

Incorporation and Testing of Revised Algorithms for the Aquatic Plant Growth Model, ECOL

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Growth of aquatic plants growth in river systems responds to phosphorus enrichment and creates fluctuations in dissolved oxygen. Most aquatic plant models simulate the growth of a single generalized specie and therefore cannot account for the wide variability in growth patterns shown by differing species. ECOL, an aquatic plant growth model developed in the late 1970s, was incorporated into the Grand River Simulation Model (GRSM) to model the growth of the three main plant species found in the Grand River watershed: *Cladophora glomerata*, *Potamogeton pectinatus* and *Myriophyllum spicatum*. ECOL calculates plant uptake of phosphorus, biomass production and loss, and the resulting production and consumption of dissolved oxygen (DO), using a 2h time step.

New algorithms to improve the sub-models in ECOL for light, temperature and phosphorus were developed and tested in this study. The present work evaluated and corrected sources of error in GRSM96, recalibrated the improved model and identified and quantified remaining weaknesses. The resulting model, GRSM98AH, has an average error between computed and observed DO of 19.6%, which was regarded as satisfactory.

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19.1 Introduction

Ontario has many lakes and rivers and protection of their water quality is a high priority. Good water quality is critical not only for a healthy aquatic ecosystem for fisheries and macroinvertebrates but also for human consumption and recreational purposes. Maintaining good water quality in southern Ontario is particularly challenging because of the multiple anthropogenic influences of agriculture and urbanization.

Government agencies dedicated to the protection of the environment are responsible for the oversight of public lands and waters. The Grand River Conservation Authority (GRCA), located in southwestern Ontario, is responsible for many management decisions affecting the water quality of the Grand River and its tributaries. One of the tools used by the GRCA in assessing alternative scenarios for water quality improvement in the Grand River watershed is the Grand River Simulation Model (GRSM), developed in the 1970s by the GRCA and the Ministry of Environment (MOE). GRSM96 is a continuous water quality model, unique because it includes a multi-species aquatic plant growth subrou-tine, ECOL. GRSM has been used previously (CH2M Gore and Storrie, 1996) for water management decisions. Attempts to improve the model are ongoing.

In 1996, the GRCA proposed a rigorous approach to the improvement and calibration of GRSM and approached researchers at the Universities of Guelph and Waterloo to undertake this task. In 1997, a literature review uncovered new equations that had been published in current studies of aquatic plant growth (Carr, 1997). Their suitability for GRSM, and more specifically for the ECOL subrou-tine, was examined and some were selected for incorporation into ECOL96 and GRSM96. This work develops new algorithms for incorporating these equations into ECOL96, tests the new model, herein called ECOL98AH and GRSM98AH, and discusses the relevance of these tests to future developments for ECOL and GRSM. Table 19.1 provides an explanation of the terminology used for naming the models and sub-routines investigated in this work.

Table 19.1 History of model and sub-routine terminology.

Model/Sub-routine	Version	Date
GRSM	generic Grand River Simulation Model	None
ECOL	generic ECOL sub-routine	None
GRSM96	GRSM that this research made changes to	May 1996
ECOL96	ECOL that this research made changes to	May 1996
GRSM98AH	GRSM that this research produced	Nov 1998
ECOL98AH	ECOL that this research produced	Nov 1998
ECOLAH	intermediate ECOL model used in this research	Nov 1998

19.2 Model Description

19.2.1 Structure of GRSM

GRSM is a computer-based mathematical model for water flows and quality in the Grand and Speed Rivers in southwestern Ontario. The modeled reach of the Grand River extends from the confluence of the Conestoga and Grand Rivers to below the oxbow turn in the Grand River, downstream of Brantford. The modeled reach of the Speed River, a major tributary of the Grand River, extends from the confluence of the Eramosa and Speed Rivers to the confluence of the Speed and Grand Rivers. The reaches are presented in Figure 19.1. Altogether, eighteen sub-reaches on the Grand River and seven sub-reaches on the Speed River are modeled.

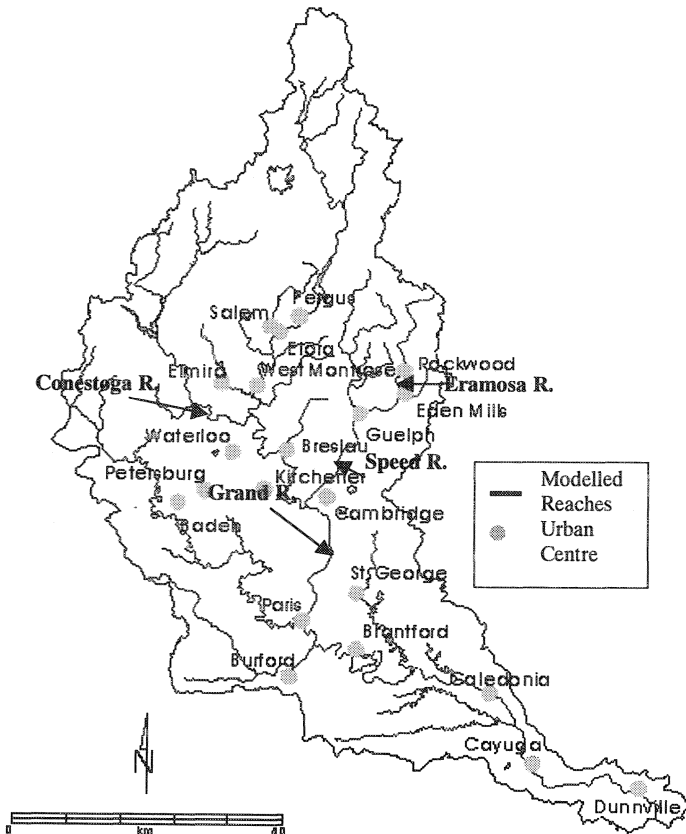


Figure 19.1 Modeled reaches of the Grand River watershed.

In GRSM, water quality and hydraulic parameters, such as temperature, flow rates, and biomass density, are held constant along the length, width and depth of the sub-reach. The average reach is 7 km long, but sub-reaches are generally shorter in locations where more changes in parameter values are expected. The model calculates major water quality indicators such as total phosphorus, plant tissue phosphorus, biochemical oxygen demand (BOD) and biomass density, but the central computed water quality indicator for GRSM is dissolved oxygen (DO). All the water quality parameters, including DO, are calculated for every reach at 2 h time intervals. Routines in GRSM include routing procedures, water flow and quality calculations resulting from the various inputs to and withdrawals from the river, and an aquatic plant growth procedure, ECOL.

19.2.2 ECOL Subroutine

ECOL was originally developed in the 1970s as a stand-alone, continuous, aquatic plant growth model. Using solar radiation, stream temperature and nutrient concentrations as the main inputs, ECOL simulates the net change in biomass densities of three species of aquatic plants for each time-step through production (photosynthesis), respiration, and washout. The three plant species originally modeled were periphyton, *Cladophora glomerata* and *Potamogeton pectinatus*. In 1996, periphyton was replaced by *Myriophyllum spicatum* due to the significant increase of Milfoil in the Grand River (CH2M Gore and Storrie Ltd., 1996). *M. spicatum* and *P. pectinatus* are rooted macrophytes while *C. glomerata* is an attached algae.

