Using modeling to understand plasticity in freshwater macrophytes. Implication for validation process

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Abstract

We evaluated the error of estimate brought while undertaking some classical hypotheses in modeling plant growth in a dynamic way or linked with imprecision in measurements of physiological characteristics of the plant or in the environmental data. This study reported also a possible application of modeling to understand plant plasticity.

We synthesized classical models based on a carbon mass balance approach and run for populations of Ranunculus peltatus, a spreading macrophyte in rivers of North-Eastern France. Simulations were performed for five contrasting combinations of environmental parameters.

Among the 48 models tested, we demonstrate highly variable results in terms of maximum biomass reached and plant temporal biomass production. The way plant architecture was approximated contributed significantly to biomass results. From the simulations, we selected a family of models matching the existing field data. Among these, one was selected arbitrarily. Using this model, we underlined that (1) light availability and temperature were key main environmental factors for plant growth and should be measured with high precision; (2) optimum temperatures for photosynthesis, respiration, and maximum activities for all physiological processes were the most sensitive constants entering the model; and (3) taking into account plant plasticity (i.e., their capabilities to modify their physiological and morphological characteristics to adapt to lack of resources or seasonal environmental changes) greatly modifies biomass production, especially when adapting to nutrient stress or to seasonal temperature variation. All these results may contribute significantly to the improvement of existing dynamic models and especially of the validation process. This approach is also of huge interest for understanding aquatic plant plasticity.

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Introduction

Models of plant growth are mathematical representations of the physiological process associated with plant metabolism (Van Dijk and Janse, 1993; Carr et al., 1997). Most models use a mass-balance approach based on the carbon cycle, and are applied for the simulation of homogeneous populations of freshwater plants (Carr et al., 1997). They have been developed to examine the effect of rooted macrophytes on aquatic ecosystems and simulate management methods on macrophyte growth (Wright and McDonnell, 1986; Davis and McDonnell, 1997). Nevertheless, mathematical representation not only plays a critical role in the estimation of plant biomass production, but also provides access to exploring the photosynthetic response of a plant to different conditions and to understanding complex processes difficult to study using classical experimental approaches.

The most important problem in using such an approach is that some aggregation of pattern and process is essential. It is impossible to model all the complexities of physiological parameters even in a homogeneous population. We are therefore required to approximate, to seek features of plant behavior which we can model. The rigor with which the model is verified and the ability of the model to provide good estimates of plant production under a range of environmental conditions will determine its strength in emulating the physiological processes involved in plant growth (Carr et al., 1997). Hence it is quite important to know whether the model used is robust and whether it can be used to make useful predictions with acceptable risk. In addition, complex processes may be simplified and traduced into several mathematical relationships. These simplifications are poorly argued and will increase the error of estimation. However, few comparative studies between results obtained from different mathematical formulation for the same physiological process are available (Frenette et al., 1993). Apart from the risk of error linked with the choice of mathematical formulation, further error may arise from the precision of the measurements of environmental parameters and from the selection of each physiological constant. That is why before validating a model, preliminary studies should be made to determine on which parameters either environmental variable or physiological constant of the plant, measuring effort should be focused.

This preliminary stage seems to have been skipped in most models or has not been published. Nevertheless, this stage is among the key steps when elaborating a model.

The present study concerns this preliminary step. It is part of a general project on the use of modeling to understand and explain plastic responses of aquatic macrophytes at the individual level according to environmental conditions. The freshwater plant selected for the model is *Ranunculus peltatus* Schrank, which is a submersed native hydrophyte species. Occurring in shallow streams, this rooted macrophyte develops a main shoot up to 3m long and from which several secondary ramets expand (Cook, 1966; Garbey et al., in press a). Its plasticity, both morphological and physiological, has been shown experimentally (Cook, 1966; Garbey et al., in press b). Modeling such a hydrophyte needs, therefore, to adapt models usually realized in lacustrine ecosystems to shallow running waters (Best, 1981; Collins and Wlosinsky, 1985; Hoostmans 1994; Best and Boyd, 1996, 2001; Best et al., 2001). In addition, the classical models usually characterized plant growth with fixed physiological parameters. The validation of such approaches should be questioned for highly plastic species such as *R. peltatus* (Maberly, 1985; Santamaria and Van Vierssen, 1997). The present work aims at evaluating the risk of error linked with these different hypotheses usually undertaken in models. It particularly aims at (i) making a synthesis of the different existing models of macrophyte growth and investigating the suitability of adapting one of them to the evaluation of growth at the individual basis; (ii) underlining key environmental data determining plant growth, and hence measuring with precision to improve the model selected; (iii) analyzing which physiological constants are the most determinant in plant growth and which should therefore be determined with accuracy; and (iv) evaluating variation obtained in results, calculated through the model, while simulating physiological plasticity.

