Modeling of algae blooming and macrophyte development in Lake Veluwe

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Abstract; A model of three species of phytoplankton (diatom, green and blue green algae) coupled with macrophyte and sedimentary model has been developed for shallow lake. Phosphorus and nitrogen return fluxes from the bottom sediment to overlying water are simulated by model for the sediment -water exchange of nutrients. The development of *potamogeton pectinatus* L. is simulated by macrophyte model. The verification of the model for phytoplankton, phosphorus, ammonium, nitrate return fluxes was conducted using observed data in Lake Veluwe in 1986. The fitness between observed and its computed values suggest that the model is capable of reproducing the real picture of phytoplankton and *Potamogeton* P.L. development in Lake Veluwe for short and long term time period. One of the rationale conclusion from the model for Lake Veluwe is that the declining of phytoplankton concentration followed the water quality is improved, as consequences light can be penetrated into deeper water column and macrophyte can be grown. All model equations and the application of the model as tool for analyzing and describing interactions between the biological processes, nutrients recycling, macrophyte developing in Lake Veluwe is subject of this study.

1. Introduction

Lake ecosystem experiences large fluctuation in submerged macrophyte biomass (Carpenter and Lodge, 1986). Submerged macrophyte affects on ecosystem through physical, chemical, biological processes and vice versa macrophyte development is determined by environmental conditions. In shallow eutrophic lakes where algae concentration is abundant, light penetration is inhibited and, thus becomes determinant condition for macrophyte development. Macrophyte biomass will result in changes in production of the ecosystem (Carpenter and Lodge, 1986). Heavy crops of macrophytes inhibit the production of phytoplankton by shading effects. When macrophytes are dominant, phytoplankton production is reduced by as much as two orders of magnitude for periods, and the macrophyte crop may be reduced in years with persistent large phytoplankton crops (Mitchell, 1989). In recent years, the restoration of highly turbid, eutrophic waters is highly demanded. Since the understand of the interactions between ecological components is essential, mathematical model is available as a tool for solving problems encountered in the management (Hootsmans, 1994). This study is devoted to develop a numerical model linking submerged macrophytes *Potamogeton pectinatus* L. under the development of three species of phytoplankton (diatom, green and blue green algae) and the exchanges of nutrients between the sediment and overlying water.

2. Model description

Ecological model consists three submodels that describe phytoplankton development, nutrient dynamics in the sediment and in the overlying water, and submerged macrophyte growth in a shallow lake. These models are summarized as follows.

2.1 Phytoplankton model

Three species of algae (diatom, green, blue green) are considered in the model. Chlorophyll-a is considered as an indicator of phytoplankton biomass both for total phytoplankton concentration or for single species. Phytoplankton growth follows the limitation by the light intensity according to Steele function (1962), by the internal phosphorus, and the internal nutrient to functions proposed by Hamilton and Schladow (1994a) and by the external silica concentration for diatom following a Michaelis-Menten equation, and the environmental temperature function by Eppley (1972). Phytoplankton biomass is resulted by four processes: growth, respiration, mortality and zooplankton grazing. The model equations and the explanations of the variables are listed in table 1. There are 14 state variables in this submodel.

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Table 1. Model equations of phytoplankton and nutrient concentrations in the water column.