Biomass Production, Respiration and Washout

Biomass production (gain in biomass) is affected by solar radiation, stream temperature and available nutrients, while respiration and washout both result in a loss of biomass. All three processes (production, respiration, and washout) are dependent on the biomass density at the previous time-step. Therefore the values calculated by each process increase as the biomass densities increase.

These species-specific limitations to production are modeled as simple proportions of the optimal photosynthesis rate:

$$\text{PROD}_i = \text{PHOTO}_{\max} * B_{i-1} * L_{Li} * L_{Ti} * L_{PHOSi} * L_{Ni} * L_{PLANTI} * \Delta T \quad (19.1)$$

where: PROD_i = gross productivity at time step i (g increased biomass/m²)

$\text{PHOTO}_{\max}$ = maximum photosynthetic rate (g increased biomass/g biomass-h)

B_{i-1} = biomass density at previous time step (g biomass/m²)

- L_{Li} = light limitation factor at time step i (dimensionless)
 L_{Ti} = temperature limitation factor at time step i (dimensionless)
 L_{PHOSi} = phosphorus limitation factor at time step i (dimensionless)
 L_{Ni} = nitrogen limitation factor at time step i (dimensionless)
 L_{PLANTi} = plant inhibition factor at time step i (dimensionless)
 ΔT = time step (h)

The plant inhibition factor is a generic limitation factor to account for all factors affecting plant growth factors not explicitly modeled in ECOL, as discussed in the literature review. The inhibition factors are designated by plant species, sub-reach and month.

Biomass respiration is based on the unit respiration rate of each species at 20°C. A temperature coefficient is used to adjust the respiration rate for temperatures above and below 20°C. Increased respiration rates caused by increased DO levels are also taken into account in the respiration equation:

$$RESP_i = R20 * B_{i-1} * TC_i * \Delta T * \frac{DO_{i-1}}{DO_{i-1} + 1.5} \quad (19.2)$$

- where:
- $RESP_i$ = biomass loss by respiration at time step i (g decreased biomass/m²)
 - $R20$ = unit respiration rate at 20°C (g decreased biomass/ g biomass-h)
 - TC_i = temperature coefficient factor for species time step i (dimensionless)
 - DO_{i-1} = dissolved oxygen concentration at previous time step (mg/L)

Biomass washed out is calculated as a fraction of the existing biomass as shown in (19.3). The washout fraction is a function of water temperature for *C. glomerata* and *P. pectinatus*. *M. spicatum* has a constant washout fraction, independent of water temperature.

$$WASH_i = W_i * B_{i-1} * \Delta T \quad (19.3)$$

- where :
- $WASH_i$ = biomass washed out at time step i (g biomass/m²)
 - W_i = biomass washout fraction at time step i (h⁻¹)

For each time step, a new biomass density for each species is calculated by summing the gains in biomass, through production, and the losses in biomass, through washout and respiration:

$$B_i = \text{PROD}_i - \text{RESP}_i - \text{WASH}_i \quad (19.4)$$

where: B_i = the total biomass of the species calculated for the time step i (g biomass/m²)

From the production and respiration rates of the plants and the resulting net biomass, the consumption and release of dissolved oxygen (DO) is computed. When periods of high aquatic plant biomass occur, DO may fluctuate widely over a 24 h period since the biomass will produce oxygen from net photosynthesis (photosynthesis - respiration) in the daylight hours and consume oxygen from respiration at night. The oxygen produced and consumed by net biomass production and respiration, respectively is calculated in (19.5) and (19.6):

$$\text{O2P}_i = \text{TPROD}_i * \text{O2ASSIM} \quad (19.5)$$

$$\text{O2UP}_i = \text{TRES}_i * \text{O2ASSIM} \quad (19.6)$$

where: TPROD_i = production of total biomass at time step i (g biomass/m²)

TRES_i = respiration of total biomass at time step i (g biomass/m²)

O2ASSIM = O_2 assimilation ratio for all plants (g O_2 /g biomass)

O2P_i = O_2 produced by photosynthesis at time step i (g O_2 /m²)

O2UP_i = O_2 taken up by respiration at time step i (g O_2 /m²)

19.2.3 Assumptions in GRSM and ECOL

As with all models, GRSM and ECOL contain numerous simplifying assumptions to reduce required input data, decrease computation and represent unknown, complex processes. Of the numerous simplifications that may produce significant error in the model, four factors have been identified as most likely to affect the accuracy of modeling plant growth in ECOL: 1) long reach lengths, 2) no cross-section variability, 3) inability to separate total phosphorus into organic and inorganic phosphorus, and 4) inability to have zero aquatic plant biomass density within a reach. Other simplifying assumptions such as grazing pressure on aquatic plants, substrate type, and riparian shading are accounted for in more general terms such as plant inhibition factors or sediment oxygen demand rates.

The assumptions of spatial averaging and biomass minima are considered to be beyond the scope of this work. The assumptions of phosphorus dynamics, grazing pressure, substrate type, velocities, and riparian shading are considered in the following literature survey.

19.3 Literature Review

In this section, literature covering factors not directly modeled in ECOL is reviewed from the perspective of how ECOL could be enhanced to indirectly account for these factors. An overview of existing aquatic plant models is presented with comparisons to ECOL. The role of basic model functionality testing in determining model validity is also briefly discussed.

19.3.1 Factors Not Modeled in ECOL

Ecological simulation models cannot be expected to capture all natural processes because of the infinite number of interactions that may occur within an ecological system and because the system remains open to the biosphere. Modeling the growth of aquatic macrophytes is no exception as there are many phenomena that must be taken into account, and the body of water, in which the vegetation grows, may be subject to numerous unanticipated inputs and outputs. Examples of phenomena not directly modeled by ECOL are: the effects of herbivorous grazers, river current, riparian shading, substrate type, sediment and root uptake of phosphorus, and phosphorus speciation.

Factors such as exotic aquatic plant species, pest infestation and disease can also drastically affect aquatic plant growth. Because these factors are innately random and are not representative of a typical growth season, their usefulness in a management water quality model is minimal and therefore they will not be discussed further.

Herbivore-Plant Interactions

In any body of water that supports aquatic plant life, there are many organisms that will use these plants for food or shelter, or both. In the case of herbivorous organisms, this translates to an increase or decrease in the biomass density of the plants according to the population and growth rates of the organisms. Mammals, waterfowl, fish, crustaceans, and insect larvae are some of the main herbivores affecting aquatic plants. The impact of herbivory on biomass can be significant. A review of grazer impact by Lodge (1991), for instance, demonstrated that herbivorous activities can cause dramatic changes in macrophyte biomass, productivity and relative species abundance.