General model formulation

The framework of this macrophyte model is standard and follows a mass-balance approach based on the carbon cycle with $\dot{B} = P - R - W - S$ where B, P, R, W and S are scalar functions of time

representing successively the Biomass, gross Photosynthesis, Respiration, plant Washout by river flow and Senescence. Three time scales were used: *to*, *t*, and *τ,* that are, respectively, the hour, the day, and the month. The time interval studied comprised 150 days and started on April 1st and ended on September 1st. This period corresponded roughly to the *R. peltatus* active growing period (Garbey et al., 2004). B corresponded to the above-ground biomass. Below ground biomass was neglected as it represents less than 1% of the plant total biomass (Garbey, unpublished data). Flowering was modeled as a function of accumulated heat following the degree-days hypothesis (Thornley and Johnson, 1990). The date of the beginning of flowering, t*, was determined when the necessary degree-days were reached. In *R. peltatus*, the critical temperature of 5°C and an accumulation of 380°C temperature degrees above 5°C for the beginning of flowering were chosen (Dawson, 1980). As in other *Ranunculus Batrachium* species, flowering initiates a physiological change in shoots which entailed their buoyancy and senescence (Dawson, 1976).

Photosynthesis

Photosynthesis is the only term in the model responsible for the growth of the biomass. Photosynthetic rate ρ(to, t, τ) was assumed to be a function of maximum photosynthetic activity (Pm), limited by environmental parameters such as water temperature (θ), intensity of light received on the plant surface (I) and nutrient availability (N) (Tab.1; eq. 1). Photoinhibition was neglected. Two different expressions of the dependence of photosynthesis on temperature were found in the literature. With the assumption that the river is shallow enough that temperature could be considered as uniform, (θ) can be modeled either with a Lehman function that reaches its maximum at an optimal temperature denoted θp (Dufayt, 2000) (eq. 1.1.1), or as a derivative of the Q10 or Van't Hoff equation (Wright and McDonnell, 1986; Evervecq et al., 2000; Scheffer et al., 1993; Asaeda and Karunaratne, 2000) (eq. 1.1.2). The traditional approach to model growth with respect to nutrients has been to use the Michaelis-Menten formulation (Tab.1 ; eq. 1.2). The half saturation constant (k_N) corresponds to the nutrient concentration (N) where photosynthetic

activity is one-half of P_m (Carr and Chambers, 1998; Dufayt, 2000; Asaeda et al., 2001). This formulation assumes a single enzyme-limited process. The limiting nutrient selected was the water soluble reactive phosphorus, as its dominant role in controlling the development and abundance of macrophytes was clearly demonstrated (Westlake, 1973; Carr and Chambers, 1998). Photosynthesis according to light was modeled as a function of available light (I(to,t)), biomass density (b(z)) to a z water depth and various extinction coefficients (Tab. 1). We denoted z ϵ [0, H] the vertical coordinates of the depth in the river with z=0 corresponding to the water surface. Chalker (1980) showed that the rate of change of P *vs.* I is a function of P, which can be expanded as a power series $\frac{\partial P}{\partial I} = a_0 + a_1 P + a_2 P^2 + a_3 P^3 + \mathrm{K}$. Three models for k(I) were derived depending on the approximation made of this equation. A quadratic approximation gives a first model (Jassby and Platt, 1976; Zimmerman et al., 1994) (eq. 1.3.1), whereas a linear approximation of the same law should give a second one (Dufayt, 2000; Best and Boyd, 2001) (eq. 1.3.2.). A third model is the Michaelis-Menten law (McBride, 1992; Hootsmans and Vermaat, 1994; Calado and Duarte, 2000) (eq. 1.3.3) with the half saturation constant k_i corresponding to the light intensity where photosynthetic activity is one-half of Pm. I(to,t) is computed from Io(to,t), which is the sunlight arriving at the earth's surface (eq. 1.4). Before reaching the plant, Io(to,t) extincts via riverine vegetation (Os: percentage of shadowing by riverine vegetation; c_4: light extinction coefficient by riverine vegetation). The impact of the shadow effect might be modeled in function of Io(to,t) by a weight function (Dufayt, 2000) (Tab. 1 ; eq. 1.4). Light attenuates exponentially in the water following a Beer-Lambert law in function of the extinction through mineral components (Ot) and macrophyte beds (c_5) (Best, 1981; Canale and Auer, 1982; Wright and McDonnell, 1986; Kirk, 1994; Asaeda et al., 2000, 2001) (eq. 1.4). Water turbidity (Ot) was fixed at 0.32 m^{-1}. Io(to,t) was computed using a common routine calculating either photoperiod λ and light intensity according to latitude, longitude and time of the year. Io was hence calculated in function of the hour. These calculations were derived from classical mechanics that give the position of the sun as a function of the earth location and angles on its planar orbit running

