

THE FORMULATION OF A GENERALIZED MODEL FOR  
SIMULATING AQUATIC MACROPHYTE PRODUCTION

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## ABSTRACT

A model simulating macrophyte production has been formulated based on the reduction of  $P_{max}$  by various loss terms: respiration, excretion, mortality, sloughing, and grazing. Functions include morphological changes influenced by depth, variations in fruiting habits, overwintering productivity, and sediment preference. Four dissimilar species have been chosen for model calibration and validation to assure a generalized model capable of predicting macrophyte dynamics under diverse conditions. The model has been initially developed to describe the processes of macrophyte production and mortality as part of a larger detritus formation and nutrient cycling model in the littoral zone of Lake George.

## INTRODUCTION

Macrophytes are aquatic plants which are generally rooted in the sediment and have morphologically discernable tissues such as leaves, stems, and roots. They vary considerably in morphology and growth habit. They inhabit the littoral zone of most lakes and can grow at depths of up to 9 to 10 m (Sculthorpe, 1967; Sheldon and Boylen, 1975<sub>b</sub>). Many grow only a few centimeters high while others may attain heights of several meters. Growth can be totally submergent or partially emergent, either as erect structures or as floating leaves. Many species have extensive root systems while others have few. The role of roots in nutrient uptake by aquatic plants is not well understood. Reproduction may be by vegetative propagation or fruiting and plants may overwinter as either seeds, rhizomes, or winter buds (tightly compacted masses of leaves born in the nodes of the parent plant). Many species grow only during the summer, dying back to some overwintering structure, while others remain productive to varying degrees throughout the winter. They are an important component of many freshwater ecosystems playing a significant role in primary productivity as well as in nutrient cycling (Sculthorpe, 1967; Wium-Anderson and Anderson, 1972).

The Eastern Deciduous Forest Biome, U.S. International Biological Program, has produced a model to predict aquatic macrophyte growth (Titus, et al., 1972). It is a complex model accurately describing the growth of Myriophyllum spicatum growing in Lake Wingra, Wisconsin,

at a depth of from 0 to 2 m. Growth-related processes have been partitioned into 10 cm depth classes of water column. Myriophyllum spicatum overwinters as a mass of roots with short viable shoots. Growth is seasonal: beginning after ice off, producing two biomass peaks during the summer, and dying in the early autumn. Because of the highly specific nature of this model it has been more expedient to construct a simpler, more general model than to attempt to adapt and validate the Myriophyllum model for Lake George, New York.

The generalized macrophyte growth model has been formulated with two objectives in mind: first, to give a predictable mathematical representation of macrophyte growth which is simplistic and yet incorporating, as much as possible, the more important aspects of macrophyte growth behavior; and secondly, to have a model which will give an accurate estimate of the annual contribution by macrophytes to the detrital pool. Detritus formation, through macrophyte mortality and sloughing, is seen as a major influence in limnetic, littoral zone dynamics. It is for this reason that a model to describe the processes of macrophyte production and mortality is being developed as part of a larger detritus formation and nutrient cycling model in the littoral zone of Lake George.

### DISAGGREGATION OF THE MODEL

For several seasons many aspects of rooted macrophyte physiology and community structure have been studied in Lake George, New York (Boylen and Sheldon, 1973; Sheldon and Boylen, 1975a, b, c, d; Sheldon, Boylen, and Park, 1975). Over 40 species of submergent macrophytes have been found to grow in the littoral zone. Various generalizations of macrophyte growth behavior can be seen in one or more of these species. To guide conceptualization of our model and for purposes of subsequent calibration and validation, 4 macrophyte species have been chosen. These plants vary in seasonal productivity, depth preference, structural morphology, reproductive or propagative habit, and sediment preference.

#### Potamogeton amplifolius

This species displays two different growth habits. In the marshes around Lake George it grows prolifically in 0 to 3 m of water. There plants begin to grow in mid-April after the ice melts. Subsequently they grow to the surface and by early July develop floating leaves and emergent flowers and fruits. All plants die back in the early autumn.