$$\begin{aligned}
 \frac{dChl_i}{dt} &= G_{max_i} \theta^{T-20} Chl_i \min \left[f(I_i), f(P_i), f(N_i), f(Si_i) \right] - k_{res_i} \theta^{T-20} Chl_i - k_{mor_i} \theta^{T-20} Chl_i - k_{zoo} ZOO \theta^{T-20} Chl_i \frac{Chl_i - Chl_{mini}}{K_{ZOO} + Chl_i} pref_i \\
 \frac{dP_i}{dt} &= UP_{max_i} \theta^{T-20} Chl_i \frac{IP_{max_i} - IP_i}{IP_{max_i} - IP_{mini}} \frac{P}{K_P + P} - k_{res_i} \theta^{T-20} IP_i - k_{mor_i} \theta^{T-20} IP_i - k_{zoo} ZOO \theta^{T-20} pref_i \frac{Chl_i - Chl_{mini}}{K_{ZOO} + Chl_i} IP_i \\
 \frac{dN_i}{dt} &= UN_{max_i} \theta^{T-20} Chl_i \frac{IN_{max_i} - IN_i}{IN_{max_i} - IN_{mini}} \frac{NO + NH}{K_N + NO + NH} - k_{res_i} \theta^{T-20} IN_i - k_{mor_i} \theta^{T-20} IN_i - k_{zoo} ZOO \theta^{T-20} pref_i \frac{Chl_i - Chl_{mini}}{K_{ZOO} + Chl_i} IN_i \\
 \frac{dP}{dt} &= k_{res_i} \theta^{T-20} IP_i + k_{mor_i} \theta^{T-20} (IP_i - IP_{mini}) + k_{zoo} ZOO \theta^{T-20} pref_i \frac{Chl_i - Chl_{mini}}{K_{ZOO} + Chl_i} (IP_i - IP_{mini}) \\
 &+ k_{miner} \theta^{T-20} BOD.YPBOD - Chl_i UP_{max_i} \theta^{T-20} \frac{IP_{max_i} - IP_i}{IP_{max_i} - IP_{mini}} \frac{P}{K_P + P} + Re lease P \frac{AREA}{VOL} \\
 \frac{dNH}{dt} &= k_{res_i} \theta^{T-20} IN_i + k_{mor_i} \theta^{T-20} (IN_i - IN_{mini}) + k_{zoo} ZOO \theta^{T-20} pref_i \frac{Chl_i - Chl_{mini}}{K_{ZOO} + Chl_i} IN_i - IN_{mini} + k_{ON} \theta^{T-20} BOD.YNBOD + Re lease NH \frac{AREA}{VOL} \\
 &- Chl_i UN_{max_i} \theta^{T-20} \frac{IN_{max_i} - IN_i}{IN_{max_i} - IN_{mini}} \frac{NH + NO}{K_N + NH + NO} P_{NH} - k_{nit} \theta^{T-20} NH \frac{DO}{K_{NO} + DO} \\
 \frac{dNO}{dt} &= -Chl_i UN_{max_i} \theta^{T-20} \frac{IN_{max_i} - IN_i}{IN_{max_i} - IN_{mini}} \frac{NH + NO}{K_N + NH + NO} (1 - P_{NH}) + k_{nit} \theta^{T-20} NH \frac{DO}{K_{NO} + DO} + Re lease \frac{AREA}{VOL} \\
 \frac{dSi}{dt} &= -G_{max_i} \theta^{T-20} Chl_i \min \left[f(I_i), f(P_i), f(N_i), f(Si_i) \right] - k_{res_i} \theta^{T-20} Chl_i + k_{mor_i} \theta^{T-20} Chl_i + k_{zoo} ZOO \theta^{T-20} Chl_i \frac{Chl_i - Chl_{mini}}{K_{ZOO} + Chl_i} pref_i + k_{USi} \theta^{T-20} USi \\
 \frac{dDO}{dt} &= G_{max_i} \theta^{T-20} Y_{OC} UC \min \left[f(I_i), f(P_i), f(N_i) \right] - k_{res_i} \theta^{T-20} Y_{OC} C_C Chl_i + UN_{max_i} \theta^{T-20} Y_{NP} \frac{IN_{max_i} - IN_i}{IN_{max_i} - IN_{mini}} \frac{NH + NO}{K_N + NH + NO} (1 - P_{NH}) Chl_i \\
 &- k_{nit} \theta^{T-20} \frac{DO}{K_{NO} + DO} Y_{NI} NH - \frac{CO}{P_1} - k_{mor_i} \theta^{T-20} Chl_i Y_O UC + k_B \theta^{T-20} \frac{DO}{K_{BOD} + DO} BOD + K_O (Q_{sat} - DO) \\
 O_{sat} &= 14.652 - 0.41022T + 7.99 \times 10^{-3} T^2 - 7.7774 \times 10^{-5} T^3; f(I) = \frac{I_i}{I_{sat}} \exp \left(1 - \frac{I_i}{I_{sat}} \right); f(P_i) = \frac{IP_i - IP_{mini}}{IP_i}; f(N_i) = \frac{IN_i - IN_{mini}}{IN_i}; f(Si_i) = \frac{Si_i}{Si_i + K_{Si}} \\
 P_{NH} &= \frac{NH}{HSCNH + NH}; I_{aver} = I \cdot 1 - \exp(-\eta h_{aver}) / \eta h_{aver}; \eta = \eta_w + \eta_{Chl} Chl + \eta_{MAC} MAC; h_{aver} = \frac{h - h_{max}}{h_{max}} \frac{AREA(h).dh}{h = 0} \Big/ \frac{h - h_{max}}{h_{max}} \frac{AREA(h).dh}{h = 0}
 \end{aligned}$$