around the sun (Danloux-Dumesnils, 1985). The Lorraine mean latitude and longitude were selected to enter the model (48°N, 7°E). The assumption was made that only 45% of the irradiance reaching the water surface is presumed photosynthetically active (PAR) and 10% of the remainder is reflected by the water surface (Van Dijk and Janse, 1993; Asaeda and Karunaratne, 2000).

Respiration

Respiration corresponds to the consumption of carbon used to maintain the cell activity and has been modeled in a number of ways in the literature (McCree, 1970; Wright and McDonnell, 1986; Dufayt, 2000). It is decomposed mostly into a temperature dependent function (l(θ)) and a function of biomass and photosynthesis (m(P,B)) (eq. 2). This l(θ) function may be formulated in two different ways, analogue to f(θ) in photosynthesis (eq. 2.1.1 and 2.1.2) (Wright and McDonnell, 1986). Respiration losses of carbon are split between maintenance respiration and/or growth respiration. Models taking into account both respirations proposed a linear combination of biomass and photosynthesis, as growth respiration is proportional to the gross photosynthetic rate P, and maintenance respiration is related to the dry weight of plant material, B (McCree, 1970) (eq. 2.2.2). However, some models neglect the growth respiration and model respiration as a function of biomass (eq. 2.2.1). The constant, Rp related to growth respiration was not evaluated in *R. peltatus.* Hence, only the variant 2.2.1 was tested.

Washout

Washout is solely taken into account in models, though its ecological importance has been shown for several macrophytes in running waters (Dawson, 1978; Wright and McDonnell, 1986). Washout was modeled as a function of biomass and water velocity (eq. 3). The mechanical resistance of the plant to friction with water was assumed to be time independent. Washout depends essentially on shear force on the river bottom, which is proportional to square velocity. It was therefore modeled as Dufayt (2000) (eq. 3.1.1). Washout may also take into account the fact that under a certain force, the washout may be null

(Water Agency, 1999) (eq. 3.1.2). This expression was a function of the minimum current velocity for the fragmentation of shoots (v_{min}), the reference current velocity (v_{ref}), and the associate washout rate (c_{11}). This formula was calibrated using two sets of data from Dufayt (2000) and Water Agency (1999) concerning respectively *Ranunculus fluitans* and *R. peltatus.* The speed of the flow of the river $v(\tau,t)$ was decomposed into its average value per month $v_o(\tau)$ and random fluctuations $v_1(\tau,t)$ that have peak values during rain storms (Tab.1; eq. 3.2). The function p: (1, ..,30) $\rightarrow$ (0,1) is an equiprobability, and w_3 is a barrier that reflects the frequencies of rain storms; w_2 and w_4 are white noise functions. F is a diffusion-convection operator that simulates the effect of relaxation on the flow speed in the river after a storm followed by renormalization. Generally, washout should be a stochastic process and it may not be well modeled by a simplified deterministic model as above.

Senescence

Senescence was modeled by setting the death rate at a certain fraction of plant biomass per day when the environmental conditions for growth deteriorate (Tab.1 ; eq. 4). The timing and values of relative death rates of plants were derived from literature data and field observations. We supposed that senescence was uniformly distributed among plants independently of the environment. We chose for $a_o(t)$ an hyperbolic tangent profile that reflects our field observations (Garbey et al., in press). In particular, we assumed that this effect has its turning point at mid-flowering period. Values for Sm rank from 0.0002 to 0.0008d^{-1} of total biomass (Wright and McDonnell, 1986; Collins and Wlosinski, 1985; Hootsmans and Vermaat, 1994; Best and Boyd, 1996, 1999, 2001). Being the most frequently quoted, the value 0.0005d^{-1} was entered in the model.

