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Charisma: a spatial explicit simulation model of submerged macrophytes

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Abstract

An important problem in lake management is the replacement of submerged plant species by competing species with undesirable properties. Although dynamics of rooted aquatic macrophytes have been extensively modeled, competition between different species has hardly been addressed so far. We present an individual-based spatially explicit model ('Charisma') designed to simulate the growth of one or more competing species of submerged macrophytes. The model behavior easily becomes rather complex and puzzling if we study more than one species. This probably reflects the complexity as it really occurs in nature, but poses a challenge for calibrating and understanding the model. To control this complexity, we used a flexible design facilitating the elimination of feedback loops and processes to trace the causes of the complex behavior of the model. The resulting 'realistic, yet transparent' model appeared useful in many aspects for bridging the existing gap between theory and reality. As an example, we present an analysis of competition between the charophyte *Chara aspera* Deth. ex Willd. and pondweed *Potamogeton pectinatus* L. The model suggests that alternative equilibria may arise as a result of two positive feedbacks: the enhancement of transparency by macrophytes and a feedback caused by bicarbonate competition.
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1. Introduction

Submerged aquatic plants have significant effects on many abiotic and biotic components of the ecosystem of shallow lakes and streams (Søndergaard and Moss, 1998). One of the most persistently reported effects is that vegetation enhances water clarity, although the mechanisms causing this effect may vary from case to case (see review: Scheffer, 1998). Proposed mechanisms are a reduction of wave resuspension by macrophytes, an allopathic impact on the algal community, and provision of shelter for zooplankton and fish.

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Growth of macrophytes is regulated by various environmental factors such as available light, temperature, nutrients including bicarbonate, sediment stability, wave action, changes in water level, and by grazing by several species of birds and fish (Scheffer, 1998). The feedback loops between vegetation growth an environmental factors such as turbidity, can make the response of macrophyte development to environmental change highly nonlinear. Since we know still relatively little about many potentially important aspects, such as foraging behavior of grazing birds deterministic growth models are a rather unreliable tool for quantitative predictions of vegetation dynamics (Scheffer, 1991). Nonetheless, simulation models can be highly valuable to integrate available knowledge in order to obtain a better understanding of the potential causes of observed patterns. Also, such models may generate new hypotheses that can subsequently be tested either in the field or in the laboratory.

Several simulation models of macrophytes have been developed to investigate the effect of macrophytes on their environment and vice versa. Such models have been reviewed by Best (1990) and more recently by Carr et al. (1997). Some of these models describe the macrophyte vegetation as a whole, without differentiation of species level (Wright and McDonnell, 1986; Collins and Wlosinski, 1989; Park and Uchrin, 1997; Janse, 1998; Muhammetoglu and Soyupak, 2000). More frequently, the simulation models describe the growth of one species, using detailed physiological data on particular species on interest such as *Myriophyllum spicatum* L. (Titus et al., 1975; Best et al., 2001), *Ceratophyllum demersum* L. (Best, 1981), *Hydrilla verticillata* (L.F.) Royle (Chen and Coughenour, 1996; Best et al., 2001), *Potamogeton pectinatus* L. (Scheffer et al., 1993; Van Dijk and Janse, 1993; Hootsmans, 1994; Asaeda and Van Bon, 1997; Hootsmans, 1999), *Ruppia cirrhosa* Petagna (Grande) (Calado and Duarte, 2000) and *Zostera marina* L. (e.g. Short, 1980; Verhagen and Nienhuis, 1983; Wetzel and Neckles, 1987; Bach, 1993). Other models are mainly focused on spatial processes (Chiarello and Barrat-Segretain, 1997; Wortmann et al., 1997). So far, however, competition between macrophyte species has hardly been

addressed in models (Wortelboer, 1990; Davis and McDonnell, 1997).

In this paper, we present the model Charisma, an individual-based macrophyte model, that can be used in a spatially explicit way. The number of interacting species in the model can range from one to many. As an example we use the model to analyze the competition between the charophyte species *Chara aspera* Deth. ex Willd and pondweed *P. pectinatus* L. The physiological rules of the model are based upon those used in the model MEGAPLANT (Scheffer et al., 1993) and extended with bicarbonate limitation (Van den Berg et al., 2002) and some spatially explicit processes.

As we will show the behavior of the model can be rather complex and puzzling if we study more than one species. To control this complexity, the model has a flexible design facilitating analyses of simplified versions. We demonstrate this by shutting off several feedback loops and processes, showing which processes cause the complex behavior of the model. Furthermore, we use Monte Carlo techniques (Klepper et al., 1994) to trace which parameters have the most significant effect on the model output, how effects of different parameters are correlated.

2. The model

Much of the formulations are based on an earlier model (Scheffer et al., 1993), extended along two lines. Firstly, the model is made spatially explicit by associating all plants and overwintering structures (hibernacula) with grid cells of a certain dimension, and adding spatial processes, such as seed dispersal. Secondly, we made it possible to simulate competition for light and nutrients between two or more macrophyte species. The model is also designed in an individual-based way. We use the super-individual concept (Scheffer et al., 1995) as an efficient and flexible way to simulate a large number of individuals. The essence of this approach is that in addition to features such as individual biomass, length of sprout and the position on the grid, each model individual has one extra property, namely

the number of individuals that it actually represents. In the analyses presented in this paper we represent the population by only two super-individuals per grid cell per species. One of these originates from tubers and one from seeds.

The model is implemented in an object oriented modeling framework (Van Nes, unpublished), which provides an extended user-interface, instantaneous visual presentation of results and tools for sensitivity analysis. As programming language Delphi was used (Borland, 1997), which uses an object-oriented Pascal version. Charisma uses a fixed integration step of 1 day, but the photosynthetical rate for each day was determined in more detail by three-point Gaussian integration (Goudriaan, 1986) both over the depth profile and time. The model and a technical description are available on internet (http://www.dow.wau.nl/aew/charisma/).

2.1. Seasonal cycle

The basis of the model is the seasonal cycle (Fig. 1). Plants can survive the winter as shoots and as
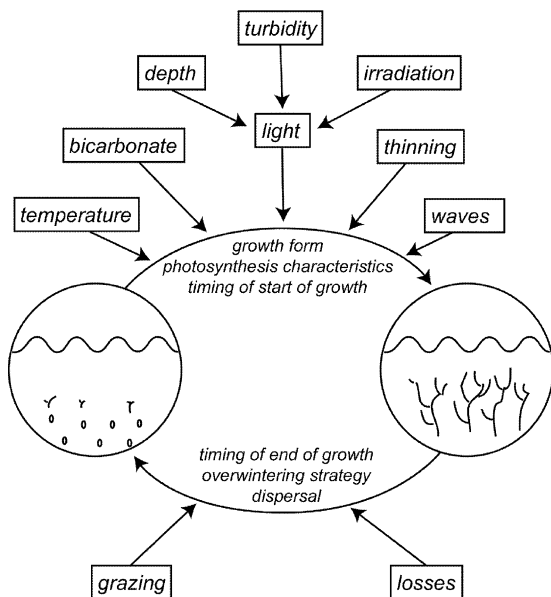