In the open lake preferred growth depth of the species is 3 to 5 m. Plants grow 1 to 3 m in height, rarely reaching the surface. They do not develop floating leaves and seldom fruit. Reproduction is restricted to vegetative propagation and many plants overwinter in a productive state. Internodal distance is short for plants growing at

shallow depths, long for plants at deeper depths.

Potamogeton robbinsii

Growth in Lake George shows a strong preference for 5 to 7 m depth, although it is not absolutely restricted to this depth range. Plants grow to a height of less than 0.5 m. They never fruit but reproduce by vegetative propagation. Many plants overwinter in a productive state.

Vallisneria americana

Growth in Lake George is preferred at 1 to 5 m depth, and plants grow to be 0.3 to 0.6 m tall regardless of the depth at which they are found. All plants can be observed to start growth from rhizomes in mid-June. Reproduction is by vegetative propagation until September, at which time each plant dies back to a tuber-like rhizome formed in the sediment at the base of the plant. Rhizomes are formed at all depths at approximately the same time. Plants growing at 1 to 2 m depth do not reach the surface except for fragile flower stalks developing from the base of the plant in mid-August. Seeds are formed but their viability is unknown (Arber, 1920). Plants growing at depths greater than 1 m never flower. There is no production during the winter.

Najas flexilis

This species grows in 1 to 7 m of water in Lake George, and plants grow less than 0.3 m tall regardless of depth. They do not propagate vegetatively, but develop from seeds which germinate in late June.

Plants fruit in late August, producing several dozen seeds per plant. These plants never reach the surface. Fruiting occurs at approximately the same time regardless of the depth at which they are growing. Shortly after fruiting the plants die.

These four groups were selected as representing most types of submergent macrophytes found in the north temperature zone of the U.S. By modeling all four groups, we are assured of a general model capable of predicting macrophyte dynamics under diverse conditions. The model provides extensive flexibility not possible in modeling a single species under rather predictable physiological conditions. Modeling considerations have been given to morphological changes influenced by depth, including alterations in fruiting habits; possibility for continuous photosynthetic activity unbounded by seasonal change; and sediment preference of the macrophyte in question. Extensive data on distributional patterns and physiological rates under varying environmental conditions have been obtained for Lake George. These data will permit both calibration and validation of the model.

#### FORMULATION OF THE MODEL

Net growth of macrophytes can be considered in terms of the interactions among several physiological processes. In our conceptualization, the macrophyte is treated as a whole, not differentiated into leaves, stem, and labile carbohydrates as proposed for Myriophyllum spicatum by Titus et al., (1972). The special processes involved in the production of overwintering material are treated separately, and their

effects are included in the equations for predicting plant growth:

$$\frac{dBM}{dt} = P - (R + E + M + SL + G) \quad [1]$$

where  $\frac{dBM}{dt}$  is the rate of change of total living macrophyte biomass with respect to time. Gross primary productivity (P) provides energy and reduced carbon for growth; loss terms include respiration (R), excretion (E), mortality (M), sloughing (SL), and grazing (G).

The differential equation for predicting the growth of overwintering material is:

$$\frac{dBW}{dt} = F + S \quad [2]$$

where BW is the overwintering biomass, F represents fruit production, and S describes rhizome or winter bud production.

#### Primary productivity

Growth through primary production is a function of nutrient concentration and light ( $U_T$ ), temperature (TEMP), substrate preference (SUB), water velocity (WTVL), fruiting, rhizome or winter bud production, and biomass. It is defined as:

$$P = P_{MAX} * U_T * TEMP * SUB * WTVL * BM - (F + S) \quad [3]$$

where P<sub>MAX</sub> is the maximum growth rate possible at optimum conditions and is modified by reduction factors to correct for non-optimal conditions. The effect of nutrients on photosynthesis utilizes saturation kinetics:

$$U_1 = \frac{S_1}{K_1 + S_1} \quad [4]$$

where  $S_1$  is nutrient concentration and  $K_1$  is the half-saturation constant. This construct is commonly used for nutrient limitation in

phytoplankton models (Chen, 1970; Ditoro, O'Connor and Thomann, 1971; Part, et al., 1974). The nutrients initially considered to be possible limiting factors are orthophosphate, nitrate and ammonia, and inorganic carbon. Limitation due to micronutrients could be taken into account by this function as well.