Modeling R. peltatus architecture: from clumps to individual plants

Except for the term on washout that has polynomial dependence on biomass and the auto-shadowing extinction factor, the above models are linear with respect to the biomass. Indeed, if initial biomass is

doubled; calculated biomass is also doubled. Consequently the models may be used to predict the biomass of an individual plant as well as the biomass per square meter. B is essentially dependent on the density of biomass in the water column (b(z)). b(z) varies with respect to the plant architecture. We tested three different simplifications of *R. peltatus* architecture: (i) *R. peltatus* is distributed uniformly over the water column (Van Dijk and Janse, 1993) (Tab.1; eq.5.1); (ii) *R. peltatus* is a canopy former and all its biomass is located in the canopy occupying an S water depth that was fixed at 0.1cm (eq. 5.2); (iii) *R. peltatus* has an intermediate architecture with biomass split into the canopy and into the H-S water depth (Fig. 1). The canopy is characterized by a very dense biomass whereas H-S comprises low biomass. The proportion of the plant located in the canopy was assumed to be related to the average current velocity and water depth. The angle between the plant main shoot and the horizontal river bottom was noted α and was function of $v(\tau)$. Plants with a L-meter-main shoot reached the water surface and began to form a canopy when $L\sin(\alpha)$ is larger than H (Tab.1 ; eq. 5.3). L was calculated using an empirical relationship linking individual plant biomass (Bi, gFW) to plant length (L, m): $L = 0.026\ x\ Bi$. This formula was obtained via regression analysis using a 140-individual data set. The conversion coefficient for dry weight to fresh weight was fixed at 0.04 (Garbey, unpublished data) and from carbon content to dry weight at 0.373 (Madsen and Maberly, 1991).

All physiological parameters entering the model were synthesized in Tab. 2. The value retained corresponded to the most cited data selected from a literature review on ecophysiological data on *R. peltatus* and when not available on *Ranunculus* spp. From the different model descriptions, 96 models could be tested (Tab. 3). Among those, 48 were selected with respect to the available ecophysiological data for *R. peltatus*.

Model simulation

Description of the study sites

Simulations were made for five study sites. These sites were chosen in order to test the model against sites with populations of plants growing in highly different environmental conditions and especially with respect to hydrological regime (Tab. 4). Further, the simulation of biomass production in a relatively high number of sites may bring valuable information and would enable selection of a few appropriate models, though a validation step is needed for conclusive selection of a model. The sites A, B and C were characterized by stable hydrological regime whereas the sites D and E were frequently flooded. The characteristics of each site were studied through monthly chemical and physical surveys in 2000 (Garbey et al., 2004) (Tab. 3). Only one measure per month is available for flow speed and water temperature. In order to extrapolate these data at the day time scale, we used a least square polynomial fitting added with a random noise of amplitude of what we observed in the field. We chose a one-degree amplitude for temperature and implemented crisis events in flow fluctuations simulating rain storms (See "Washout" section). Studies performed on some of these sites report maximum biomass of *R. peltatus* ranking from 50 to 300 gDW/m² for site D and from 100 to 210 gDW/m² for site E in June (Water Agency, 1999; Garbey, 2000).

Performance tests

A sensitivity analysis of a simulation model is required to assess the variables or physiological constants affecting at most model behavior. The impact of each environmental parameter on plant biomass was analyzed by simulating a change in a given environmental parameter, all others remaining the same. The variation of the initial value was chosen in order to reflect measurement imprecision linked with the monitoring of these parameters. We selected variation amplitude of 10µg/l for nutrients, 10cms for water depth, 10% for shading percentage, 1°C for temperature and 0.2 m/s for current velocity. With respect to physiological parameters entering the model, a more classical sensitivity analysis was used. We investigate the impact of a 2% variation of each physiological parameter, the others remaining constant on the relative variation of biomass simulated.

A good indicator of the impact of each parameter in the model is given by approximating the change on biomass within a day if a parameter is changed by few percentage points. This method was used for the sensitivity analysis of 16 constants included in the models.

Simulating *R. peltatus* physiological plasticity

If plants essentially respond to short-term environmental fluctuations in an unregulated manner without active changes in resource utilization, acclimative responses are observed upon exposure to different environmental conditions for longer periods, and this in most aquatic plants. We selected three main plastic behaviors that are observed in *R. peltatus* and that are classically reported strategies developed to adapt to changes in environmental conditions or stress.