Fig. 1. Seasonal cycle of the vegetation with environmental factors and plant characteristics that can be adjusted in the model (redrawn from: Scheffer et al., 1993).

two possible types of overwintering structures ('hibernacula'): tubers and seeds. (For simplicity, in the model oospores of *C. aspera* are considered seeds and the *C. aspera* bulbils are considered tubers.) At a pre-set day in spring, growth is initiated by transforming a certain fraction of the seeds and tubers in a grid cell to young sprouts. The growth of the sprouts is supplemented with a fixed daily percentage (default 10%) of the remaining hibernaculum biomass (cf. Hodgson, 1966). Consequently, plants get an exponentially decreasing input from their seeds and tubers. At a pre-set age, the macrophytes start allocating a part of their biomass in seeds and tubers, up to a maximum fraction of their biomass, which they reach at a second fixed age. Thereafter this fraction stays constant. At the pre-set end of the growing season, this part of the plants is transformed into biomass of overwintering structures and added to the propagule bank of the grid cell associated with the parent plant. Seeds can optionally be dispersed to neighboring grid cells by a dispersion function.

2.2. Growth form

The weight of the shoots is defined by a fixed root-shoot ratio (default 0.1), but during the growth season a fixed part of the biomass is allocated to reproduction organs. The length of young sprouts increases proportionally with its biomass according to a fixed weight per meter sprout (cf. Ikusima, 1970). If the plants reach their maximum length or the water surface, further growth causes a proportional increase over the whole length of the plants. Optionally, however, plants like pondweeds (*P. pectinatus*) invest part of their production in shoots spreading just under the water surface. The fraction of the biomass of the sprout that spreads over the water surface is defined by a parameter.

2.3. Growth rate

The daily growth of the plants in weight (ΔW) depends on gross photosynthesis (P), respiration (R_m) and mortality (M).

$$\Delta W = W_s P - W(R_m + M) \tag{1}$$

In which: W_s is the weight of the sprouts, excluding reproduction organs (g) and W is the individual plant weight (g). Respiration is formulated as a fixed maintenance respiration (r_{20}), only dependent on temperature by a Q_{10} formulation (default value of Q_{10} is 2):

$$R_m = r_{20} Q_{10}^{(T-20)/10} \tag{2}$$

Growth respiration is balanced with maximum photosynthesis rate in the parameter P_{max}.

Photosynthesis of the plants is affected by in situ light (I), temperature (T), bicarbonate (C) and distance (D) from the top of the plants following saturation functions (see also Fig. 2):

$$P = P_{max} \frac{I}{I + H_I} \frac{C}{C + H_C} \frac{1.35T^3}{T^3 + 14^3} \frac{H_D}{H_D + D} \tag{3}$$

The parameter P_{max} represents the specific daily production of the plant top at 20 °C in the absence of resource limitation. The default values are based on photosynthesis measurements.

The Monod or Michaelis–Menten function is adequate for describing the photosynthetic response to light (Carr et al., 1997). The default half-saturation constants for light (*C. aspera*: $H_I = 14$ µE m^{-2} s^{-1}; *P. pectinatus*: $H_I = 52$ µE m^{-2} s^{-1}) are based on growth experiments (Van den Berg, unpublished).

The Hill function describing the temperature dependence of photosynthesis was fitted to literature data by Scheffer et al. (1993).

Photosynthesis is assumed to decrease with distance to the plant top due to tissue aging or periphyton growth. The half-saturation distance ($H_D = 1$ m) is set using data from Ikusima (1970).

In the presented analyses we assumed that the plants are not phosphorus or nitrogen limited (Best et al., 1996).

In the eutrophic lakes we study, carbon limitation probably occurs frequently (Van Wijk, 1989; Vadstrup and Madsen, 1995; Van den Berg et al., 2002). Carbon limitation is described with a Monod function on the bicarbonate concentration (C). Though the plants have a higher affinity for CO_2 over bicarbonate (Vadstrup and Madsen, 1995), the CO_2 concentration is usually below their compensation point during the growth season (Van den Berg et al., 2002). In experiments is showed that *C. aspera* is less sensitive to carbon limitation ($H_C = 30$ mg l^{-1}) compared to *P. pectinatus* ($H_C = 60$ mg l^{-1}) (Van den Berg et al., 2002).

Since the in situ light intensity follows a daily cycle and varies with depth, photosynthesis is calculated on several moments of the day at several depths in the vegetation. The thickness of the plant biomass in the surface layer of canopy-forming species is neglected, but self-shading in this layer is included by integrating the photo-
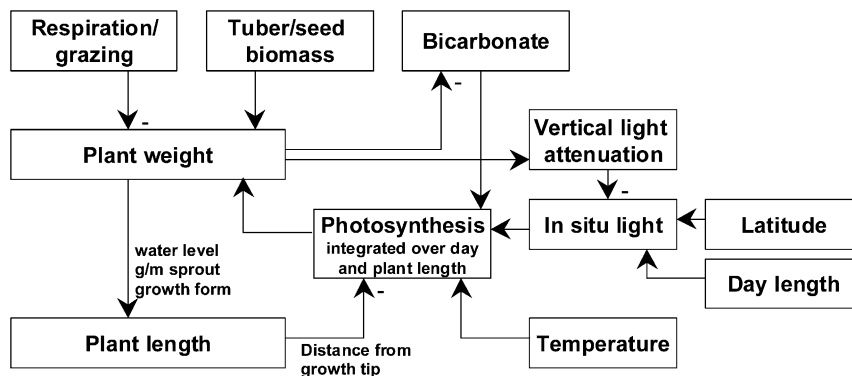

Fig. 2. Schematic overview of the factors that determine the net macrophyte growth in terms of weight (g) and length (m) during the growing season.

synthesis over an infinitely thin surface layer, using Gaussian integration.

2.4. Mortality

Four mortality causes are explicitly included in the model: wave damage, losses due to herbivory, mortality due to competition at high plant densities and seasonal die-off. Optionally, an additional background mortality can be used. Obviously, a negative growth rate leads to a loss of biomass. Losses can be effectuated through a decrease in either the number of plants or the average individual weight. Due to the clonal growth of plants, the concept of individual is somewhat obscure for aquatic vegetation. We use pragmatic rules for the allocation of losses: (1) negative growth results in a loss in number of plants; (2) herbivory results in a loss in individual weight only; (3) background mortality and wave mortality result in a loss in numbers if the plants have not yet reached the water surface, otherwise in weight loss. Note that, computationally, the individual weight is only relevant for sprouts that have not yet reached the water surface where it determines the sprout length and therefore the light conditions.

At high plant densities mortality occurs in the model, following the thinning law, which relates the individual weight (W) to the population numbers (N^*) (see review by Westoby (1984)):

$$N^* = \left(\frac{7000}{W}\right)^{-3/2} \tag{4}$$

We assume that the losses in numbers are compensated by a faster growth of the remaining plants. Thus, thinning implies readjusting the individual weight of the remaining plants in such way that there is no loss in overall vegetation biomass.