Where NO-nitrate concentration in water (mgN.m⁻³); P_{NH}-preference factor for ammonium uptake; Si-reactive silica concentration (mg Si.m⁻³); Chl_i-chlorophyll-a concentration of diatom, green and blue green algae (mg.m⁻³); IP_i internal phosphorus concentration (mgP.(mg Chl)⁻¹); IP_{max_i}-maximum internal phosphorus concentration (mgP.(mg Chl)⁻¹); IP_{min}-minimum internal phosphorus concentration (mgP.(mg Chl)⁻¹); UP_{max_i} maximum rate of phosphorus uptake (d⁻¹); K_P-half saturation constant for phosphorus uptake (mg.m⁻³); IN_i-internal nitrogen concentration (mgN.(mg Chl)⁻¹); IN_{max_i}-maximum internal nitrogen concentration (mgP.(mg Chl)⁻¹); IN_{min}-minimum internal nitrogen concentration (mgP.(mg Chl)⁻¹); UN_{max_i} maximum rate of nitrogen uptake (d⁻¹); K_N-half saturation constant for nitrogen uptake (mg.m⁻³); Chl_{mini} minimum chl-a level for zooplankton grazing (mg.m⁻³); G_{max_i}-maximum rate of phytoplankton growth (d⁻¹); θ-temperature multiplier for growth of phytoplankton(-); k_{res_i}-rate coefficient for respiration of phytoplankton (d⁻¹); k_{mor}-rate coefficient for mortality of phytoplankton (d⁻¹); k_{zoo}-rate coefficient for zooplankton grazing on phytoplankton (d⁻¹); ZOO-zooplankton biomass (g.m⁻³); K_{ZOO}-half saturation constant for grazing on phytoplankton(mg.m⁻³); pref_i-grazing preference factor for different species of phytoplankton (-); P-soluble reactive phosphorus (mg.Pm⁻³); BOD-biological oxygen demand (mg.m⁻³); YPBOD-ratio of mg Prelease to mg oxygen utilised in organic decay; Re lease P release rate of phosphorus from the sediment (mg.Pm⁻²d⁻¹); AREA-area of the sediment (m²); VOL-volume of the lake (m³); N-ammonium concentration (mg.Nm⁻³); YNBOD-ratio of mg Nrelease to mg oxygen utilised in organic decay; Re lease P release rate of ammonium from the sediment (mg.Nm⁻²d⁻¹); Y_{OC}-stoichiometric ratio of oxygen to carbon for photosynthesis and respiration; C_C-ratio of carbon to chl-a; Y_{NP}-stoichiometric ratio of oxygen to nitrogen for nitrate reduction; Y_{NI}-stoichiometric ratio of oxygen to nitrogen for nitrification; k_B-rate coefficient for detrital breakdown; K_{BOD}-half saturation constant for the effect of dissolved oxygen on detrital breakdown; K_O-exchange coefficient (d⁻¹)

2.2 Sediment -water exchange model for nutrients

A dynamic model for prediction of nutrient fluxes across the sediment - water interface has developed in order to investigate the nutrient fluxes release from the sediment. In a natural lake, it is observed that the activity of benthic fauna plays an important role in the determination of vertical characteristics of the active bottom layer. The main transport processes in sediment are advection due to infiltration, seepage or incorporation, diffusion, bioturbation and at the interface, sedimentation and resuspension (Smits *et al.*, 1993; Chapelle, 1994). In the model, the sediment layer under consideration is divided into four sub-layers (table 2). The aerobic layer, the denitrifying layer, the upper reduced layer and the lower reduced layer. A thin stable boundary layer is supposed to exist over the sediment - water interface.. The equations and the explanations of the state variables are summarized in table 3. A set of 12 state variables of the submodel needs to be solved.

Table 2. Schematization of processes in the lake -bottom sediment and overlying water

Layer	Detritus	Nitrate	Ammonium	Dissolved Oxygen	Phosphate
Z0 Water column	Sinking Incorporation Mineralization Degradation Humification	Denitrification Nitrification	Ammonification Nitrification Adsorption Dispersion	Photosynthesis Oxidation BOD Respiration	Mineralization Sorption Dispersion
Newly deposited detritus	Degradation Incorporation		Ammonification	COD	Release
Z1 aerobic layer		Dispersion Nitrification Flux to denitrifying layer	Seepage Degradation Nitrification Dispersion Seepage	Degradation	Adsorption Seepage Mineralization Bioturbation
Z2 denitrifying layer			Degradation	Nitrification	Dispersion
Z3 upper reduced layer		Denitrification	Seepage Dispersion	Deoxygenation	Seepage Burial Mineralization Dispersion
Z4 lower reduced layer	Bioturbation Burial Degradation	Denitrification	Degradation	Deoxygenation	Seepage Burial Mineralization
Inactive bottom layer	Inactive	Inactive	Seepage	Inactive	Seepage Burial