(i) Plastic adjustment to seasonal changes in water temperature

For a wide diversity of aquatic species, seasonal differences in the thermal regime resulted in a shift in optimal temperature for net photosynthesis (Maberly, 1985; Pilon and Santamaria, 2001). In general the observed shifts consisted of higher environmental temperatures generally leading to higher optimal temperatures, and *vice versa*. However, in many cases the range of acclimative adjustment in the photosynthetic response is small, and for the majority of species the recorded optima were substantially higher than predominant water temperatures. Simulating this adjustment in the *R. peltatus* model was achieved by decreasing θp from 19.7 to 17.7°C until the initiation of flowering t* which corresponds approximately to May or the beginning of June depending on the site. A hyperbolic tangent profile simulated the increase of θp from 17.7 to 19.7°C after t*. Then θp was fixed at 19.7°C for the end of the season. Such a formula was selected to reflect the short number of days necessary to acclimate to seasonal temperature fluctuations (a few days).

(ii) Plastic adjustment in response to a light stress

The phenotypically plastic responses to variation in instantaneous irradiance consist classically of greater photosynthetic activity in decreasing light levels. This trend may be attributed to a higher chlorophyll content and consequently greater assimilatory capacity in the shade-adapted shoots (Barko and Smart, 1981; Bowes et al., 1977; Pilon and Santamaria, 2001). For instance, Maberly (1993) highlighted a 2.6 fold higher light utilization efficiency for plants growing at 3.5m-water depth than at 0.5m. We simulated plant adaptation to low light availability by reducing maximum photosynthetic rate from 0.011 to 0.010 and increasing light use efficiency from 0.000078 to 0.0001. Site A with more than 75% of shading was taken as an example of light stress condition.

(iii) Plastic adjustment of maximum saturation constant according to nutrient stress

Less data are available on plant acclimation to nutrient stress. We simulated this by reducing the saturation constant for nutrients from 4.7 to 3µg/l, which corresponded to a 36% reduction. We took populations from site A with less than 19µg/l of $P\text{-}PO_4^{3-}$ in water as an example of nutrient stress conditions.

Results

Comparison of the models

Forty-eight models were tested using combinations of two formulas for temperature, three for dependence of photosynthesis on light, three for washout and three for simulating plant architecture (Tab.4). To illustrate the variability of results found, we selected only models with the third approximation of plant architecture, which predicts that biomass is split between the canopy and the rest of the water column. Highly variable results for maximum biomass were found through the 18 models tested (Tab. 5). For instance, the second variant used for washout (models 7 to 12) entailed nearly the complete washout of plants resulting in very low biomass production in all sites. Maximum biomass produced was highly sensitive to temperature. Modeling photosynthesis and respiration dependence on temperature using the second formula (models 4, 5, 6, 10, 11, 12, 16, 17, 18) decreased approximately three times the maximum

biomass compared to using the first formula. Published data gives a biomass range similar to results obtained with the first formula of plant photosynthesis dependence on temperature (Water Agency, 1999) (models 1, 2, 3, 12, 13, 14). Among these models, the differences stand in the formula used for light and between variants 1 and 3 for washout. These models corresponded to different site biomass signatures, the most aberrant being the highest biomass found for the oligotrophic and shaded site A compared to the eutrophic and moderately shaded site C (model 3). Strong overestimates of biomass were found using the third form of dependence of photosynthesis on light compared to published data.

Among the 18 models tested, only four (models 1, 2, 13 and 14) seemed to be pertinent, though giving quite different results. In the following section of results, we selected model 13 as an example but the same analysis could have been done with the other three models. Precise validation will be necessary to isolate which among this family of models is the most predictive. In the following analysis, results for sites B and D were not mentioned as they closely resemble sites A and E, respectively. In determining plant growth, photosynthesis and senescence were two major processes (Fig. 2). Depending on the site, loss of carbon by respiration corresponded to approximately 30 to 40% of carbon produced by photosynthesis. Respiration and photosynthesis evolved proportionally. Washout had a quite low importance in the carbon loss but was characterized by an irregular variation corresponding to storm events. Senescence significantly decreased biomass, especially at the end of the season.

We simulated results obtained with the three approximations of *R. peltatus* architecture (Fig. 3). Approximating *R. peltatus* architecture as being homogeneously distributed in the water column gave the lowest biomass, whereas the highest biomass was obtained while simulating *R. peltatus* biomass as split between the canopy and the rest of the water column. Simulating biomass as concentrated in the canopy gave intermediate results. This was due to the strong autoshadowing effect provoked by the dense biomass concentration in a thin water column. Using the first simulation underestimated the maximum biomass reached by 5 to 16%, compared to the third, more realistic one (Fig. 3). Using the second simulation contributed to an underestimate of 1 to 12%. This range of error with plant architecture

formulation was similar for the biomass obtained at T=150d for site A. However, for sites C and E, the error of estimates was increased and reached 12 and 11% respectively for the first formulation, and 5.6 and 7.3% for the second one. Nevertheless, all simulations reached peak biomass at the same time with only one or two days of variation. The error of estimate was higher for sites with a high biomass production than for sites with a low biomass production due to stressful environmental conditions.