In very shallow regions (< 0.3 m) of large lakes, aquatic macrophytes are usually absent due to uprooting or dislodging of plants by wave action (Schutten and Davy, 2000). This is mimicked in the model by means of a depth-related mortality (M_W) which is maximal (M_{max}) at the shoreline and decreases with the water depth (Z) following a Hill-function with a default half-saturation depth (H_W) of 0.15 m (Scheffer et al., 1993):

$$M_W = M_{max} \frac{H_W^p}{H_W^p + Z^p} \tag{5}$$

The exponent (p) of the Hill function is set to a default value of 4 to obtain a steep reduction in depth-related mortality.

Grazing by birds during the growth season can be an important factor for macrophyte communities (Mitchell et al., 1988). Optionally, it can be simulated by setting a fixed grazing rate in g m^{-2} representing, for instance, the consumption capacity of the local coot population, and a limit in terms of vegetation density below which grazing ceases. In winter, tuber banks can be reduced considerably by bird grazing (Van Eerden et al., 1998), which can be mimicked in the model by setting the threshold density to which hibernacula are reduced in winter. At default there is no grazing.

Seasonal die off is the most radical mortality. As described earlier, it occurs at a pre-set day of the year and implies transformation of a proportion of the biomass into seeds and tubers. These overwintering structures subsequently also experience a certain mortality rate. This results in seed/tuber bank dynamics where a mortality rate and spring germination are counterbalanced by an input which occurs each autumn.

2.5. In situ light

The availability of light is the primary factor controlling photosynthesis in most aquatic systems (Carr et al., 1997), implying that an accurate description of light availability is essential. Irradiance follows a daily cycle and light is attenuated in the water column, resulting in a spatio-temporal pattern. Daily solar irradiance in the model follows a sine wave over the year fitted to data for Dutch shallow lakes. The photosynthetically active radiation (PAR) is assumed to be 50% of the total irradiance. Irradiation at any time of the day is a function of the day length, which is calculated from the latitude, and the time of the year following equations suggested by Kirk (1983).

Reflection of light at the water surface is fixed at 10%, neglecting the impact of variation in solar angle and waves. Light attenuation in the water column follows the Lambert–Beer law. In addition (self-)shading by macrophytes is included in the model using specific light attenuation coefficients of plant material (K_p) (Ikusima, 1970; Scheffer et al., 1993), summed over all simulated species. The adjusted Lambert–Beer law thus becomes:

$$I_z = I_0 e^{-Kz - \sum K_p B_{<z}} \tag{6}$$

In which: I_z is irradiation at depth z; I_0 is irradiation at surface; K is light attenuation coefficient of the water; $B_{<z}$ is the total shoot biomass of a species above depth z. The light attenuation coefficient of plant material is set at $0.02 \text{ m}^2 \text{ g}^{-1}$ (Ikusima, 1970) for both *C. aspera* and *P. pectinatus* for our simulations.

2.6. Temperature, turbidity, bicarbonate and water level

Environmental variables in the model can be either fixed, or modeled as a sinusoidal function of time or supplied as a time series. A reduction of the local turbidity by vegetation (Scheffer, 1998) is modeled assuming an instantaneous effect of vegetation biomass (B, g m^{-2}) on vertical light attenuation coefficient (K, m^{-1}) in each grid cell:

$$K^* = K_{\min} + (K - K_{\min})\frac{H_K}{B + H_K} \tag{7}$$

This implies that vegetation can reduce the vertical light attenuation coefficient down to a minimum level ($K_{\min}$, g m^{-2}). The half-saturation constant (H_K, g m^{-2}) is estimated from field data from Lake Veluwemeer (Van Nes et al., 2002a).

We parameterized the model for *C. aspera* using results from experiments and data of Lake Veluwemeer (Table 1). Parameters of *P. pectinatus* were taken from Scheffer et al. (1993), with the exception of the maximum gross production ($P_{\max}$) which has been calibrated using data on vegetation dynamics in Veluwemeer (Table 1).

3. Methods of analysis

3.1. Monte Carlo sensitivity analysis

We used the Monte Carlo sensitivity analysis to investigate which parameters have the strongest impact on model outputs. We generated 5000 sets of parameters, drawing all parameters randomly and independently from uniform probability distributions within ranges of $\pm 10\%$ around the default values. Five years were simulated with each parameter setting, and the model results (biomass, mean length, numbers, and individual weight) were stored at days 152, 182 and 213 of each year. At the end of each simulation, the model was reset to the starting number of seeds (or oospores) and tubers (or bulbils) (total 10 g m^{-2} for each species). Sensitivity coefficients were defined by linear regression between the parameter values and each model output value, scaled by the ranges used for each parameter (Klepper, 1989). Cluster analysis (average linkage) was used to form groups of parameters that had the same or opposite effect on the qualitative model results. As similarity measure the absolute sine of the angle between the vectors of sensitivity coefficients was used. As measure of the total sensitivity the length of this vector was used (Klepper, 1989).

We also added 100 dummy parameters that have no effect on the model. These dummy parameters were set arbitrarily to 1 and varied in the same way as the model parameters. This allows a test of the hypothesis that the effect of the model parameters is not different from zero. This is done by comparing the total sensitivity of each model parameter with the 99% percentile of the sensitivity coefficients of the 100 dummy parameters. Only parameters that have significantly stronger effect on the model than the dummy variables were included in the cluster analysis.

3.2. Scanning of asymptotic regimes

'Asymptotic regimes', are defined as the behavior of the model after infinitely long simulations. Simple models in constant environments can converge to an equilibrium. In our case the simplest asymptotic regime is a seasonal cycle.

Table 1

Default parameters for *Chara aspera* and *Potamogeton pectinatus*. 'Oospores' are called 'seeds' in the model, and 'bulbils' are named 'tubers' *P. pectinatus* only reproduces using tubers. All biomass values are in grams ash-free dry weight