Table 3. Model equations of sediment - water exchange of nutrient.

$$\begin{aligned}
 \frac{dDet_s}{dt} &= q \cdot a \cdot M \cdot Chl_a - u \cdot Det_s - s \cdot Det_s; z_1 = \sqrt{2 \cdot \alpha_1 \cdot D_{Oxy} \cdot k_{O_2} / OC}; \\
 OC &= OC_b / z_1 + ac \cdot k_{deg1} \cdot Det_1 + p_1 \cdot an \cdot k_{nit1} \cdot NH_4 + COD / z_1 \\
 COD &= (1 - fra) \cdot ac \cdot [k_{deg1} \cdot Det_1 (z_1 + z_2) + k_{deg2} \cdot Det_2 \cdot z_2 \\
 z_2 &= 2 \cdot (NO_1 - NO_c) / \sqrt{D_{nit} / k_{deg2}}; OC_b = ac \cdot k_{degb} \cdot Det_b \\
 \frac{dDet_1}{dt} &= F_{d_{w1}} - F_{d_{w2}} - k_{deg1} \cdot Det_1; \frac{dDet_1}{dt} = \frac{F_{d_{w1}} - F_{d_{w2}} \cdot Det_1}{z_1 + z_2 + z_3} - k_{deg1} \cdot Det_1 \\
 \frac{dDet_4}{dt} &= \frac{F_{d_{w3}} \cdot Det_1 - F_{d_{w3}}}{z_4} - k_{deg4} \cdot Det_4; F_{d_{w1}} = sc \cdot Det_s; F_{d_{w2}} = rc \cdot Det_s \\
 F_{d_{w3}} &= \frac{2D_b}{z_1 + z_2 + z_3 + z_4} \cdot \frac{Det_1}{1 - \alpha_1} - \frac{Det_1}{1 - \alpha_1} \\
 \frac{dNO_1}{dt} &= \frac{-F_{n_{w1}} + F_{n_1}}{\alpha_1 \cdot z_1} + k_{nit1} \cdot NH_4 - k_{den1} \cdot NO_1 \\
 \frac{dNO_2}{dt} &= \frac{-F_{n_1} + F_{n_2}}{\alpha_1 \cdot (z_2 + z_3)} + k_{nit2} \cdot NH_2 - k_{den2} \cdot NO_2 \\
 \frac{dNO_4}{dt} &= \frac{-F_{n_3}}{\alpha_4 \cdot z_4} + k_{nit4} \cdot NH_4 - k_{den4} \cdot NO_4; F_{n_3} = 2 \cdot (\alpha_1 + \alpha_2) \cdot D_{nit} \cdot \frac{NO_4 - NO_2}{z_2 + z_3 + z_4} \\
 F_{n_{w1}} &= 2 \cdot \alpha_1 \cdot D_{nit} \cdot \frac{NO_1 - NO_{w1}}{z_1 + z_2} + F_{n_1} = 2 \cdot \alpha_1 \cdot D_{nit} \cdot \frac{NO_2 - NO_1}{z_1 + z_2} \\
 \frac{dNH_1}{dt} &= \frac{F_{a_1} - F_{a_{w1}} + F_{a_1} + F_{a_{w1}} - F_{a_{w1}}}{p_1 \cdot d_1} + \frac{aa \cdot k_{deg1} \cdot Det_1}{\alpha_1} - k_{nit} \cdot NH_1 \\
 \frac{dNH_2}{dt} &= \frac{-F_{a_1} + F_{a_2} + F_{a_{w1}} - F_{a_{w1}}}{\alpha_1 \cdot (z_2 + z_3)} + \frac{aa \cdot k_{deg1} \cdot Det_1}{\alpha_1} \\
 \frac{dNH_4}{dt} &= \frac{-F_{a_3} - F_{a_{w3}} - F_{a_{w3}} - F_{a_{w3}}}{\alpha_4 \cdot z_4} + \frac{aa \cdot k_{deg1} \cdot Det_4}{\alpha_4} \\
 F_{a_1} &= 2 \cdot \alpha_1 \cdot D_{amm} \cdot \frac{NH_1 - NH_2}{z_1 + z_2}; PO_{p1} = f_{p1} \cdot PO; PO_{d1} = f_{d1} \cdot PO / \alpha
 \end{aligned}$$