Impact of each parameter on plant biomass production

The analysis of the impact of each environmental parameter on plant biomass was investigated by a simulation of a change in a given parameter, all others remaining the same. For instance, the sensitivity of the model to nutrient availability was tested by calculating biomass production for an increase and a decrease in 10µg/l of the initial concentration, all other parameters remaining fixed (Fig. 4). Variation in nutrient availability has a significant impact on biomass in the oligotrophic site (site A) and has poor effect when the concentration of nutrients in the water is sufficient (sites C and E). Indeed a maximum increase of 140% was found for site A compared to 2 to 12% for sites E and C, respectively. A variation of 10 cms of the initial water depth entailed at maximum less than 2% variation in the calculation of biomass, highlighting the low sensitivity of the model to variations in water depth. In contrast, a 10% variation and a 1°C variation of temperature greatly influenced biomass calculation with a maximum variation reaching more than 200% for shading and 70% for temperature compared to the biomass simulated with the initial value. Finally, a variation of 0.2m/s for current velocity implied a variation from 0-30% at maximum.

Impact of variation of the physiological parameters on biomass production

Sensitivity analysis showed either positive or negative impacts of variation of the physiological parameters on plant biomass, and this impact varied in function of time (Fig. 5). Key parameters that affected at most the model behaviour comprised Pm, θp, θr and Sm, which may entail a maximum

variation of 5-10% in biomass results, whatever the site considered. For site A, c3 and Rm induced a relative increase in biomass of 2% at maximum. For site E, c1 entailed up to 4% of increase in total biomass. In contrast, some constants such as c_4, c_{11} and v_{min} contribute to less than 1% variation of the biomass in all sites. Some constants corresponded to variable importance depending on the site. For instance, a 2% increase of v_{ref} entailed a 1% increase of the biomass for site D whereas less than 0.002% was found for site C. A general trend was that the model is less sensitive when simulations give low biomass production, such as for site C compared to the productive site B. Sensitivities of the model with respect to c_{11}, v_{ref} and v_{min} followed a stochastic evolution, being higher during storm events.

Simulating plastic behaviour of R. peltatus

Benefits of plastic adjustments for adapting to seasonal changes in water temperature differed depending on the site and hence on the environmental conditions (Fig. 6). For instance, the highest biomass variation reached up to 81% between plastic and non plastic individuals for population from site E with an increase of 57.9% of the maximum biomass attained. Further, a strong phenological change was detected with a maximum biomass reached 36 days earlier for plastic plants than for non plastic plants. Nevertheless, smallest variations were found for populations from site A: a maximum increase in biomass of 33% was found with a 27.5% difference for peak biomass. However, only a few days of delay in plant phenology was noticed for non plastic plants. Finally, for site C, the highest variation reached 46%, whereas only 30.6% of increase was found between the two maximums of biomass. The peak biomass was reached 15 days earlier for plastic plants. For all three sites, biomass at the end of the period of simulation was higher for plastic than for non plastic individuals.

Plastic adjustments in response to stresses in resources lead to contrasting benefits. In response to light stress, the maximum increase in biomass production was 15% and occurred at the end of the season (Fig. 7a). The maximum of biomass was reached on day 67 for plastic and non plastic plants and differed by 8.5%. However, with respect to nutrient stress, plastic adjustment resulted in more than 75% of maximum

increase in biomass at the end of the season (Fig. 7b). Peak biomass was 31% greater and was reached five days later for plastic plants compared to non plastic plants.

General discussion

Synthesis and comparison of modelling approaches

This work enabled us to synthesise a modelling approach for freshwater macrophytes and test some of the simplifications of the dependence of the main physiological process on environmental parameters. Compared to the data available on the biomass production of some sites, it was quite easy to select a few models that seemed pertinent in simulating *R. peltatus* growth. However, the validation process was not done, and we are not yet able to underline the best model that would most equate to natural situations. Nevertheless, this work underlined the importance of modelling plant growth for populations developing in ecologically different sites. Indeed, the most useful models are the ones that not only fit to field observations in a particular site but also adequately represent the relative differences among sites. When this condition is not fulfilled, the envelope of applicability of such models is strictly limited.