The effect herbivory has on the densities of macrophytes and attached algae in the Grand and Speed Rivers is unknown. During field studies in (Mangile, GRCA, 1997, and from personal observations) crayfish were routinely found in areas of high aquatic plant density. In one study it was predicted that the success of crayfish foraging was limited to waters with lower velocities than 0.5 cm/s (Hart, 1992), which could apply to some reaches on the Grand and Speed Rivers, especially in late summer during low flow periods. Macroinvertebrate larva (species unknown) were found in high densities on *P. pectinatus* for a period in the later summer, during the 1997 field program (Mangile, GRCA, 1997, and from the personal observations) particularly at the Blair station and further downstream, on the Grand River. Mallards and Canadian geese were also observed in areas where river velocities were suitably slow. The sub-routine ECOL assumes, however, that the decrease in plant biomass density due to herbivore-plant interactions is insignificant compared to the three main factors modeled: temperature, light and nutrients. ECOL takes account of herbivory through a plant inhibition factor, which is specific for each species, sub-reach and month, and can be calibrated to account for herbivorous activity. Spatial variations in grazer impacts can also be represented by the inhibition factor since it is defined by sub-reach. Lastly, temperature and flow effects on grazers could be represented by the inhibition factor on a monthly basis. Modeling effects of herbivory may be difficult because growth patterns and/or migration of these organisms can be influenced by subtle environmental clues.

Substrate Type

Six main classifications in substrate type for rivers can be used: bedrock, boulders, cobble, gravel, sand, and silts and clays, given in decreasing particle size. The only effect of the substrate that is modeled in GRSM is the sediment oxygen demand (SOD) by giving a rate of SOD for each sub-reach for each month. Since SOD affects the dissolved oxygen level, which in turn affects the respiration rates of the plants, the net plant growth in the ECOL subroutine is affected. However, there are other aspects of the substrate type that may influence plant growth. For instance, in a study on macrophyte production in a marsh in southern France, it was shown that *M. spicatum* had a lower biomass density than *P. pectinatus* when grown on sediments with low organic matter (2-4%) concentration (van Wijck et al., 1994).

In Report #14 of the Grand River Basin Water Management Study (Walker et al., 1982) the Grand River was defined as having a stony (gravel to cobble) substrate while the Speed River was defined as bedrock and stony. From field reports there is great variation in substrate type in both rivers. There are large areas in both the Speed and Grand with complete silt or bedrock substrates, and in the Grand River there are large areas of boulders and sand (Mangile, GRCA, 1997, and from personal observations). Field observations revealed that areas

primarily comprising silt, sand or smooth bedrock substrate typically did not support aquatic vegetation (Mangile, GRCA, 1997, and from personal observations). The absence of plants on sand and smooth bedrock was likely to be due, in part, to the very low organic content found in or on these substrates. Since the silt regions also were correlated with slower flow and increased depth, it is also possible that grazing or increased depth suppressed the growth of the macrophytes in these locations.

Riparian Shading

Riparian shading can include trees, brush, or any other living or inanimate phenomenon that leads to the reduction of light reaching the water surface of the river or lake. The calculations in ECOL do not consider land-based shading, thus hindering GRSM's ability to assess the management option of riparian shading. In a study on the irrigation and drainage canals of the Nile Delta, shading by riparian vegetation was found to be an effective management technique for submerged macrophytes compared to emergent aquatic vegetation (Khedr et al., 1997).

Although both the Grand and Speed Rivers have natural riparian shading, the extent that shading reduces light may be insignificant overall since both rivers have an average width at low flow of over 35 m (Walker et al., 1982). Normally, riparian vegetation is considered to be an option for reducing aquatic vegetation for streams where the width of flow is smaller than the widths of the Speed and Grand Rivers (Dawson, 1978). According to Khedr et al. (1997), the effect of shading is inversely proportional to the width of the channel, leading the authors to suggest shading as a management alternative for the control of macrophytes only in narrower channels.

River Velocity

The ECOL subroutine does not explicitly account for the influence of flow variation on plant biomass. The amount of plant biomass washed out is calculated as a fraction of the existing biomass density for each species. The fraction of biomass washed out either accounts for the increased death and detachment at some 'washout' temperature or is set at a minimum washout fraction of 0.1%. Scouring or sloughing effects of high velocities are neglected in the model.

In the Badfish Creek in Wisconsin, *P. pectinatus* was found to have a strong negative correlation with current velocity (Madsen and Adams, 1989). However, in this case, the authors theorized that it was the high biomass density that was causing the lower velocities in the stream. *P. pectinatus* in the Nechako River was found to be most abundant at sites with slower current velocities (< 0.2 m/s) (French and Chambers, 1996).

During the spring melt and associated runoff, the Grand and Speed Rivers experience increased flows, which may lead to scouring of the previous year's aquatic plants. Field observations revealed the presence of more large floating plant debris in the Grand River after periods of high rainfall (Mangile, GRCA, 1997, and from personal observations). However, whether the velocities of the Speed and Grand Rivers significantly influence the biomass densities of the three plant species modeled is unknown since the percentage of observed debris to total biomass present was not determined.

Phosphorus Uptake by Sediment or Roots

Phosphorus has a high potential to interact with sediment, but none of those interactions are modeled in ECOL. As a result, the availability of this nutrient to plants may be overestimated in ECOL. In fact, some studies have demonstrated that sediment has more control over long-term phosphorus than aquatic vegetation or periphyton (Reddy et al., 1996; McCallister and Logan, 1978). Reddy et al. (1996) estimated that 56 to 77% of the phosphorus taken up by above ground aquatic vegetation during periods of active growth is released within six months of senescence. Gumbrecht (1993) found only 20% of the removed phosphorus to be in the aquatic plants harvested in a wastewater treatment pond and therefore dismissed direct uptake and subsequent harvest as the most important removal process of phosphorus.

In ECOL, the growth of the two rooted macrophytes, *M. spicatum* and *P. pectinatus*, in response to phosphorus is based on the water column phosphorus. Smith and Adams (1986) demonstrated that most of the phosphorus uptake by *M. spicatum* was through the roots while most of the phosphorus release was through the shoots. Other studies have also indicated that root uptake of phosphorus exceeds that of shoot uptake (Barko and Smart, 1980; Carignan and Kalff, 1980) due to the higher concentration of phosphorus in sediment pore water (Carignan, 1982). One hypothesis is that the missing algorithms for calculating root uptake of phosphorus may be implicitly modeled through existing algorithms of water column phosphorus uptake if water column and interstitial phosphorus are related. Where sediments are saturated with phosphorus, the diffusion of phosphorus from the sediments to the water column may maintain phosphorus at 'saturated' levels in the water column. The aquatic plant growth would reflect the saturated conditions of both the sediments and the water column.