$$\begin{aligned}
 F_{a_3} &= (\alpha_1 + \alpha_4) D_{amm} \cdot \frac{NH_4 - NH_2}{z_1 + z_2 + z_3 - z_1}; PO_{ad1} = f_{ad1} \cdot PO; PO_{p1} = f_{p1} \cdot PO \\
 PO_{ad1} &= Cac(1 - \alpha) \cdot \frac{PO_{d1}}{K_s + PO_{d1}} \\
 \frac{dPO_1}{dt} &= \frac{F_{p_{boun}} + F_{p_{sed}} - F_{p_{w1}} + F_{p_2} + F_{p_{seep2}} - F_{p_{seep2}} + F_{p_{bio2}} - F_{p_{ber2}} \cdot PO_1}{z_1 + z_2} \\
 &+ ap \cdot k_{deg1} \cdot PO_1 \\
 \frac{dPO_3}{dt} &= \frac{-F_{p_2} + F_{p_3} + F_{p_{seep2}} - F_{p_{seep3}} - F_{p_{bio2}} + F_{p_{bio3}} + F_{p_{ber2}} \cdot PO_1 - F_{p_{ber3}}}{z_3} \\
 &+ ap \cdot k_{deg1} \cdot PO_3 \\
 \frac{dPO_4}{dt} &= \frac{-F_{p_3} + F_{p_{w3}} - F_{p_{w3}} - F_{p_{w3}} + F_{p_{w3}} \cdot PO_3 - F_{p_{w3}} \cdot PO_4}{z_4} + ap \cdot k_{deg1} \cdot PO_4 \\
 &+ \frac{f_{d13} \cdot PO_1}{\alpha_1} - f_{d10} \cdot PO_{w1} \\
 F_{p_{boun}} &= ap \cdot k_{deg1} \cdot Det_1; F_{p_{w1}} = 2 \cdot \alpha_1 \cdot D_{po} \cdot \frac{f_{d13} \cdot PO_1}{z_0 + z_1 + z_2} \\
 F_{p_2} &= 2 \cdot D_{po} \cdot \frac{f_{d13} \cdot PO_3 - f_{d11} \cdot PO_1}{z_1 + z_2 + z_3 + z_0}; k = k_{10} \cdot k^{1-20} \\
 &+ \frac{f_{d14} \cdot PO_4}{\alpha_4} - \frac{f_{d13} \cdot PO_3}{\alpha_1} \\
 F_{p_3} &= (\alpha_1 + \alpha_4) D_{po} \cdot \frac{f_{d14} \cdot PO_4}{z_3 + z_4} \\
 F_{p_{bio2}} &= 2 \cdot D_{po} \cdot \frac{(f_{pre3} + f_{ad3}) PO_3 - f_{ad1} \cdot PO_1}{(z_1 + z_2 + z_3)(1 - \alpha_1)} \\
 &+ \frac{(f_{pre4} + f_{ad4}) PO_4}{1 - \alpha_4} - \frac{(f_{pre3} + f_{ad3}) PO_3}{1 - \alpha_1} \\
 F_{p_{bio2}} &= 2 \cdot D_{po} \cdot \frac{(f_{pre4} + f_{ad4}) PO_4}{(z_3 + z_4)(1 - \alpha_1)} \\
 D &= D_{molecular} + (bio - 1) D_{biobarton}
 \end{aligned}$$