The light limitation term is that of Steele (1965):

$$U_I = \frac{2.72 * FP}{E' * Z} \left[ e^{\left[ \frac{I_0}{I_s * FP} \right] e^{-E'Z}} - e^{-\left[ \frac{I_0}{I_s * FP} \right]} \right] \quad [5]$$

where limitation is based on the effective light intensity defined by the photoperiod (FP), the incident solar radiation ( $I_0$ ), saturating light intensity ( $I_s$ ), depth of water column (Z), and the corrected extinction coefficient ( $E'$ ).  $E'$  is considered as the sum of extinction due to the water plus a linear function of refractive biomass:

$$E' = E + (L * B_m) + (X * B_D) + (Y * B_E) \quad [6]$$

where  $E$  is the extinction coefficient of water, and  $L$ ,  $X$ , and  $Y$  relate the increase in light extinction to macrophyte (BM), seston (BD), and epiphytic biomass (BE) respectively.

The construct used to mimic the interaction of limitation due to nutrients and light, developed by Bloomfield, et al (1973) and described by Scavia and Park (1975) is:

$$U_T = \frac{n}{\prod U_i} \quad [7]$$

where  $U_T$  describes the total effect of the individual limitation factors ( $U_i$ ) given above.

The effect of temperature on photosynthesis is assumed to be universal, although the magnitude of the effect at a given temperature is species specific. Maximum photosynthesis will proceed at some optimum temperature (TOPT) and at a linear rate under sub-optimal temperatures defined by  $Q_{10}$ , the change in rate due to a  $10^\circ$  change in temperature. Photosynthesis will cease at some maximum temperature (TMAX). In equation 8 the average water column temperature is expressed as T. The empirical relation describing this function was developed by Shugart et al., (1974), with a slight modification suggested by Bloomfield et al., (1973) and described in detail by Scavia and Park (1975):

where:

$$\text{TEMP} = V e^{X X (1-V)}$$

$$V = \frac{T_{\text{MAX}} - T}{T_{\text{MAX}} - T_{\text{OPT}}}$$

$$X = \left[ W^2 \left( 1 + \sqrt{1 + \frac{40}{W}} \right)^2 \right] / 400$$

$$W = \ln(Q_{10}) (T_{\text{MAX}} - T_{\text{OPT}})$$

[ 8 ]

The substrate upon which the macrophyte is growing is considered in a function that designates optimal growth on preferred substrates and sub-optimal growth on others. A large number of in situ observations of macrophyte growth habits in Lake George have allowed consideration of this function (Sheldon, Boylen and Park, 1975):

$$\text{SUE} = e^{- \left| \text{SOPT} - \text{SED} \right| \cdot \beta}$$

[ 9 ]

where SOPT represents the optimum grain size for the species in question, SED is the observed grain size (site specific), and  $\beta$  is an empirical

coefficient.

A function to express the effect of water velocity,  $WTVL$ , is included to represent replenishment of nutrient supply around the leaves of the attached plant (Titus et al., 1972):

$$WTVL = KWV * WATVEL$$

[10]

where  $KWV$  is a coefficient used to relate nutrient supply (and thus productivity) to water velocity ( $WATVEL$ ).

The fruiting process, either in terms of the production of seeds or shoots for overwintering, will be at the cost of primary productivity because of the transfer of energy and reduced carbon from production to fruiting. The formulation of fruit production is as follows:

$$F = S_1 (FP) * S_1 (T) * S_1 (BM) * FR * P$$

[11]

This equation is controlled by a number of switch functions ( $S_1$ ); a switch will equal 1 when conditions are favorable and 0 when conditions are not favorable. The switches are used to predict biological changes in the physiology of the plant (i.e., fruiting when environmental conditions are met). The environmental criteria include photoperiod, water temperature, and macrophyte biomass. A species-specific function relating plant biomass and average height is used to determine whether or not the plant has reached the surface, at which time fruiting will take place.

It is assumed that the amount of plant biomass present when fruiting begins will produce a physiologically-determined amount of fruit. Initiation of fruiting is based on the above switches and is specific for a given species, fruiting will continue at a rate ( $FR$ ) proportional

to the photosynthetic rate (since fruit production is based on available carbon produced through photosynthesis) until the given amount of fruit is produced.