19.3.2 Other Aquatic Plant Models

Most water quality models incorporate some limited effects of aquatic plants, normally to account for diurnal fluctuations in dissolved oxygen, but there is wide range in the degree of detail in the models. Some water quality models, such as

QUAL2E as applied in the River Sava, Slovenia, implicitly assume inclusion of biomass production and respiration through SOD rates (Drolc and Koncan, 1996). The Segment Travel River Ecosystem Autograph Model (STREAM) uses fixed photosynthetic and respiration rates and does not relate the nutrients, such as soluble phosphorus, to the potential for aquatic plant growth (Park and Lee, 1996). Other models, such as WEED go into great detail, such as calculating different production rates for separate parts of the plant (Titus et al., 1975). The WASP model considers the effects of algae and bacteria on DO and uses Michaelis-Menten kinetics to model biological response to phosphorus and nitrogen (Ambrose et al., 1993).

Michaelis-Menten kinetics is the most commonly used approach for modeling nutrient response for aquatic plant growth. There is more debate over the choice of temperature and light algorithms for adjusting photosynthetic and respiration rates. Many of the algorithms developed for photosynthesis have the problematic response of an unbounded exponential, where temperatures over the maximum or below the minimum do not result in a decrease in the photosynthetic rate. Washout is generally derived from empirical formulas. Of all the models investigated in the literature, the Spring Creek rooted macrophyte model in Pennsylvania (Wright and McDonnell, 1986), and the QUAL model (Collins and Wlosinski, 1989), most closely resemble ECOL in terms of both the algorithms used and the link to dissolved oxygen as a water quality criterion. Even before changes are made to ECOL96, the ability to model multiple plant species is the main obvious advantage which ECOL has over other aquatic plant models.

19.3.3 Testing of Model Functionality

Model functionality was tested by altering model input data sets within realistic ranges to see whether the computed response is reasonable. Not considered as a rigorous examination of the validity of the model, such as verification, model functionality testing is to be used either as a first examination of the reasonableness of new algorithms or as further confirmation that the model is behaving realistically. For example, if the input value of suspended solids concentration was increased, one would expect a decrease in plant biomass production because of the attenuation of photosynthetically available light. If this is not observed in the results, further examination of the results is required to determine the cause (such as the water body too shallow for effective light attenuation, or the suspended solids concentration already above a level affecting maximum light attenuation). Sensitivity analysis is a form of model functionality testing in which the direction of change (+ or -) of model results are compared to the anticipated direction of change when decreasing or increasing certain parameters. In a study of 3D regional biogeochemical models, model functionality testing was used to build the model in a step-wise manner (Robinson and McKay, 1990). The

approach taken in their model design was first to construct simplified models with a minimal number of biogeochemical components, and then, step-by-step, to introduce further components and detailed intercomponent interactions based on reasonable results at each incremental phase. In Painter and Jackson's (1989) model of *Cladophora* growth, the output of the model was checked against the current understanding of *Cladophora* physiology. That is, at optimal nutrient and light levels, the maximum growth rate was expected to occur at the optimal temperature. Model functionality testing provides a simple model testing methodology that has the ability to detect gross inaccuracies or unexpected model results.

19.4 Plant Growth Algorithms

In this section, the main algorithms of ECOL are reviewed, and special emphasis is given to the algorithms recommended from an earlier literature survey (Carr, 1997). Comparisons are made between existing (in ECOL96) and proposed (for ECOL98AH) algorithms. The model prior to algorithm alterations is termed GRSM96 and the proposed algorithms are described for incorporation into GRSM98AH.

19.4.1 GRSM96 Phosphorus Limitation Equations

Originally, the limiting factor for phosphorus, PFAC, was the ratio of the total phosphorus in the water column of a sub-reach to the phosphorus required by the plants in that same sub-reach. The phosphorus limiting factor (PFAC) did not vary with internal phosphorus concentration already present in the plants so a phosphorus storage factor (STFAC) was used to account for changes in internal plant phosphorus concentrations:

$$\text{PFAC} = \frac{\text{PSUPPLY}}{\text{PDEMAND}} + \text{STFAC} \quad (19.7)$$

where: PFAC = phosphorus limitation factor (dimensionless)
 PSUPPLY = water column phosphorus (g TP)
 PDEMAND = total phosphorus demand by plants (g TP)
 STFAC = fraction of water column phosphorus taken up by plant tissue (dimensionless)

Total phosphorus demand by plants is calculated in GRSM96 by summing the required total phosphorus for each species as calculated in (19.8):

$$PDEMAND = PHOTO_{\max} * L_T * B * REQFAC * SAREA * \Delta T \quad (19.8)$$

where:

- $PHOTO_{\max}$ = photosynthetic rate (g biomass/g biomass-h⁻¹)
 L_T = temperature limitation factor (dimensionless)
 B = biomass density (g biomass/m²)
 $PASS$ = phosphorus assimilation ratio (g P/ g biomass)
 $REQFAC$ = nutrient utilization efficiency factor (dimensionless)
 $SAREA$ = surface area of sub-reach (m²)

The GRSM96 phosphorus limitation factor, PFAC, is linearly related to the total phosphorus in the water column. When total phosphorus levels are high, a frequent occurrence on the Grand and Speed Rivers (PWQMN, MOEE), ECOL96 calculates unreasonably high PFAC values, which are then constrained to a maximum of 1.2.

19.4.2 Proposed Changes to Phosphorus Limitation Equations

The literature suggests that aquatic plant growth does not respond linearly to water column total phosphorus (Auer and Canale, 1982) but rather hyperbolically, as derived from Michaelis-Menten kinetics. Most of the aquatic plant models reviewed in the literature used Michaelis-Menten related equations to model plant growth response to nutrients. These included the *Salvinia molesta* model (Toerien et al. 1983), MEGAPLANT (Scheffer et al., 1993), the Australian estuary *Cladophora* model (Gordon and McComb, 1989), the rooted macrophyte growth model (Wright and McDonnell, 1986), and CE-QUAL-R1 (Collins and Wlosinski, 1989). The following Michaelis-Menten based equation was developed by Auer and Canale (1982) to model phosphorus uptake by *Cladophora* in Lake Huron from both external water column phosphorus and internal plant phosphorus (Auer and Canale, 1982):

$$P_{up} = P_{upmax} * \frac{SRP}{Km + SRP} * \frac{Kq}{Kq + (Q1 - Qo)} \quad (19.9)$$

- where:
- P_{up} = phosphorus uptake rate by plant (%P/h)
 P_{upmax} = maximum phosphorus uptake rate by plant (%P/h)
 Km = half-saturation constant for uptake as a function of external water column phosphorus concentration (μg/L)
 Kq = half-saturation constant for uptake as a function of internal plant phosphorus concentration (%P)
 Qo = minimum phosphorus concentration for plant (%P)

- SRP = phosphorus concentration in water column, if known
use Soluble Reactive Phosphorus (SRP), which is plant
available ($\mu\text{g/L}$)
- Q1 = phosphorus concentration in plants (%P)

The half-saturation constants are defined as the amount of phosphorus (internal or external) at which the phosphorus uptake rate is half of the maximum uptake rate. They are empirically derived and species-specific. Using this approach, the uptake of phosphorus increases as P concentrations in the water increase and as P concentrations in the plant decrease.