Chl_a chlorophyll-a concentration in overlying water ($mg\ m^{-3}$); Det_s detritus concentration in overlying water ($g\ C\ m^{-3}$); Det_1 detritus concentration in boundary layer ($g\ C\ m^{-3}$); Det_2 detritus concentration in the sediment ($g\ C\ m^{-3}$); NO nitrate concentration in the sediment ($g\ C\ m^{-3}$); NH ammonium concentration in the sediment ($g\ C\ m^{-3}$); PO_{ad1} adsorbed phosphate concentration in the sediment ($g\ P\ m^{-3}$); PO_{p1} precipitated phosphate concentration in the sediment ($g\ P\ m^{-3}$); PO_{d1} dissolved phosphate concentration in the sediment ($g\ P\ m^{-3}$); $F_{a_{boun}}$ ammonification flux from the boundary layer ($g\ N\ m^{-2}d^{-1}$); $F_{d_{w1}}$ bioturbation flux of detritus ($g\ C\ m^{-2}d^{-1}$); $F_{p_{bio}}$ bioturbation flux of phosphate between layers ($g\ P\ m^{-2}d^{-1}$); COD chemical oxygen demand ($g\ O_2\ m^{-2}d^{-1}$); F_{a_1} dispersive ammonium flux between layers ($g\ N\ m^{-2}d^{-1}$); $F_{a_{w1}}$ dispersive ammonium return flux to overlying water ($g\ N\ m^{-2}d^{-1}$); $F_{n_{w1}}$ dispersive nitrate return flux to overlying water ($g\ N\ m^{-2}d^{-1}$); F_{p_1} dispersive phosphate flux between layers ($g\ P\ m^{-2}d^{-1}$); $F_{p_{w1}}$ dispersive phosphate return flux to overlying water ($g\ P\ m^{-2}d^{-1}$); PO_{ad} dissolved phosphate concentration ($g\ P\ m^{-2}d^{-1}$); $F_{d_{w1}}$ flux of detritus incorporated in the upper layer ($g\ C\ m^{-2}d^{-1}$); $F_{d_{w2}}$ flux of detritus settled from overlying water ($g\ C\ m^{-2}d^{-1}$); z_0 thickness of water boundary layer (m); α porosity; α_1 incorporation rate of detritus in the sediment (d^{-1}); sc sedimentation rate of detritus ($m\ d^{-1}$); t time; Ws specific weight of the sediments ($kg\ m^{-3}$); ap stoichiometric constant for phosphate in detritus ($g\ P/g\ C$); k_{deg} degradation rate of detritus in the bottom (d^{-1}); k_{den} denitrification rate (d^{-1}); k_{nit} nitrification rate (d^{-1}); q - nutrient fraction which becomes when phytoplankter dies; a - the fraction of nutrient per unit of phytoplankton type; k_{O_2} - correction factor for oxygen concentration; O_2 - oxygen concentration in overlying water ($g\ m^{-3}$); f_{ad} - fraction reduced substances permanently removed; NO_c - critical nitrate concentration ($g\ N\ m^{-3}$); $F_{d_{w3}}$ - burial flux based on bottom volume ($m\ d^{-1}$); Cac - adsorption capacity ($g\ P\ kg^{-1}$ dry matter); bio - amplification factor for bio-irrigation ($-$); F_{n_1} nitrate flux to the denitrifying layer ($g\ N\ m^{-2}d^{-1}$); PO - organic phosphate concentration ($g\ P\ m^{-3}$); OC_b oxygen consumption flux in the boundary layer ($g\ O_2\ m^{-3}d^{-1}$); OC oxygen consumption rate ($g\ O_2\ m^{-3}d^{-1}$); $F_{p_{boun}}$ phosphate release flux from the boundary layer ($g\ P\ m^{-2}d^{-1}$); PO_{p1} precipitated phosphate concentration ($g\ P\ m^{-2}d^{-1}$); z_1 the thickness of the 1st layer (m) M the natural mortality of phytoplankton (per day); u the mineralization rate constant of detritus (per day); s the sedimentation rate constant (per day); D diffusion coefficient ($m^2\ d^{-1}$); f adsorbed, dissolved, precipitated or organic phosphate fractions; α stoichiometric constant for nitrogen in detritus ($g\ N/g\ C$); α_1 stoichiometric constant for oxidation of detritus ($g\ O/g\ C$); α_2 stoichiometric constant for nitrification ($g\ O/g\ N$); kp phosphate precipitation rate (d^{-1}); K_s half saturation phosphate concentration ($g\ P\ m^{-3}$ pore water)

2.3 Macrophyte model of Potamogeton pectinatus L

The macrophyte model describing Potamogeton pectinatus L. has been developed coupling with parameters taken from phytoplankton model. Schematization of shoot, secondary shoot, root, mother tuber and new tuber for Potamogeton pectinatus L is given in fig. 1.

Fig. 1- The definition of shoot, secondary shoot, root, mother tuber and new tuber for *Potamogeton pectinatus* L.

The equations governing macrophyte development of root, shoot, secondary shoot, mother tuber and new tuber are presented in table 4.