The production of rhizomes or winter buds will be governed by switch functions similar to those in equation 11:

$$S = S_i (FP) * S_i (T) * S_i (BM) * SR * P \quad [12]$$

The switches for photoperiod and temperature are the same as for fruiting; however, the opposite is true for plant height. This is construed to produce overwintering material in the form of rhizomes or winter buds for the situation where all environmental criteria are met, but where the plant has not grown to the surface, thus precluding fruiting (except in Najas flexilis). The relationship between rhizome or winter bud production and photosynthetic production is given as SR.

Respiration

The loss of biomass due to respiration is thought to be a function of biomass and temperature and is expressed as:

$$R = KR * BM * TEMP \quad [13]$$

The maximum respiration rate at optimum temperature (KR), again species specific, is corrected for non-optimal temperatures as described in equation 8 above.

Excretion

The loss of biomass through excretion is related to the respiratory by-products. It is predicted by the equation:

$$E = KE * R \quad [14]$$

where KE represents the relationship between respiration and excretion and is the fraction of biomass "wasted" during respiration. The respiratory loss of biomass is given in equation 13.

Mortality

Natural or non-predatory mortality is considered to be the physiological death of the whole plant and is related to 3 basic functions -- intrinsic death, temperature, and physiological processes such as fruiting:

$$M = \frac{(KM * BM)}{U_T} * e^{(T-TCRIT)} * fn (F or S) \quad [15]$$

The physiological vigor of the plant is assumed to be a function of nutrient and light availability. As the conditions for growth become poor the limitation term,  $U_T$ , becomes small and the intrinsic mortality (KM) is increased. When the water column temperature surpasses the critical temperature (TCRIT), there is an exponential increase in mortality. The fruiting processes, which dramatically reduce the vigor of the plant as the fruits mature, also add to plant "die-back". The effect of production of overwintering material on mortality is modeled to increase exponentially with time, beginning at the start of fruit, rhizome, or winter-bud production (tx):

$$fn (F or S) = \begin{cases} e^{KMF (t-tx)} & ; t > tx \\ 1 & ; t \leq tx \end{cases} \quad [16]$$

and ending when the overwintering biomass is reached (see above).

KMF is the rate constant relating this factor to the overall mortality

term and  $t$  is time.

### Sloughing

Sloughing is determined by a relation between the leaf area index (LAI) and the optimum leaf surface area (LOPT), a species specific parameter. LAI can be experimentally determined by relating leaf surface area to the corresponding area of sediment surface and reducing it to a function of plant biomass. Sloughing will not occur when the leaf area index is less than the optimum; when LAI exceeds LOPT, sloughing will occur at some basal rate (KS) modified by the amount the optimum is exceeded:

$$SL = (LAI - LOPT) * KS * BM$$

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### Grazing

Predatory mortality or grazing, is envisioned as a function of macrophyte biomass as well as a function of the various herbivores such as fish, ducks, and macro-invertebrates. This term is seen as minor at this stage of model development, but plans for experimental determination of their effects are in progress.

## DISCUSSION

This model has been designed to mimic the general physiological responses of submergent aquatic vascular plants. Four species with considerable dissimilarities in these responses have been chosen for model calibration and validation. Data collection since 1972 include measurements on physiology, morphology, and ecology of these species growing in the littoral zone of Lake George. Biomass determinations ( $\text{g DWt/m}^2$ ) have been made over a 0 to 9 m transect in 2 bays -- in the southern and northern basins of Lake George, respectively. Measurement of photosynthetic rates under environmental conditions, temperature optima and maxima, light saturation, effect of water velocity and sloughing, have been made for each species as well as many observations on fruiting and propagation habits, depth and sediment preferences, and the relationship between plant leaf area index, biomass and height. Experiments to measure nutrient concentrations in the sediment of macrophyte beds, nutrient uptake kinetics, and respiration and excretion rates by the plants are currently being completed.

At present we have chosen to reduce gross primary productivity (Eq. 1) by losses due to respiration, excretion, mortality, sloughing and grazing. The production of a labile carbohydrate pool or photosynthate is not incorporated into this model as it is in other production models (Titus, et al., 1972; Shugart, et al., 1974) because in its simplicity the model is designed only to simulate growth. As model implementation proceeds, incorporation of photosynthate production may become advantageous.