Among the modelled physiological processes of plant loss and gain of carbon, photosynthesis and senescence are two key processes. Washout contributed less than previously thought in biomass determination. This may be explained by the lack of information on this biological process, and therefore by the difficulty describing a corresponding appropriate mathematical relationship and calibrating it efficiently. Plant washout is very difficult to study through experimental work. Only a few studies report experimental evaluation of plant fragmentation by current velocity and flooding (Wright and MacDonnell, 1986; Dufayt, 2000), and results obtained seem to be reliable only in a narrow range of environmental conditions. More effort should be directed to the acquisition of data about this process. When modelling biomass production of a homogeneous population, individual characters of plants are important to take into account (Best and Boyd, 2001). This is especially true while simulating plant architecture, as shown through the present work. Such variability may be explained by the strong influence of plant architecture

on light interception and hence on photosynthetic activity. A correct estimation of biomass density may consist of taking into account only biomass in the canopy, which in most cases led to less than 5% error of estimate. Care must be taken, nevertheless, in highly productive sites where a better estimate of biomass distribution should be done.

Impact of environmental parameters on plant biomass production

One of the major results found in the present study is the hierarchical model sensitivity to variations in environmental parameters. It shows that if a precise and regular survey is needed for determining light availability and temperature, less effort may be required for the measurements of water depth, current velocity and nutrients in most sites. In site A, the lowest sensitivity of biomass production to temperature variation may be explained by the occurrence of other strong limiting factors such as nutrient and light limitation. In such cases, a higher precision for the measurement of nutrient availability is required. In order to complete these measurements, frequency and approximation error should be tested for the two determinant parameters, light availability and temperature, so as to perform the validation process. It is likely that a short time step for these measurements such as a daily survey would be necessary.

The dependence of plant growth on environmental parameters may further be complicated, especially with respect to CO_2 and O_2, both limiting factors that were not taken into account in the present model. CO_2 is the preferred form of carbon for photosynthesis in aquatic plants. However its concentration is generally low especially when the pH of water is above 6.5 (Sand-Jensen, 1983). Madsen and Maberly (1991) demonstrated that photosynthetic rates of *R. peltatus* in a stream could be strongly limited by inorganic carbon. Another example of gas limitation is the influence of water O_2 concentration on plant respiration. For instance, Dawson et al. (1981) observed that respiration in *Ranunculus calcareus* increased linearly with dissolved oxygen over the range 5-15mg/l. However, few models have attempted to take this parameter into account and the mathematical formulation for this relationship is hence lacking. A refinement in the modelling process would concern the dependence of plant growth on nutrients. In the

present study, only the water concentration of phosphorus was taken into account. However in some cases, *R. peltatus* growth is highly sensitive to shortages in ammonium (Maberly, Pers. Com.). The sediment compartment may also comprise a significant source of nutrients for plant uptake and the phosphorus and ammonium concentration in the interstitial water of sediments as well as the nutrient exchange between water and sediment should be taken into account.

Using modelling to understand physiological plasticity in freshwater plants

As far as we know using modelling to study plant physiological plasticity in aquatic systems has not been attempted until the present study. Our results show that small variations in some physiological parameters resulted in strong modification in biomass results. It is most interesting to compare these results with physiological plasticity highlighted experimentally in freshwater plants. The adaptation shown experimentally equates to slight variations of physiological parameters highlighted by the model as determining plant biomass. When simulating, plastic adjustments to seasonal fluctuation of water temperature leads to a compression of the life-cycle and enables plants to achieve a better growth and to reproduce within the growing period. With respect to stress, physiological plasticity may benefit plant adaptation to low nutrient availability more so than to low irradiance. However, careful attention should be drawn to these first results as experimental work on physiological acclimation is quite recent and has been studied only on a few macrophyte species (Pilon and Santamaria, 2001, 2002). The transposition of these data to the simulation of plasticity in *R. peltatus* may hence not be perfectly adequate. Much work must be done to collect physiological data of species in a wide range of environmental conditions to be able to study such plasticity. Besides, since many aquatic plants show a high degree of morphological plasticity, strong photomorphogenic effects may reduce the need for acclimative changes in physiological processes such as photosynthesis. The modelling approach we used may be completed by taking into account morphological plasticity. A similar project was initiated in some understorey plant species by Pearcy and Yang (1996). It consisted of modeling trade-offs existing between resources allocated to

nutrient uptake *vs.* light harvesting. Plant architecture was precisely modeled, and the modeling included morphological and physiological adaptation with their associated calculated costs and benefits. Finally, intraspecific plasticity, for instance the distinction of sun leaves (floating leaves) from shade leaves (submerged leaves), that displays different shade tolerance (Spence and Chrystal, 1970) may also be simulated in a more complex model.