The next step was to apply this equation to the model. There was sufficient information in the literature for the coefficients to develop an equation that described the effects of both internal and external phosphorus for the species *C. glomerata*. The equations for calculating the phosphorus limitation factors for this species are (Auer and Canale, 1982):

$$\text{CLADP} = 1 - \frac{Q_0}{Q_2} \quad (19.10)$$

$$Q_2 = Q_1 + (P_{\text{up}} - \text{PHOTO}_{\text{max}} * Q_1) * \Delta T \quad (19.11)$$

- where:
- Q2 = the new plant phosphorus concentration (%P)
 - Q1 = the last plant phosphorus concentration (%P)
 - P_{up} = plant phosphorus uptake rate (%P/h)
 - $\text{PHOTO}_{\text{max}}$ = maximum photosynthesis/growth rate (h^{-1})
 - Q_0 = minimum phosphorus concentration (%P)
 - CLADP = phosphorus limiting growth for *C. glomerata* (dimensionless)

The other two species did not have sufficient information in the literature to take into account the internal phosphorus concentration and could not be derived from *Cladophora* data. Plant physiology differences between attached algae like *Cladophora* and rooted macrophytes, like *M. spicatum* and *P. pectinatus*, do not allow for legitimate comparison. Initial values for half-saturation constants for external phosphorus were derived from the literature.

It is recommended, at least until more internal phosphorus response research is conducted, that Michaelis-Menten kinetics, as used in the above aquatic plant models, be used to represent external phosphorus response of *P. pectinatus* and *M. spicatum*:

$$L_p = \frac{\text{SRP}}{\text{SRP} + K_m} \quad (19.12)$$

where: SRP = phosphorus concentration in water column; if known, use Soluble Reactive Phosphorus (SRP), which is plant-available (mg/L)
 Km = half-saturation constant for external P concentration, SRP (mg/L)
 L_P = limiting growth factor for phosphorus (dimensionless)

19.4.3 GRSM96 Temperature Limitation Equations

The original equations for the temperature limitation on the optimal growth rates of the three species took into account the maximum and optimal temperatures, and a calibration factor, termed the shape factor. The shape factor and its corresponding unity factor maintain the temperature limit (L_T) below 1. The following form of the equation was used for each species:

$$L_T = e^{[UniFac \cdot (T - T_{opt})]} * \left(\left| \frac{T_{max} - T}{T_{max} - T_{opt}} \right| \right)^{ShaFac} \quad (19.13)$$

where: L_T = temperature limiting factor (dimensionless)
 T = observed stream temperature (°C)
 T_{opt} = optimum temperature for species growth (°C)
 T_{max} = maximum temperature for species growth (°C)
 ShaFac = shape factor (dimensionless)
 UniFac = ShaFac/(T_{max}-T_{opt}) (°C⁻¹)

The GRSM96 temperature equation accounts for neither a minimum temperature for plant growth, nor a range of optimum temperatures for growth. Because of differing ages of plant tissue and differing tissue type, it is improbable that a plant species in the natural world would have one single temperature that would give a maximum growth rate. Maximum growth is more likely to occur over a range of optimum temperatures. Lastly, qualitatively speaking, the graphical plots produced from this equation appear to be unnaturally symmetrical.

19.4.4 Proposed Temperature Limitation Equations

A newer approach to modeling the temperature limitation factor (Thornton and Lessem, 1978) makes use of maximum and minimum temperatures, as well as a range of optimum temperatures. The range of optimum temperatures is warranted by the wide range of optimum temperatures reported in the literature. The new form of the temperature limitation factors consists of two curves, one

for the temperatures from the minimum to the lower optimum and one for the temperatures for the upper optimum to the maximum. The product of these two curves is the limitation factor for any given temperature (Thornton and Lessem, 1978):

$$L_T = K_A(T) * K_B(T) \quad (19.14)$$

where:

$$K_A(T) = \frac{k_1 * e^{[k_1 * (T - T_{min})]}}{1 + k_1 * \{e^{[k_1 * (T - T_{min})]} - 1\}} \quad (19.15)$$

$$K_B(T) = \frac{k_4 * e^{[k_4 * (T_{max} - T)]}}{1 + k_4 * \{e^{[k_4 * (T_{max} - T)]} - 1\}} \quad (19.16)$$

$$\gamma_1 = \frac{1}{T_{opt2} - T_{min}} * \ln \left(\frac{k_2 * (1 - k_1)}{k_1 * (1 - k_2)} \right) \quad (19.17)$$

$$\gamma_2 = \frac{1}{T_{max} - T_{opt3}} * \ln \left(\frac{k_3 * (1 - k_4)}{k_4 * (1 - k_3)} \right) \quad (19.18)$$

k_1, k_2, k_3, k_4 = min, lower opt, upper opt, and max reaction rates (dimensionless) (0.1, 0.98, 0.98, 0.1)

T = observed stream temperature (°C)

T_{min} = min temperature (°C)

T_{opt2} = lower optimum temperature (°C)

T_{opt3} = upper optimum temperature (°C)

T_{max} = max temperature (°C)

When plotted, the new temperature limitations show a broader range of optimum growth temperatures. This may be caused by tissue of varying ages or composition, which would have different associated optimum temperatures.

19.4.5 GRSM96 Light Limitation Equations

The light limitation factor in ECOL96 and ECOL98AH are both calculated from the photosynthetically available radiation at plant depth (PARD). The PARD was calculated by the Lambert exponential attenuation formula based on the concentration of suspended solids in the water column and a multiplier, called a

self-shading factor. The self-shading multiplier was constant upon reaching a significant biomass density and represents the decrease in light due to in-stream biomass shading. The following is an example of the algorithm to calculate the photosynthetically available light in ECOL96:

$$PARD_{SS} = WATI * e^{[-KE*(DEPTH-PLANT_DEPTH)]} \quad (19.19)$$

where: $PARD_{SS}$ = photosynthetically available radiation at plant depth due to SS (Langleys/min)
 $WATI$ = amount of light just underneath water surface (Langleys/min)
 KE = light attenuation factor due to suspended solids (m^{-1})
 $PLANT_DEPTH$ = depth of plant growth (set at .9 m)
 $DEPTH$ = depth of stream flow (m)

The shading caused by existing plant biomass was accounted for by the application of a shading factor to the photosynthetically available light (after the attenuation by SS) to calculate a total value of photosynthetically available light shown in (19.20) and (19.21).

$$PARD_{TOT} = PARD_{SS} * SHADE \quad (19.20)$$

$$SHADE = \cos(B / SHADE_FACT) \quad (19.21)$$

where: $PARD_{TOT}$ = photosynthetically available radiation at plant depth due to SS and plant biomass (Langleys/min)
 $SHADE$ = shading multiplier for species (dimensionless)
 $SHADE_FACT$ = shade factor for species ($g \text{ biomass}/m^2$)
 B = plant biomass density ($g \text{ biomass}/m^2$)

At high biomass densities, $SHADE$ becomes an unrealistic negative value. The trigonometric relationship is not documented in any of the models found in the literature and the scientific reasoning behind the algorithm is unclear.