LITERATURE CITED

- Arber, A. 1920. Water plants: a study of aquatic angiosperms. University Press, Cambridge. Repr. (1963) with an introduction by Stearn, W. T., as *Historiae Naturalis Classica*, 23. Cramer, Weinheim, 436 p.
- Bloomfield, J. A., R. A. Park, D. Scavia, and C. S. Zahorcak. 1973. Aquatic modeling in the Eastern Deciduous Forest Biome, U. S.-International Biological Program, pp. 139-158. In E. J. Middlebrooks, D. H. Falenknborg, and T. E. Maloney (eds.), Modeling the eutrophication process. Utah State University, Logan, Utah.
- Boylen, C. W. and R. B. Sheldon. 1973. Biomass distribution of rooted macrophytes in the littoral zone of Lake George. EDFB Memo Report 73-65. 19 pp.
- Chen, C. W. 1970. Concepts and utilities of ecologic model. J. San. Eng. Div. Amer. Soc. Chem. Eng. 96: 1085-1097.
- Dituro, D. M., D. J. O'Connor, and R. V. Thomann. 1971. A dynamic model of the phytoplankton population in the Sacramento- San Joaquin Delta. In J. D. Hem (ed.), Nonequilibrium systems in natural water chemistry. Amer. Chem. Soc. Adv. in Chem. Series 106: 131-180.
- Park, R. A., R. V. O'Neill, J. A. Bloomfield, H. H. Shugart, R. S. Booth, R. A. Goldstein, J. B. Mankin, J. F. Koonce, D. Scavia, M. S. Adams, L. S. Clesceri, E. M. Colon, E. H. Dettmann, J. A. Hoopes, D. D. Huff, S. Katz, J. F. Kitchell, R. C. Kohberger, E. J. LaRow, D. C. McNaught, J. L. Peterson, J. E. Titus, P. R. Weiler, J. W. Wilkinson, and C. S. Zahorcak. 1974. A generalized model for simulating lake ecosystems. *Simulation* 23: 33-50.
- Scavia, D. and R. A. Park. 1975. Documentation of selected constructs and parameter values in the aquatic model CLEANER. Submitted to Ecological Modeling.
- Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold Ltd., London. 610 pp.
- Sheldon, R. B. and C. W. Boylen. 1975a. Annual succession of submergent macrophytes in a freshwater lake. In preparation.
- Sheldon, R. B. and C. W. Boylen. 1975b. Depth penetration by aquatic vascular plants. In preparation.

- Sheldon, R. B. and C. W. Boylen, 1975c. Effect of trophic change on productivity and standing crop in an oligotrophic freshwater lake. In preparation.
- Sheldon, R. B. and C. W. Boylen. 1975d. Factors affecting the contribution by epiphytic algae to the primary productivity of an oligotrophic freshwater lake. *J. Appl. Env. Microbiol.*, in press.
- Sheldon, R. B., C. W. Boylen, and R. A. Park. 1975. Growth patterns of submergent macrophyte communities. In preparation.
- Shugart, H. H., Jr., R. A. Goldstein, R. V. O'Neill, and J. B. Mankin. 1974. Teem, a terrestrial ecosystem model for forests. *Oecol. Plant.* 9: 231-264.
- Steele, J. H. 1965. Notes on some theoretical problems in production ecology, p. 383-397. In C. R. Goldman (ed.), Primary production in aquatic environments. *Mem. Inst. Ital. Idrobiol.* 18 Suppl. Univ. California Press, Berkeley.
- Titus, J. E., M. S. Adams, P. R. Weiler, R. V. O'Neill, H. H. Shugart, Jr., R. S. Booth, and R. A. Goldstein. 1972. Production model for Myriophyllum spicatum L. EDFB Memo Report 72-108. 17 pp.
- Wium-Anderson, S., and J. M. Anderson. 1972. The influence of vegetation on the redox profile of the sediment of Grane Langsø, a Danish Lobelia lake. *Limnol. Oceanogr.* 17: 948-952.