Parameter	Description	Unit	C. aspera	P. pectinatus
SeedsStartAge	Age of the plants where seed formation starts	days	30[b]	30[b]
SeedsEndAge	Age of the plants where SeedFraction is reached	days	60[b]	60[b]
TuberStartAge	Age of the plants where tuber formation starts	days	30[b]	30[b]
TuberEndAge	Age of the plants where TuberFraction is reached	days	60[b]	60[b]
hCarbonate	Half-saturation carbonate concentration of growth	mg l^{-1}	30[b]	60[b]
hCarboReduction	Half-saturation biomass of carbonate reduction by plants	g m^{-2}	30[b]	60[b]
pCarbonate	Power of Hill function of carbonate dependent growth	–	1[b]	1[b]
cTuber	Fraction of tuber weight lost daily when sprouts starts growing	fraction	0.1[d]	0.1[d]
pMax	Maximal gross photosynthesis	h^{-1}	0.006[a]	0.008[a]
Q10	Q10 for maintenance respiration	–	2[d]	2[d]
Resp20	Respiration at 20 °C	day^{-1}	0.00193[c]	0.00206[d]
MaxLength	Maximum length of macrophyte	m	0.35[a]	4[d]
MaxWeightLenRatio	Weight of 1 m young sprout	g m^{-1}	0.03[c]	0.1[d]
RootShootRatio	Proportion of plant allocated to the roots	Fraction	0.1[a]	0.06[d]
SpreadFrac	Fraction of sprout weight spread under the water surface	Fraction	0[a]	0.5[d]
FracPeriphyton	Fraction of light reduced by periphyton	Fraction	0.2[d]	0.2[d]
HExtReduction	Half saturation biomass of extinction reduction	g m^{-2}	40[a]	70[a]
hPhotoDist	Distance from plant top at which the photosynthesis Is reduced factor 2	m	1[d]	1[d]
hPhotoLight	Half-saturation light intensity (PAR) for photosynthesis	µE m^{-2} s^{-1}	14[b]	52[b]
hPhotoTemp	Half-saturation temperature for photosynthesis	°C	14[e]	14[d]
pExtReduction	Power in Hill function of extinction reduction	–	1[a]	1[a]
PlantK	Extinction coefficient of plant issue	m^{-2} g^{-1}	0.02[c]	0.02[c]
pPhotoTemp	Exponent in temp. effect (Hill function) for photosynthesis	–	3[e]	3[d]
sPhotoTemp	Scaling of temperature effect for photosynthesis	–	1.35[e]	1.35[d]
BackgroundMort	Background mortality	day^{-1}	0[f]	0.0006[f]
HwaveMort	Half-saturation depth for mortality	m	0.1[a]	0.1[a]
MaxAge	Maximum age of plants	day	175[a]	175[a]
MaxGrazing	Maximum grazing rate	g m^{-2} day^{-1}	0[f]	0[f]
MaxWaveMort	Maximum loss of weight in shallow areas	Fraction	0.2[a]	0.2[a]
pWaveMort	Power of Hill function for wave mortality	–	4[a]	4[a]
Thinning	Apply the thinning rule?	–	True[f]	True[f]
GerminationDay	Day of germination of seeds	dayno	114[b]	–
ReproDay	Day of dispersal of seeds	dayno	250[b]	–
SeedBiomass	Individual weight of seeds	g	0.00002[c]	–
SeedFraction	Fraction of plant weight allocated to seeds	year^{-1}	0.13[b]	–
SeedGermination	Fraction of seeds that germinate	year^{-1}	0.2[a]	–
SeedImport	Import of seeds	No m^{-2} year^{-1}	0[f]	–
SeedInitialBiomass	Initial biomass of seeds	g m^{-2}	2[f]	–
SeedMortality	Mortality of seeds	day^{-1}	0.0019[a]	–
SeedRadius	Max. dispersal radius for 90% of the seeds	m	0[e]	–
TuberBiomass	Individual weight of tubers	g	0.00018[b]	0.05[d]
TuberFraction	Fraction of plant weight allocated to tubers	year^{-1}	0.22[b]	0.2[d]
TuberGermination	Fraction of tubers that germinate	year^{-1}	1[b]	1[d]
TuberGermDay	The day that tubers germinate	dayno	114[b]	100[b]
TuberImport	Import of tubers	No. m^{-2} year^{-1}	0.1[f]	2[f]
TuberInitialBiomass	Initial biomass of tubers	g m^{-2}	8[f]	10[f]
TuberMortality	Mortality of tubers	day^{-1}	0[b]	0[b]

[a] Calibrated;

[b] Estimated from field observations (Van den Berg, unpublished results);

[c] Unpublished measurements van den Berg;

[d] Scheffer et al. (1993);

[e] Assumed to be the same as *Potamogeton pectinatus* in Scheffer et al. (1993);

[f] Option.

For models with ordinary differential equations (semi-) analytical methods are available to analyze the effect of parameters or environmental factors on the equilibria. We are not aware of such methods for individual based models. Therefore we used several 'brute force' numerical procedures, which all include simulation until convergence to a certain seasonal cycle has occurred. Such procedures can be used to scan the effects of different initial conditions or different of environmental factors or parameter settings on the asymptotic regimes.

More precisely, we used the following procedure to scan the asymptotic regime of the model over a range values for a certain parameter or environmental factor. We start with an arbitrary initial biomass of overwintering structures (default 10 g m^{-2}) in a state where vegetation can develop (either in clear or shallow water). The yearly cycle is allowed to stabilize by letting the model run for 200 years. Subsequently, the biomass is plotted at an arbitrarily chosen day in summer (default day 183 (1 or 2 July)) for 5 successive years. Thereafter, one state variable or parameter is changed over a certain range in a number of small steps (default 41), each time using the previous final state as a new starting point for the simulations. In each of these small steps, the model is first run for 100 years to stabilize, and subsequently the new summer biomass is plotted in 5 successive years (to check whether convergence to a 1-year cycle occurred).

In order to check for hysteresis due to alternative attractors we subsequently repeat the procedure, moving along the parameter range that we scanned in opposite direction. Thus, we remove all plants, seeds and tubers, let the vegetation colonize the bare location starting from a tiny yearly import of oospores and bulbils of 0.1 m^{-2} year^{-1}, and do 41 steps backwards along the gradient. If the model has alternative stable states, this can be reflected by a different result on the forward and backward scans. In complex situations (e.g. with several competing species), it is not guaranteed that the alternative equilibria are found with this method. Therefore, we can alternatively use a less efficient method: again by changing a parameter or environmental factor step by step, not using the previous final state as new starting point, but with several very different initial conditions.

4. Results

4.1. Monte Carlo sensitivity analysis

For sensitivity analysis we used a version of the model with two competing species (*C. aspera* and *P. pectinatus* using a fixed water depth of 1 m and a fixed turbidity (vertical light attenuation coefficient of 2 m^{-1}). Analysis of results from 10.000 randomly selected parameter sets, showed that only 45 of the 90 examined parameters had a 'significant effect', i.e. exceeded the 0.99 percentile of the sensitivity scores of 100 dummy variables included in the analysis. Fig. 3 shows the results of this analysis and the accompanying cluster analysis of the parameters with a significant effect. To check whether 'non-significant' parameters really had no effect, a second analysis was done (with 5000 parameter sets) on only those 'non-significant' ones. The result indicated that 17 of these parameters had nonetheless a significantly stronger effect than the dummy variables. This shows that the power of the analysis decreases when there are parameters with a strong effect on the outcomes. A next analysis excluding also the 17 weakly significant parameters confirmed that the remaining 18 parameters really had no significant effect on the model outcome.