19.4.6 Proposed Light Limitation Equations

The proposed method for ECOL98AH of calculating light limitation factors maintains the Michaelis-Menten relationship for the limitation factor. However, the ability of plant biomass density to attenuate light is modeled in the same manner as the suspended solids. A weedbed light attenuation coefficient and plant density are introduced to the Lambert attenuation equation (19.22):

$$\text{PARD}_{\text{TOT}} = \text{WATI} * e^{-[\text{KE} * (\text{DEPTH} - \text{PLANT_DEPTH}) + \text{Kw} * \text{B}]} \quad (19.22)$$

where: Kw = weedbed light attenuation coefficient (g biomass/m^2)

19.5 Methods

The following list outlines the methodology used to incorporate the new algorithms in ECOL98AH and subsequently evaluate their suitability for GRSM98AH:

1. perform an initial calibration on GRSM98AH using sub-reach 10 (Speed River sub-reach),
2. perform a sensitivity analysis on input parameters of ECOL98AH (in GRSM98AH),
3. evaluate how GRSM98AH responds to a normal range of alternate data sets (model functionality),
4. recalibrate all sub-reaches with available observed DO data based on insights gained through item 2 and 3, and
5. calculate standard and relative error of estimate between computed (GRSM98AH) and observed dissolved oxygen (James, 1994).

19.6 Results and Discussion

The results from the calibration process, sensitivity analysis, and model functionality tests are discussed in the following sections. The average of 80% agreement between observed data and computed results was deemed to be satisfactory. From the calibration results and field observations, it is hypothesized that macroinvertebrates play a significant role in the net plant biomass produced. In terms of non-temperature parameters, the sensitivity analysis revealed that biomass computed in ECOL98AH is most sensitive to changes in the maximum photosynthesis rates, unit respiration rates, wash-out fraction and the half-saturation light constants. Sensitivity of temperature parameters was demonstrated using a frequency distribution plot. Model functionality tests provided insight into model response under numerous realistic alternate scenarios. As a result of the model functionality tests, changes to temperature parameters were incorporated into the model.

19.6.1 Calibration

An average agreement of 80% between the available sets of computed DO and observed DO was achieved with revisions to phosphorus, temperature and light algorithms and plant inhibition factors. The standard error of estimate for computed DO versus observed DO was 1.9 mg/L. For a severe case of depleted levels of DO under 3 mg/L, this error in the model (1.9 mg/l) would allow the correct classification of the waters as being under the MOE guideline of 5 mg/L (MOE, 1994).

As an example, Figure 19.2 presents the DO calibration results for sub-reach 6 and the associated biomass densities are plotted in Figure 19.3. Similar plots of observed and computed DO were produced for the two other sub-reaches which had available observed DO data (sub-reach 2, Grand River at Bridgeport and sub-reach 10, Speed River).

There was a need to adjust the plant inhibition factors for sub-reaches 2 and 6, which may indicate spatially-differing constraints to growth. Because the maximum photosynthetic rates were initially set for sub-reach 10, these rates intrinsically included the plant inhibition factor that applied for the environmental conditions in sub-reach 10. As only one species, for one month, required an adjustment to the plant inhibition factor, sub-reach 2 appears to have the same degree of constraints to growth as sub-reach 10. Sub-reach 6 required more adjustment to the plant inhibition factors, indicating different constraints to growth from non-modeled environmental pressures.

The need for decreased inhibition factors (which leads to a decrease in biomass density) to maintain a good agreement between observed and computed DO may be linked to macroinvertebrate fauna observed at this site (Mangile, GRCA, 1997, and from personal observations). This finding is consistent with other reports in the literature showing that macroinvertebrates have significantly decreased the densities of macrophyte and algal stands (Bergey, 1995; Creed and Sheldon, 1993).

19.6.2 Sensitivity Analysis

Few of the aquatic plant models found in the literature described a sensitivity analysis on the plant growth related parameters and therefore, few meaningful comparisons could be made between sensitivity in ECOL98AH and in other models. ECOL98H results were most sensitive to the following non-temperature parameters: the washout fraction, the half-saturation constant for light, the unit respiration rate at 20°C and the maximum photosynthesis rate, all of which were species-specific. The results from the macrophyte model, MEGAPLANT (Scheffer et al., 1993), were found to be the most sensitive to the maximum photosynthesis rate. Model results from ECOL96 were sensitive to the

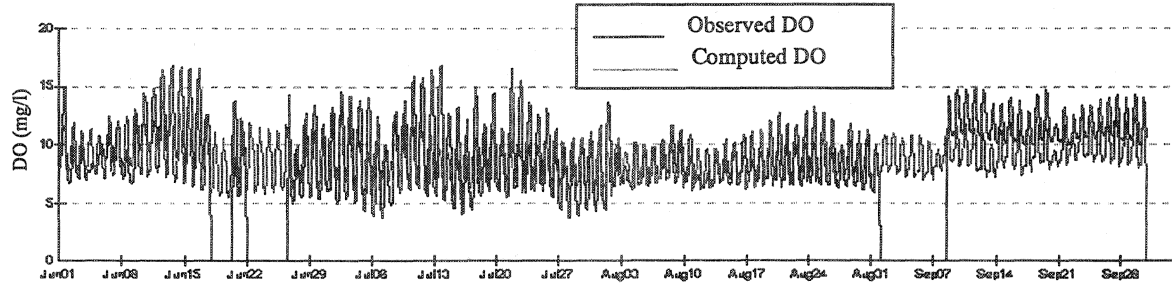


Figure 19.2 Computed versus observed DO for sub-reach 6 (Grand River at Blair).

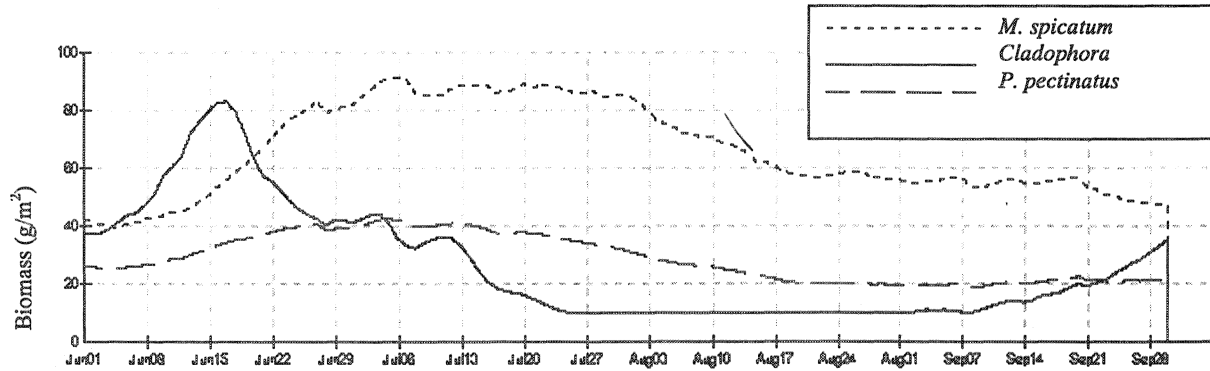


Figure 19.3 Computed biomass for sub-reach 6 (Grand River at Blair).

half-saturation constant for light and the unit respiration rate (CH2M Gore and Storrie, 1996, Walker et al., 1982). Therefore, the parameters with greatest influence on model results in ECOL98AH were consistent with sensitivity analyses on other aquatic plant models.