Table 4. Model equations for macrophyte development in shallow lake

$\frac{dB_{shl}}{dt} = Ph_{shl} - RESP_{shl} - (1 - C_{dead})DEAD_{shl} + TUBF - ELSEC \cdot \max[0, F_{shl}] - f_{shl} \cdot \epsilon_{shl} \cdot B_{shl}$ $\frac{dB_{sec}}{dt} = Ph_{sec} - RESP_{sec} - (1 - C_{dead})DEAD_{sec} + ELSEC \cdot \max[0, F_{shl}] - f_{sec} \cdot \epsilon_{sec} \cdot B_{sec}$ $\frac{dB_{root}}{dt} = GR_{root} - RESP_{root} - (1 - C_{dead})DEAD_{root} - NTUBF \cdot f(j)$ $\frac{dB_{tub}}{dt} = -RESP_{tub} - DECAY_{tub} - TUBF$ $\frac{dB_{ntub}}{dt} = GR_{ntub} - RESP_{ntub} - DECAY_{ntub} + NTUBF \cdot f(j) + f_{shl} \cdot \epsilon_{shl} \cdot B_{shl} + f_{sec} \cdot \epsilon_{sec} \cdot B_{sec}$ <p>where</p> $f_{shl} = Ph_{shl} - RESP_{shl} - (1 - C_{dead})DEAD_{shl} + TUBF$ $f_{shl} = 0 \text{ if } Ph_{shl} - RESP_{shl} - (1 - C_{dead})DEAD_{shl} + TUBF - ELSEC \cdot \max[0, F_{shl}] \geq 0$ $f_{shl} = 1 \text{ if } Ph_{shl} - RESP_{shl} - (1 - C_{dead})DEAD_{shl} + TUBF - ELSEC \cdot \max[0, F_{shl}] < 0$	$f_{sec} = 0 \text{ if } Ph_{sec} - RESP_{sec} - (1 - C_{dead})DEAD_{sec} + ELSEC \cdot \max[0, F_{shl}] \geq 0$ $f_{sec} = 1 \text{ if } Ph_{sec} - RESP_{sec} - (1 - C_{dead})DEAD_{sec} + ELSEC \cdot \max[0, F_{shl}] < 0$ $Ph_{shl} = k_{CO2} \cdot PMAX \cdot \frac{P}{K_P + P} \cdot \frac{N}{K_N + N} \cdot \frac{PAR}{K_{PAR} + PAR} \cdot \frac{K_{age}}{K_{age} + Age} \cdot B_{shl}$ $Ph_{sec} = k_{CO2} \cdot PMAX \cdot \frac{P}{K_P + P} \cdot \frac{N}{K_N + N} \cdot \frac{PAR}{K_{PAR} + PAR} \cdot \frac{K_{age}}{K_{age} + Age} \cdot B_{sec}$ $\gamma_{shl} = r_{shl} \cdot \frac{k_{shl}}{k_{shl} + Ph_{shl} - RESP_{shl} + C_{dead} \cdot DEAD_{shl}}; RESP_{sec} = \alpha_{sec} \cdot B_{sec}$ $\gamma_{sec} = r_{sec} \cdot \frac{k_{sec}}{k_{sec} + Ph_{sec} - RESP_{sec} + C_{dead} \cdot DEAD_{sec}}; GR_{root} = G_{root} \cdot B_{root}$ $RESP_{shl} = \beta_{shl} \cdot B_{shl}; DEAD_{root} = \gamma_{root} \cdot B_{root}; DEAD_{root} = \gamma_{root} \cdot B_{root};$ $DEAD_{sec} = DR_{sec} \cdot B_{sec}; TUBF = \alpha_{tub} \cdot B_{tub}; RESP_{tub} = \beta_{tub} \cdot B_{tub}; DECAY_{tub} = \gamma_{tub} \cdot B_{tub}$ $\max[0, F_{shl}] = 0 \text{ if } F_{shl} \leq 0; \max[0, F_{shl}] = F_{shl} \text{ if } F_{shl} > 0;$
<p>where B_{shl} shoot biomass ($g \cdot m^{-2}$); B_{sec} secondary shoot biomass ($g \cdot m^{-2}$); B_{root} root biomass ($g \cdot m^{-2}$); B_{tub} tuber biomass ($g \cdot m^{-2}$); Ph_{shl} gross photosynthesis of shoot ($g \cdot m^{-2} \cdot d^{-1}$); Ph_{sec} gross photosynthesis of secondary shoot ($g \cdot m^{-2} \cdot d^{-1}$); C_{dead} fraction of dead biomass available for growth; $DEAD_{shl}$ dead of shoot biomass per day ($g \cdot m^{-2} \cdot d^{-1}$); $RESP_{sec}$ respiration of secondary shoot ($g \cdot m^{-2} \cdot d^{-1}$); $DEAD_{sec}$ dead of secondary shoot biomass per day ($g \cdot m^{-2} \cdot d^{-1}$); $TUBF$ biomass of tuber coming from tuber for shoot growth per day $g \cdot m^{-2} \cdot d^{-1}$; γ_{shl} dead rate of shoot (d^{-1}); γ_{sec} dead rate of secondary shoot (d^{-1}); α_{tub} rate of tuber bank biomass available for biomass initiation (d^{-1}); β_{shl} respiration rate of shoot (d^{-1}); β_{tub} respiration of tuber bank (d^{-1}); γ_{tub} respiration of tuber bank (d^{-1}); γ_{root} is the decay rate of tuber bank ($g \cdot g^{-1} \cdot d^{-1}$); γ_{root} dead rate of root (d^{-1}); k_{CO2} conversion of O_2 to afdw (ash-free dry weight) $g \cdot g^{-1} \cdot O_2$; $PMAX$ maximum rate of gross photosynthesis ($g \cdot O_2 \cdot g^{-1} \cdot d^{-1}$); PAR insolation in PAR (photosynthetically active radiation) half way averaged over the day ($\mu E \cdot m^{-2} \cdot d^{-1}$); Age age of the shoot or secondary shoot d; K_P half saturation constant for phosphate phosphorus concentration in pore water sediment ($g \cdot P \cdot m^{-3}$); K_N half saturation constant for nitrogen concentration in pore water sediment ($g \cdot N \cdot m^{-3}$); K_{PAR} half saturation of PAR; $ELSEC$ - effect of light on development of new secondary shoots; ϵ_{shl} - fraction of shoot biomass transferred to new tuber biomass; ϵ_{sec} - fraction of secondary shoot biomass transferred to new tuber biomass; GR_{root} - growth root biomass ($g \cdot m^{-2} \cdot d^{-1}$); $NTUBF$ - fraction of root biomass for the formation of new tuber; $f(j)$ - initial julian day of new tuber formation; G_{root} - root growth rate (d^{-1}); r_{shl} - maximum dead rate of shoot biomass (d^{-1}); r_{sec} - maximum dead rate of secondary shoot biomass (d^{-1}); k_{shl} - half saturation constant for shoot dead ($g \cdot m^{-2} \cdot d^{-1}$); k_{shl} - half saturation constant for secondary shoot dead ($g \cdot m^{-2} \cdot d^{-1}$);</p>	