The parameters that define the temperature limitation (hPhotoTemp and sPhotoTemp) appeared to have the largest impact on the model results (Fig. 3) These parameters are part of clusters of parameters that have a similar effects on the model outcomes. The parameter hPhotoTemp of *C. aspera* is part of a cluster with parameters that mostly related with the primary production of *C. aspera* (pMax, hCarbonate). A closer look at the sensitivity matrix (not shown) revealed that this cluster has effect on all model outcomes (biomass, individual biomass, numbers) of *C. aspera*. The effect on *C. aspera* increases with time (Fig. 4). The strongest effect appears only after five years of simulation. The same cluster of parameters also has a strong opposite
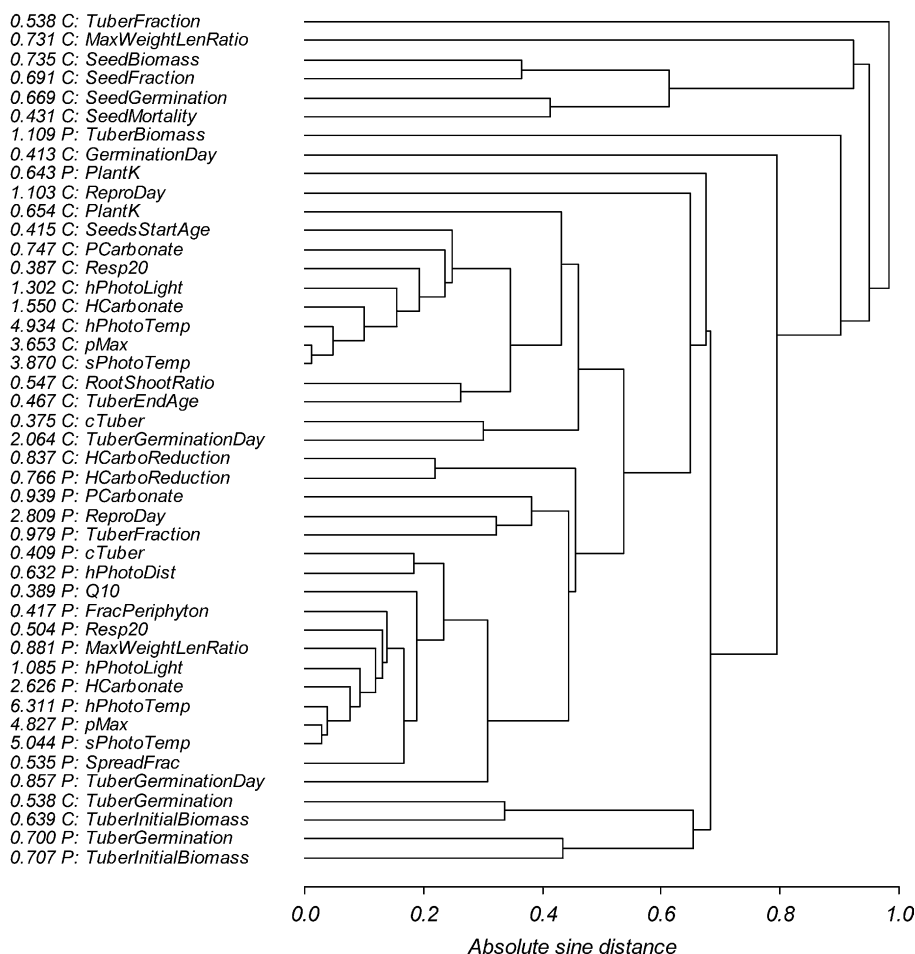
Fig. 3. Cluster analysis of the sensitivity indices of the parameters. Parameters with the same or opposite effect on the model results (biomass, numbers, and mean individual weight) are grouped together. The value before each parameter is the length of the vector of the sensitivity coefficients (Klepper, 1989), which is a measure of the total strength of the effect. The 45 parameters that are shown have a significantly stronger total effect than 99% of 100 dummy variables. C = *C. aspera*, P = *P. pectinatus*. The abbreviations of the parameters are explained in Table 1.

effect on all *P. pectinatus* outcomes, which has reached its maximum already after two years. Probably, in the first years of these standard simulations biomasses are so low that competition is not yet important, and the outcome is dominated by the initial conditions. This is confirmed by the sensitivity of reproduction parameters (for instance the cluster with TuberGerminationDay of

C. aspera) which increases hardly with time (Fig. 4).

4.2. Unraveling mechanisms of hysteresis in plant competition

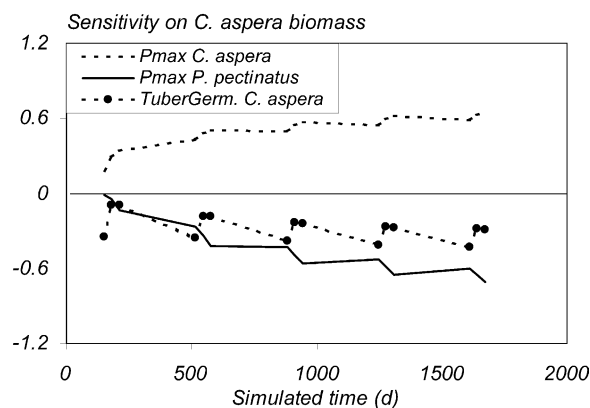As an example of how specific mechanisms in macrophyte competition can be addressed we

Fig. 4. The sensitivity coefficients of three parameters (P_{max} of *C. aspera* and *P. pectinatus* and TuberGerminationDay of *C. aspera*) on the biomass of *C. aspera* in time (5 years, 3 points in time per year).

show results of the analysis of the effect of variation in the turbidity of the water (K_d) on competition between *C. aspera* and *P. pectinatus*. For simplicity we neglect spatial aspects in this analysis, and focus on a single grid cell of 5×5 m with a water depth of 1 m. Scanning of asymptotic regimes (Fig. 5a) showed that there are two zones with alternative equilibria in this situation. In clear water, with a vertical light attenuation between 1 and 4.5 m^{-1}, there is either a mix of both species or a monoculture of *P. pectinatus*. Another small zone of alternative equilibra occurs around a light attenuation of about 6.5 m^{-1}. In this zone there can either be *P. pectinatus* or no vegetation. The model thus predicts that during eutrophication, the system changes from *C. aspera* to *P. pectinatus* dominance followed by a loss of vegetation in turbid water.

The system shows hysteresis in its response to changing water turbidity. One aspect of this pattern is unexpected: the system does not return to its initial state in clear water. To check whether the positive feedback between plants and water clarity could cause this phenomenon we took out the effect of plants on turbidity in the model. It appears that this eliminates the narrow band of hysteresis in turbid water, but not the irreversible pattern on the left-hand side of the range (Fig. 5b). Therefore, there must be another explanation for

the occurrence of alternative stable states in clear water.

We therefore checked two other aspects of competition in the model. Firstly, competition for light is asymmetrical, as *P. pectinatus*, forms a canopy above *C. aspera*, which grows as a dense mat covering the sediment. Secondly, both plants compete for bicarbonate, which is a potentially limiting nutrient. We checked the effects of these aspects on the occurrence of alternative equilibria, by repeating the analysis using different versions of the model. First, we made the competition for light symmetrical by setting the maximum length of *P. pectinatus* equal to the value of *C. aspera*. Though the area with alternative equilibria in clear water has become somewhat smaller (between 1 and 3.5 m^{-1}, see Fig. 5c), the qualitative behavior of the model is almost the same. The next step is to shut off the feedback in bicarbonate by letting the bicarbonate concentration be unaffected by the macrophytes. Now, the alternative equilibria in clear water disappear (Fig. 5d). Charophytes never become abundant, and there is only a small zone with alternative equibria in turbid water. The latter zone is caused by the turbidity feedback as shown by shutting both feedback loops off (Fig. 5e). In conclusion, the model analysis suggests that competition for bicarbonate may be a powerful mechanism causing hysteresis, allowing pondweeds to remain dominant even at low turbidities were charophytes would otherwise take over.

