \cdot g^{-1}$)	0.17	75	2.026	0.437	0.001
d. Transformed Distal 15 cm Shoot ($X^{-0.65}$) Biomass (g)	0.51	79	-0.354	1.102	0.001
			Relative Growth Rate		
e. Initial Whole Plant Biomass (g)	0.50	95	2.357	180.3	0.001
			Shoot Tissue Phosphorus		
f. Distal 15 cm Shoot Biomass (g)	0.50	88	2.479	-3.575	0.001

Table 6. Photosynthetic rate (mg $C \cdot g^{-1} \cdot h^{-1}$) ANCOVA model for Myriophyllum spicatum described 63 % ($P < 0.001$) of the total variation using the class variable the proportion of organic pond sediment (%), and the continuous variables shoot tissue phosphorus (mg $P \cdot g^{-1}$) and transformed ($X^{-0.65}$) shoot tip biomass (g). For this model, least square means (LSM) with the same letter do not significantly ($P < 0.05$) differ.

	Proportion of Pond Sediment (%)				
	0	25	50	75	100
Photo-synthetic Rate LSM	2.409 B	2.745 AB	3.067 A	2.694 AB	2.540 B
n	16	15	16	16	16
SE of LSM	0.173	0.169	0.159	0.171	0.175

Table 7. Relative growth rate ($mg \cdot plant^{-1} \cdot d^{-1}$) ANCOVA model for Myriophyllum spicatum described 67 % of the total variation using the class variable the proportion of pond sediment (%), and the continuous variables initial plant biomass (g) and shoot tissue phosphorus ($mg\ P \cdot g^{-1}$). For this model, least square means (LSM) with the same letter do not significantly ($P < 0.05$) differ.

	Proportion of Pond Sediment (%)				
	0	25	50	75	100
Relative Growth Rate LSM	19.70 C	27.60 A	26.21 A	25.34 AB	22.47 BC
n	16	15	16	16	16
SE of LSM	1.16	1.39	1.14	1.16	1.23

Literature Cited

BOX, G.E.P. and TIDWELL, P.W., 1962. Transformation of the independant variables. Technometrics, 4: 531-550.

COCHRAN, W.G., 1957. Analysis of covariance: its nature and uses. Biometrics, 13: 261-281.

EVANS, G.C., 1972. The quantitative analysis of plant growth. Univ. of California Press, Berkeley, 734 pp.

GOLTERMAN, H.L. and CLYMO, R.S. (Editors), 1969. Methods for chemical analysis of fresh waters. IBP Handbook No. 8. Blackwell Scientific Publications, Edinburgh, 166 pp.

HARPER, J.L., 1977. Population biology of plants. Academic Press, London, England, 892 pp.

LEGENDRE, L. and LEGENDRE, P., 1983. Numerical ecology. Elsevier Scientific Publishing Co., Amsterdam, 419 pp.

SAND-JENSEN, K. and SØNDERGAARD, M., 1979. Distribution and quantitative development of submerged macrophytes in relation to sediment characteristics in softwater, oligotrophic Lake Kalgaard, Denmark. Freshwater Biol., 9: 1-11.

STATISTICAL ANALYSIS SYSTEMS, 1982. SAS users' guide: statistics (1982 ed.). SAS Institute, Inc., Cary, N.C., 584 pp.

THOMAS, R.L., SHEARD, R.W. and MOYER, J.R., 1967. Comparison of conventional and automated procedures for nitrogen, phosphorus and potassium analysis of plant material using a single digestion. Agron. J., 59: 240-243.

WETZEL, R.G., 1975. Limnology. W.B. Saunders Co., Philadelphia, 743 pp.

ZAR, J.H., 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J., 620 pp.