In comparison to the growth and respiration rates, ECOL98AH maximum biomass was either insensitive or less sensitive to all the phosphorus-related parameters, including the half-saturation constants for internal and external phosphorus, the assimilation rate and the uptake rate of phosphorus and the phosphorus efficiency utilization factor. Because of the high phosphorus concentrations in the water column, it is hypothesized that the modeled system is at saturation for phosphorus and therefore is not affected by changes in phosphorus-related parameters. The same conclusion was drawn from the CH2M Gore and Storrie sensitivity analysis (1996) for the phosphorus parameters in ECOL96. ECOL98AH model results were found to be less sensitive to the light attenuation parameters, including the weedbed and suspended solids attenuation coefficients and plant depth. It is hypothesized that because the Grand and Speed Rivers are generally shallow rivers, they therefore do not have enough water column depth to effectively attenuate light from the surface to the plants.

Model results were found to be highly sensitive to the temperature-related parameters when the temperature parameters were near observed water temperature. The frequency of a given water temperature and the sensitivity of a marker temperature (maximum, optimum, minimum) were correlated. This type of sensitivity is expected because the temperature curves flatten as they extend to the minimum and maximum marker temperatures. For example, if the maximum temperature for *M. spicatum* is altered between 30°C and 40°C (the original value being 35°C), one would not expect a major change in the plant response if water temperatures never approached this range of temperatures. Titus et al. (1975) found *M. spicatum* to increase by only 10% with 10°C increase in water temperature, which may have been attributed to the average water temperatures being outside the range of the optimum growth temperatures for that species. Therefore, the sensitivity analysis for temperature-related parameters in this study were consistent with previous work on aquatic plant growth response to temperature.

19.6.3 Comparing ECOLAH to GRSM98AH

The unrealistic increase, when the water temperature series was decreased by 2°C, of computed *Cladophora* biomass density in both GRSM98AH and ECOLAH was problematic and prompted further investigation of the *Cladophora* growth pattern in the GRSM98AH model under 1995 conditions. The direction and degree of biomass change computed (i.e. significantly increasing) at the end of the growing season was suspect because there was a steeply increasing

biomass density curve at the end of September for *Cladophora*. In addition, when the model was extended into December, the unreasonably high biomass density that remained confirmed that the computed growth pattern was unrealistic.

Two factors were hypothesized to have contributed to the computation of unrealistically high *Cladophora* biomass densities. In ECOL (96 and 98AH), computed water temperatures greater than the upper *Cladophora* washout temperature trigger the model to calculate higher *Cladophora* washout values. However, there is no lower washout temperature for *Cladophora* to trigger the computation of similarly high washout at the end of the growing season. Secondly, the optimum temperature ranges for *Cladophora* inputted into ECOL98AH may have been too wide. After temporarily incorporating a function to increase *Cladophora* biomass wash-off at lower temperatures and decreasing the optimum temperature range for *Cladophora*, more realistic biomass density values were computed by both ECOLAH and GRSM98AH. However, there was no significant change in the agreement between computed and observed DO.

In the field season of 1997, Mangile (GRCA, 1997) and the writer (Humphries) both observed higher densities of macroinvertebrate larvae on the macrophytes at the Blair station, on the Grand River, compared to the Speed River and Bridgeport stations, during the mid to late summer. Model performance is weakest during this time period. Based on the literature on herbivory by macroinvertebrates, it is possible that these larva could suppress plant growth enough to cause the lower fluctuations in the observed DO data, compared to the computed DO results. The plant inhibition factor for this sub-reach was lowered, which caused a decrease in computed plant growth, for the months where lower minima of DO fluctuations were observed.

19.6.4 Model Functionality Testing

The model functionality tests confirmed the validity of the sensitivity analysis results and provided further insight into the behavior of the model. Only one test, where temperature values were decreased, produced an unexplainable result, which subsequently led to recommendations to incorporate additional changes in the temperature-related algorithms for *Cladophora*.

Increases and decreases in water column phosphorus led to expected model results for *P. pectinatus* and *M. spicatum*. The low sensitivity of *Cladophora* to changes in water column phosphorus in ECOL98AH was attributed to its (*Cladophora*'s) higher half-saturation constant, which produces a flatter limitation curve compared to *P. pectinatus* and *M. spicatum*.

Increases in total nitrates produced insignificant changes in biomass production. This supports the assumption that phosphorus is normally the limiting nutrient in eutrophic waterbodies. Furthermore, when the total nitrates

are decreased, potentially below saturation, there is a noticeable decrease in computed plant growth, indicating that nitrogen, if low enough, can become the limiting nutrient.

Biomass densities for *P. pectinatus* and *M. spicatum* increased, as expected, with increased solar radiation. However, *C. glomerata* in both models decreased with increasing solar radiation. Initially, this was considered to be an indication of a faulty model but after more testing, a satisfactory reason for this inconsistency was discovered. GRSM98AH calculates water temperature based on air temperature and solar radiation. However, because of the equations which compute water temperature use solar radiation as one of the variable, when the input solar radiation increases, the computed water temperature also increases. In GRSM98AH, the optimum temperatures inputted for *Cladophora* are low, and therefore increases in computed water temperature cause a decrease in computed *Cladophora* density. Likewise, decreases in input solar radiation, which result in lower computed water temperatures, calculates increased growth of *Cladophora*. As expected, decreases in computed *P. pectinatus* and *M. spicatum* densities coincide with decreases in solar radiation.

Changes in input suspended solids concentrations did not have a significant impact on computed plant biomass. For the shallow depths in the Grand and Speed Rivers where the most prolific aquatic plant growth occurs (Mangile, GRCA, 1997, and from personal observations), suspended solids may not have enough depth to attenuate light effectively. ECOLAH was based on a shallow reach in the Grand River and therefore does not reflect the possibility of suspended solids attenuation in deeper reaches. Because the light attenuation algorithm is only activated when the computed water column is deeper than the inputted plant growth depth, after the computed water depth increases over the model-specified plant depth, the model became sensitive to suspended solids concentrations. The designated plant depth is 0.9 m, which falls between the depths of 0.84 and 1.05; the latter depth being where sensitivity to suspended solids begins. High sensitivity to suspended solids and related parameters in GRSM96 reported by CH2M Gore and Storrie (1996) was probably determined under deeper water conditions.