5. Discussion

The model Charisma is not meant as a predictive tool but rather for the purpose of gaining insight and generating hypotheses. This is also the general aim of much simpler so-called 'minimal models'. However, these models usually ignore or highly oversimplify aspects such as seasonality, space and numerous quantitatively important processes. The niche of models such as Charisma is to explore questions with more realism, while the flexible design of the model and the analyzing tools allows a thorough scrutinization of causality of generated patterns. A good strategy for gaining insight from such model is in our opinion a
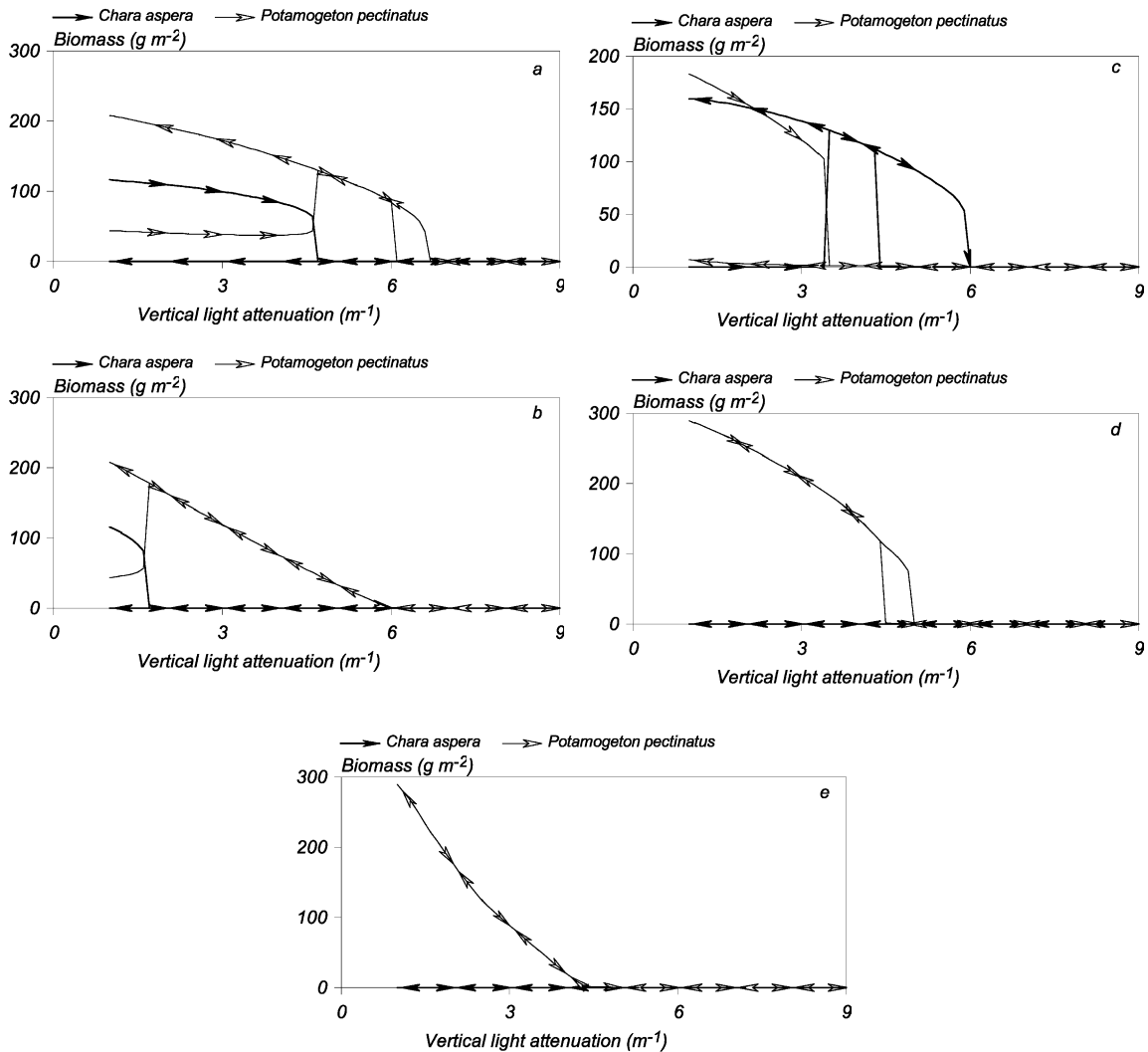
Fig. 5. The effect of a change in the vertical light attenuation on the equilibrium summer biomass (on 2 July) of *C. aspera* and *P. pectinatus* on a grid cell of 1 m. The arrows indicate the direction of the change in vertical light attenuation. (a) Default parameter settings. (b) The same analysis, but with the vertical light attenuation feedback closed. This is done by setting the effect of both species on the turbidity to zero. (c) The same analysis as a) but the maximum length of *P. pectinatus* equals that of *C. aspera* (0.35 m). (d) The same analysis but the turbidity feedback is closed. This is done by setting the effect of both species on bicarbonate to zero, and setting the bicarbonate concentration to a lower value (60 mg l^{-1}). (e) Both feedbacks closed, see (b) and (c).

thorough analysis of different versions of the model, of which some may be oversimplified. The value of this strategy is exemplified in the bifurcation analysis of the competition between the two species as described in this paper. We could show that the patterns were mainly determined by the bicarbonate feedback, and to a lesser extend by the water clarity feedback.

An often-discussed problem of complex ecological simulation models is the fact that a good fit

of the generated results to field data does not guarantee that the model is correct (Scheffer and Beets, 1994; Rykiel, 1996). Therefore, perhaps the most rewarding result is a persistent discrepancy between model predictions and field patterns. As an example consider the prediction of Charisma that once *P. pectinatus* has gained dominance it will not be replaced by *C. aspera* even if water quality is greatly improved. This contrasts with the recovery pattern in lake Veluwemeer where Charophytes eventually replace *P. pectinatus* and became completely dominant (Meijer, 2000). This suggests that other mechanisms than the modeled ones may be important in the field. A possible explanation is that winter grazing by Bewick's swans on *P. pectinatus* tubers creates bare spots that *C. aspera* can colonize, and that the resulting 'hot spots' produce enough oospores to expand into the neighboring areas, thus displacing *P. pectinatus* from other parts. Indeed, in Lake Veluwe, *C. aspera* recolonized the lake very slowly, expanding from a few initial spots gradually in about 10 years. Thus, the model is realistic and transparent enough to suggest interesting research questions.