3. Model verification and application

The verification was conducted using observed data of ammonium, nitrate, phosphorus, three species of algae (diatom, green algae and blue green algae), measured soluble reactive phosphorus concentrations, total biomass of macrophyte (*Potamogeton pectinatus* L) in Lake Veluwe (The Netherlands) from January to November, 1986 (figs 2-5). The Lake has the surface area of about 32.8 km² with average depth of 2m. The decline of *Potamogeton pectinatus* L. in the Lake are considerable from 1969 to 1975 (Schffer et al., 1994) due to the lake eutrophication. From 1979 the restoration measures were taken by reducing external phosphorus loading from 3.0 to 1.0 g P m⁻² y⁻¹ with retention time of dissolved

compounds from 0.5 to 0.25 years (van der Molen et al., 1994). As the results, diatoms and green algae were dominant from 1985 and *Potamogeton pectinatus* L. gradually recovered.

Fig. 2: The comparison between phosphate return fluxes with and without including macrophyte, measured SRP in Lake Veluwe in 1978.

Fig. 3: The comparison between measured and computed values of nitrate, ammonium and phosphorus in Lake Veluwe in 1986.

Fig. 4: The comparison between measure and computed concentration of diatoms, green and blue green algae in Lake Veluwe in 1986

Fig. 5: The comparison between observed and computed of total macrophyte biomass in Lake Veluwe in 1986.

It is evident that the discrepancies between measured and calculated data are in the acceptable ranges. It is noted that phosphorus return flux calculated in the model gives better agreement with measured SRP than that calculated without including macrophyte (fig. 2).

Fig. 6: The comparison between computed and measured phosphate return fluxes in Lake Veluwe from 1978 to 1987

Fig. 7: The comparison between measured and computed values of nitrate, ammonium and total phosphorus in Lake Veluwe from 1978 to 1987

Keeping all the model parameters, long term investigation of nutrients, phytoplankton concentrations and macrophyte development in Lake Veluwe from 1978 to 1987 has reproduced (figs 6-9). Obviously by declining phytoplankton concentration from 1978 to 1987 (fig. 8), water clarity is improved, as a result, macrophyte was largely enhanced (fig. 9).

Fig. 8: The comparison between measured and computed concentrations of Chlorophyll-a in Lake Veluwe from 1978 to 1987

Fig. 9: Total macrophyte biomass and maximum height in Lake Veluwe from 1978 to 1987.

3. Conclusions

The model results show that the model was capable of reproducing real picture of phytoplankton and macrophyte development, nutrient dynamics in Lake Veluwe for short and long term period. By reducing external phosphate loading, phytoplankton compositions in Lake Veluwe were reduced, from nitrogen limited to phosphate limited and switched from blue- green algae to green algae and diatom. The decline of phytoplankton concentrations followed the water quality is improved, as consequences light can be penetrated into deeper water column and macrophyte can be grown. The model also can be used for analyzing the interactions of phytoplankton growth, macrophyte development and nutrient dynamics in other shallow lake for lake manager.

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