Results for input air temperature increases were as expected. Computed biomass densities of *Cladophora*, which has a lower input optimum temperature range, were lowered while computed biomass of *M. spicatum*, which has a higher input optimum temperature range, increased. Input air temperature decreases in the model produced expected results for *M. spicatum*. However, the computed biomass curve for *Cladophora* again reached unreasonably high densities. When a tighter range of input optimum temperatures and the addition of an input lower wash-off temperature were applied to ECOLAH, the computed *Cladophora* curve returned to a normal range.

Changes to flow inputs did not have any significant effect on computed aquatic plant growth. Because ECOLAH was set up to have constant concentrations of phosphorus and nitrogen, input flows did not change input nutrient concentrations. Since the computed plant response to phosphorus, the limiting nutrient, is based on the input concentration and not the loading, input flows would not have an effect of increasing the plants' exposure to phosphorus. The input flows would only have an effect on algorithms relating to respiration, because of their dependence on oxygen concentrations, which can be affected by the reaeration rates, computed from flow inputs. Therefore, it appears that computed plant growth is not sensitive to oxygen concentrations, as is also concluded in Carr's review of environmental factors regulating aquatic plant production (1997).

19.7 Conclusions

The aquatic plant model, ECOL98AH, is unique because of its ability to compute the DO fluctuations caused by the net production of multiple plant species. This new model has an average error of estimation in computed DO results of approximately 20% and a relative error for computed DO of 8%. The standard error of estimation for computed DO was 1.9 mg/L.

The most sensitive non-temperature related parameters in ECOL98AH were the maximum photosynthesis rates, the unit respiration rates, the washout rates, and the half-saturation light constants while the least sensitive parameters were the light attenuation coefficients, for both suspended solids and weedbed density, and the internal half-saturation constant for phosphorus. Marker temperatures (maximum, upper optimum, lower optimum, minimum) and their corresponding reaction rates become sensitive in ECOL98AH when they were within the normal frequency water temperatures.

The replacement of older linear functions with Michalis-Menten algorithms brought ECOL98AH into line with current botanical practices for modeling aquatic plant response to phosphorus. The amended GRSM98AH, which included a tighter input optimum temperature range for *Cladophora*, responded reasonably, in term of computed biomass density and direction of response, within normal ranges of input data. It is likely that aquatic plant production in the Grand and Speed Rivers may be more sensitive to changes in temperature and light than to phosphorus because phosphorus levels are at saturation. The shallow depths do not allow water to significantly attenuate light from either suspended solid or plant biomass and thus incident radiation has little impact on computed plant production. Finally, based on literature, field observations and observed DO results, macroinvertebrates were believed to suppress plant biomass production in the Grand River at Blair (sub-reach 6).

Notation

- g_1, g_2 : specific rate coefficient for GRSM98AH lower and upper temperature curve ($^{\circ}\text{C}^{-1}$)
 DT: time step (h)
 B: aquatic plant density (g biomass/ m^2)
 CLADP: GRSM98AH phosphorus limitation factor for *Cladophora glomerata* (dimensionless)
 DEPTH: depth of stream flow (m)
 DO: dissolved oxygen (mg/L)
 k_1, k_2, k_3, k_4 : temperature reaction rates used in GRSM98AH (dimensionless)
 KA, KB: declining and rising limb of GRSM98AH temperature curve (dimensionless)
 KE: light attenuation factor due to SS (m^{-1})
 Km: half-saturation constant for water column phosphorus used in GRSM98AH algorithms ($\mu\text{g/L}$)
 Kq: half-saturation constant for internal plant phosphorus used in GRSM98AH algorithms (%P)
 Kw: light attenuation factor due to plant biomass density used in GRSM98AH algorithms ($\text{m}^2/\text{g biomass}$)
 LL, LN, LPHOS, LT: light, nitrogen, phosphorus and temperature limitation factors (dimensionless)
 LPLANT: plant inhibition factor (dimensionless)
 O2ASSIM: DO assimilation ratio (g DO/g biomass)
 O2P, O2UP: DO produced from photosynthesis and taken up by respiration (gDO/ m^2)
 PARDSS: photosynthetically available solar radiation at plant depth due to SS (Langleys/min)
 PARDTOT: photosynthetically available solar radiation at plant depth due to SS and plant biomass (Langleys/min)
 PASS: phosphorus assimilation ratio (g TP/g biomass)
 PDEMAND: total phosphorus demand by aquatic plants (g TP)
 PFAC: GRSM96 phosphorus limitation factor (dimensionless)
 PHOTOmax: maximum photosynthetic rate (g biomass/g biomass-h)
 PLANT_DEPTH: depth of plant growth (m)
 PROD: biomass gained through photosynthesis (gross productivity) (g biomass/ m^2)
 PSUPPLY: total phosphorus in water column (g TP)
 Pup: phosphorus uptake rate by aquatic plants used in GRSM98AH phosphorus algorithms (% P/h)
 Pupmax: maximum phosphorus uptake rate by aquatic plants used in GRSM98AH algorithms (% P/h)
 Q: plant tissue phosphorus used in GRSM98AH phosphorus algorithms (%P)

- Qo : minimum phosphorus concentration in plant tissue used in GRSM98AH phosphorus algorithms (%P)
- R20: unit respiration rate at 20oC (g biomass/g biomass-h)
- REQFAC : nutrient utilization efficiency factor (dimensionless)
- RESP: biomass lost through respiration (g biomass/m2)
- SAREA : surface area of sub-reach (m2)
- SHADE : shading multiplier used in GRSM96 light algorithms (dimensionless)
- SHADE_FACT :
biomass-density-dependent shading factor used in GRSM96 light algorithms (g biomass/m2)
- ShaFac : shape factor for GRSM96 temperature algorithms (dimensionless)
- SRP: soluble reactive phosphorus ($\mu\text{g/L}$)
- SS: suspended solids (mg/L)
- STFAC: GRSM96 fraction of water column phosphorus taken up by plant tissue (dimensionless)
- T: observed water temperature (oC)
- TC: temperature coefficient factor for respiration (dimensionless)
- Tmax: maximum temperature for growth used in GRSM98AH and GRSM96 (oC)
- Tmin, Topt : minimum and optimum temperatures for growth used in GRSM98AH(oC)
- Topt2, Top3 : lower and upper optimum temperatures for growth used in GRSM98AH(oC)
- TP: total phosphorus (mg/L)
- TPROD, TRES: production and respiration of total biomass (g biomass/m2)
- UniFac: calibration factor for GRSM96 temperature algorithms (oC-1)
- W: biomass washout fraction (dimensionless)
- WASH : biomass lost through washout (g biomass/m2)
- WATI : solar radiation just underneath the water surface (Langleys/min)

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