Although it is impossible to characterize sensitivity of the model in an absolute sense, relative ranking of the sensitivity to different parameters can give a clue to which aspects are most important in driving dynamics of the real system. Our sensitivity analysis indicated that macrophyte growth is particularly sensitive to temperature, which is in line with earlier model analyses (Scheffer et al., 1993), and with empirical results from lab experiments (Barko and Smart, 1981; Spencer, 1986) and field studies (Best and Visser, 1987; Scheffer et al., 1992). In view of the key role of submerged plants in many lakes, the temperature sensitivity suggests that this aspect could be an important focus of future research on effects of climate change on lake ecosystems. In an uncertainty analysis, Van Nes and Scheffer (2003) show that the model may be very sensitive to parameter changes, especially near catastrophical bifurcation points.

A good example of the way in which models such as Charisma can fill the niche between reality and minimal models is the analysis of causes and consequences of alternative stable states described in this paper. In previous work, the prediction of alternative equilibria has been based largely on results from extremely simple (1 or 2 differential equations) models without seasons (e.g. Scheffer, 1998). It is not at all obvious that persistent alternative equilibria would also be possible in situations with seasons, as the ecosystem is often thought to be 'reset' in winter (Knowlton, 1992). Our results demonstrate that for submerged macrophytes the dependency on the previous-years' population known from field studies (Kautsky, 1990) is likely to be strong enough to make alternative equilibria possible.

Also, our analysis of causes of alternative stable states goes well beyond the highly simplified plant-turbidity feedback mechanism described in minimal model studies (Scheffer, 1998). Charisma can have alternative equilibria for at least three reasons: the turbidity feedback, competition for bicarbonate, and harvesting or grazing (described in detail by Van Nes et al., 2002b). The positive feedback on the turbidity is an intuitively straightforward reason to expect alternative equilibria in macrophyte stands. However, the models employed so-far do not allow an estimate of the conditions under which hysteresis should really be expected. Using Charisma a more realistic picture has been produced showing the dependence of this phenomenon on the strength of the clearing effect and on the depth gradient and mixing processes in a lake (Van Nes et al., 2002a). Though the availability of CO_2 has been shown to explain the competition between two very different species of macrophytes in a earlier model study (Wortelboer, 1990), competition for bicarbonate, as analyzed here, has not been described before as a mechanism causing alternative attractors. The underlying positive feedback is due to the higher consumption of bicarbonate by *C. aspera*, which can also tolerate lower bicarbonate concentrations than *P. pectinatus*. Therefore if the biomass of *C. aspera* increases, the biomass of *P. pectinatus* is more strongly suppressed, which causes better light conditions for *C. aspera*. Our results are also more or less analogous to that obtained from Tilman's resource-ratio theory describing competi-

tion for two resources (Taylor and Williams, 1975; Tilman, 1977).

In nature environmental variability, the turbidity feedback, competition for bicarbonate, and harvesting or grazing will often interact to produce shifts in vegetation dynamics. Models such as Charisma allow one to explore the complex potential consequences of such simultaneously acting mechanisms, while retaining the possibility to study and understand the emerging patterns in a systematic way. Obviously, they are only one type of tool in the toolbox needed to unravel the forces that drive ecological systems in the real world. However, we feel that this type of transparent, moderately realistic models are essential to fill the notorious gap between minimal models, field pattern analyses and controlled experiments.

References

Asaeda, T., Van Bon, T., 1997. Modelling the effects of macrophytes on algal blooming in eutrophic shallow lakes. Ecol. Modell. 104, 261–287.

Bach, H.K., 1993. A dynamic model describing the seasonal variations in growth and the distribution of eelgrass (*Zostera marina* L): I. Model theory. Ecol. Modell. 65, 31–50.

Barko, J.W., Smart, R.M., 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed fresh water macrophytes. Ecol. Monogr. 51, 219–236.

Best, E.P.H., 1981. A preliminary model for growth of *Ceratophyllum demersum*. Verh. Int. Ver. Theor. Angew. Limnol. 21, 1484–1491.

Best, E.P.H., 1990. Models on metabolism of aquatic weeds and their application potential. In: Pieterse, A.H., Murphy, K.J. (Eds.), Aquatic Weeds—The Ecology and Management of Nuisance Aquatic Vegetation. Oxford University Press, Oxford, pp. 254–273.

Best, E.P.H., Visser, H.W., 1987. Seasonal growth of the submerged macrophyte *Ceratophyllum demersum* L. in mesotrophic Lake Vechten (Netherlands) in relation to insolation, temperature and reserve carbohydrates. Hydrobiologia 148, 231–244.

Best, E.P.H., Woltman, H., Jacobs, F.H.H., 1996. Sediment-related growth limitation of *Elodea nuttallii* as indicated by a fertilization experiment. Freshwater Biol. 36, 33–44.

Best, E.P.H., Buzzelli, C.P., Bartell, S.M., Wetzel, R.L., Boyd, W.A., Doyle, R.D., Campbell, K.R., 2001. Modeling submersed macrophyte growth in relation to underwater light climate: modeling approaches and application potential. Hydrobiologia 444, 43–70.

Borland, 1997. Borland Delphi 3 for Windows 95 & Windows NT, User's Guide.

Calado, G., Duarte, P., 2000. Modelling growth of *Ruppia cirrhosa*. Aquat. Bot. 68, 29–44.

Carr, G.M., Duthie, H.C., Taylor, W.D., 1997. Models of aquatic plant productivity: a review of the factors that influence growth. Aquat. Bot. 59, 195–215.

Chen, D.X., Coughenour, M.B., 1996. A mechanistic model for submerged aquatic macrophyte photosynthesis: *Hydrilla* in ambient and elevated CO_2. Ecol. Modell. 89, 133–146.

Chiarello, E., Barrat-Segretain, M.H., 1997. Recolonization of cleared patches by macrophytes: modelling with point processes and random mosaics. Ecol. Modell. 96, 61–73.

Collins, C.D., Wlosinski, J.H., 1989. A macrophyte submodel for aquatic ecosystems. Aquat. Bot. 33, 191–206.

Davis, J.F., McDonnell, A.J., 1997. Development of a partitioned-biomass model for rooted macrophyte growth. Aquat. Bot. 56, 265–276.

Goudriaan, J., 1986. A simple and fast numerical method for the computation of daily totals of crop photosynthesis. Agr. Forest Meteorol. 38, 249–254.

Hodgson, R.H., 1966. Growth and carbohydrate status of Sago pondweed. Weeds 14, 263–268.

Hootsmans, M.J.M., 1994. A growth analysis model for *Potamogeton pectinatus* L. In: Van Vierssen, W., Hootsmans, M.J.M., Vermaat, J.E. (Eds.), Lake Veluwe, a Macrophyte-dominated System under Eutrophication Stress. Kluwer, Dordrecht, pp. 250–286.

Hootsmans, M.J.M., 1999. Modelling *Potamogeton pectinatus*: for better or for worse. Hydrobiologia 415, 7–11.

Ikusima, I., 1970. Ecological studies on the productivity of aquatic plant communities IV. Light condition and community photosynthetic production. Bot. Mag. Tokyo 83, 330–341.

Janse, J.H., 1998. A model of ditch vegetation in relation to eutrophication. Wat. Sci. Tech. 37, 139–149.

Kautsky, L., 1990. Seed and tuber banks of aquatic macrophytes in the Asko area northern Baltic sea proper. Holarct. Ecol. 13, 143–148.

Kirk, J.T., 1983. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge.

Klepper, O., 1989. A model of carbon flows in relation to macrobenthic food supply in the Oosterschelde estuary (S.W. Netherlands). PhD Dissertation, LUW Wageningen, The Netherlands, 270 pp.

Klepper, O., Van der Tol, M.W., Scholten, H., Herman, P.M., 1994. Smoes-A simulation model for the Oosterschelde ecosystem. 1. Description and uncertainty analysis. Hydrobiologia 283, 437–451.

Knowlton, N., 1992. Thresholds and multiple stable states in coral reef community dynamics. Am. Zool. 32, 674–682.

Meijer, M.L., 2000. Biomanipulation in the Netherlands—15 years of experience. PhD Dissertation, Wageningen University, 208 pp.

Mitchell, S.F., Hamilton, D.P., MacGibbon, W.S., Nayar, P.K.B., Reynolds, R.N., 1988. Interrelations between phytoplankton, submerged macrophytes, black swans (*Cygnus*

atratus) and zooplankton in a shallow New Zealand lake. Internationale Revue der Gesamten Hydrobiologie 73, 145–170.

Muhammetoglu, A.B., Soyupak, S., 2000. A three-dimensional water quality-macrophyte interaction model for shallow lakes. Ecol. Modell. 133, 161–180.

Park, S.S., Uchrin, C.G., 1997. A stoichiometric model for water quality interactions in macrophyte dominated water bodies. Ecol. Modell. 96, 165–174.

Rykiel, E.J.J., 1996. Testing ecological models: the meaning of validation. Ecol. Model. 90, 229–244.

Scheffer, M., 1991. On the predictability of aquatic vegetation in shallow lakes. Mem. Ist. Ital. Idrobiol. 48, 207–217.

Scheffer, M., 1998. Ecology of Shallow Lakes. Chapman and Hall, London.

Scheffer, M., Beets, J., 1994. Ecological models and the pitfalls of causality. Hydrobiologia 275–276, 115–124.

Scheffer, M., De Redelijkheid, M.R., Noppert, F., 1992. Distribution and dynamics of submerged vegetation in a chain of shallow eutrophic lakes. Aquat. Bot. 42, 199–216.

Scheffer, M., Bakema, A.H., Wortelboer, F.G., 1993. MEGA-PLANT—a simulation model of the dynamics of submerged plants. Aquat. Bot. 45, 341–356.

Scheffer, M., Baveco, J.M., DeAngelis, D.L., Rose, K.A., Van Nes, E.H., 1995. Super-individuals a simple solution for modelling large populations on an individual basis. Ecol. Modell. 80, 161–170.

Schutten, J., Davy, A.J., 2000. Predicting the hydraulic forces on submerged macrophytes from current velocity, biomass and morphology. Oecologia 123, 445–452.

Short, F.T., 1980. A simulation model of the seagrass production system. In: Phillips, R.C., McRoy, C.P. (Eds.), Handbook of Seagrass Biology: An Ecosystem Perspective. Garland, New York, pp. 277–295.

Søndergaard, M., Moss, B., 1998. Impact of submerged macrophytes on phytoplankton in shallow freshwater lakes. In: Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo., Kristoffersen, K. (Eds.), Structuring Role of Submerged Macrophytes in Lakes. Springer-Verlag, New York, pp. 115–132.

Spencer, D.F., 1986. Early growth of *Potamogeton pectinatus* L. in response to temperature and irradiance: morphology and pigment composition. Aquat. Bot. 26, 1–8.

Taylor, P.A., Williams, P.J., 1975. Theoretical studies on the coexistence of competing species under continuous flow conditions. Can. J. Microbiol. 21, 90–98.

Tilman, D., 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58, 338–348.

Titus, J., Goldstein, R.A., Adams, M.S., Mankin, J.B., 1975. A production model for *Myriophyllum spicatum*. Ecology 56, 1129–1138.

Vadstrup, M., Madsen, T.V., 1995. Growth limitation of submerged aquatic macrophytes by inorganic carbon. Freshwater Biol. 34, 411–419.

Van den Berg, M.S., Coops, H., Simons, J., Pilon, J., 2002. A comparative study of the use of inorganic carbon resources by *Chara aspera* and *Potamogeton pectinatus*. Aquat. Bot. 72, 219–233.

Van Dijk, G.M., Janse, J.H., 1993. Modeling resource allocation in *Potamogeton pectinatus* L. J. Aquat. Plant Manage. 31, 128–134.

Van Eerden, M.R., Beekman, J.H., Smit, M., Oosterbeek, K., 1998. Patch use by Bewick's swans *Cygnus columbianus bewickii* feeding upon sago pondweed *Potamogeton pectinatus* in shallow lakes in the Netherlands: variation in exploitation threshold caused by social, environmental and time dependent factors. In: Van Eerden, M.R. (Ed.), Patchwork-Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. Thesis University of Groningen, Lelystad, pp. 187–214.

Van Nes, E.H., Scheffer, M., 2003. Alternative attractors may boost uncertainty and sensitivity in ecological models. Ecol. Modell. 159, 117–124.

Van Nes, E.H., Scheffer, M., Van den Berg, M.S., Coops, H., 2002a. Dominance of charophytes in eutrophic shallow lakes—when should we expect it to be an alternative stable state? Aquat. Bot. 72, 275–296.

Van Nes, E.H., Scheffer, M., Van den Berg, M.S., Coops, H., 2002b. Aquatic macrophytes: restore, eradicate or is there a compromise? Aquat. Bot. 72, 387–403.

Van Wijk, R.J., 1989. Ecological studies on *Potamogeton pectinatus* L. PhD Dissertation, Catholic University of Nijmegen, p. 171.

Verhagen, J.H.G., Nienhuis, P.H., 1983. A simulation model of production, seasonal changes in biomass and distribution of eelgrass (*Zostera marina*) in Lake Grevelingen. Mar. Ecol. Progr. Ser. 10, 187–195.

Westoby, M., 1984. The self-thinning rule. Adv. Ecol. Res. 14, 167–255.

Wetzel, R.L., Neckles, H.A., 1987. A model of *Zostera marina* L. photosynthesis and growth simulated effects of selected physical–chemical variables and biological interactions. Aquat. Bot. 26, 307–324.

Wortelboer, F.G., 1990. A model on the competition between two macrophyte species in acidifying shallow soft-water lakes in The Netherlands. Hydrobiol. Bull. 24, 91–107.

Wortmann, J., Hearne, J.W., Adams, J.B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modell. 98, 137–149.

Wright, R.M., McDonnell, A.J., 1986. Macrophyte growth in shallow streams: biomass model. J. Environ. Eng. ASCE 112, 967–982.