Conclusion and perspectives

Modeling may have very interesting implications in the understanding of complex mechanisms of plasticity. It can highlight some possible feedback mechanisms that may not be apparent from laboratory studies. In addition, such an approach may identify areas where research is needed (Titus et al., 1975; Scheffer et al., 1993). In the present case, work is lacking on establishing physiological parameters for *R. peltatus* photosynthesis and washout. Modeling at the individual scale would bring useful information on the link between morphological, physiological plasticity and environmental conditions. Performance of such an approach is also essential before the validation process, as it determines the level of precision and frequency of environmental monitoring necessary for successful matching between field observations and model calculations. This could in addition provide the error risk associated with the model prediction.

After the validation of the model in different ecological situations and adapting it to individual modeling, the last step of this project will consist of using it to understand plasticity at the population level. Such simulation would require the coupling between individuals in order to take into account plant competition for light and nutrients, and plant interactions with the environment. This would result in a biologically more coherent, non-linear model.

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References

Asaeda, T., Karunaratne, S., 2000. Dynamic modeling of the growth of *Phragmites australia* : model description. Aquat. Bot. 67, 301-318.

Best, E.P.H., 1981. A preliminary model for growth of *Ceratophyllum demersum* L. Verh. Intern. Verein. Limnol. 21, 1484-1491.

Best, E.P.H., Boyd, W.A., 1996. A simulation model for growth of the submersed aquatic macrophyte hydrilla (*Hydrilla verticillata* L.F. Royle). Technical Report A-96-8, US Army Engineer Waterways Experiment Station, Vicksburg, MS.

Best, E.P.H., Boyd, W.A., 1999. A simulation model for growth of the submersed aquatic macrophyte Eurasian watermilfoil (*Myriophyllum spicatum* L.). Technical report E-99-3, US Army Engineer Research and Development Center, Vicksburg, MS.

Best, E.P.H., Boyd, W.A., 2001. A simulation model for growth of the submersed aquatic macrophyte american wildcelery (*Vallisneria americana* Michx.). Technical Report ERD/EL TR-01-5, US Army Enginneer Research And Development Center, Vicksburg, MS.

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. Hydrobiol. 444, 43-70.

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

Canale, R.P., Auer, M.T., 1982. Ecological studies and mathematical modelling of *Cladophora* in Lake Huron: V. Model development and calibration. J. Great Lakes Res. 8, 112-125.

Carr, G.M., Chambers, P.A., 1998. Macrophyte growth and sediment phosphorus and nitrogen in a Canadian prairie river. Freshwat. Biol. 39, 525-536.

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.

Chalker, B.E., 1980. Modelling light saturation curves for photosynthesis: An exponential function. J. Theor. Biol. 84, 205-215.

Collins, C.D., Wlosinski, J.H., 1985. A macrophyte submodel for aquatic ecosystems. Aquat. bot. 33,191-206.

Cook, C. D. K., 1966. A monographic study of *Ranunculus* subgenus *Batrachium* (D. C.) A. Gray. Mitt. Bot. Staat. Inst. Syst. Bot. der Universität München 6, 47-237.

Danloux-Dumesnils, M., 1985. Elements d'astronomie fondamentale. Ed. Albert Blanchart.

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

Dawson, F.H., 1976. The annual production of the aquatic macrophyte *Ranunculus penicillatus* var. *calcareus* (R.W. Butcher) C.D.K. Cook. Aquat. Bot. 2, 51-73.

Dawson, F. H., 1980. Flowering of *Ranunculus penicillatus* (Dum.) Bab. var. *calcareus* (R. W. Butcher) C. D. K. Cook in the Piddle river (Dorset, England). Aquat. Bot. 9, 145-157.

Dawson, F.H., Westlake, D.F., Williams, G.I., 1981. An automatic system to study the responses of respiration and photosynthesis by submerged macrophytes to environmental variables. Hydrobiol. 77, 277-285.

Dufayt, O., 2000. Aspects biologiques et modélisation du cours d'eau: Etude expérimentale et modélisation du développement de la Renoncule flottante (Ranunculus fluitans) dans la Semois. Unpublished PhD thesis, Fondation Universitaire Luxembourgeoise, Arlon.

Everbecg, E., Gosselain, V., Viroux, L., Descy, J.-P., 2000. Potamon : a dynamic model for predicting phytoplankton composition and biomass in lowland rivers. Wat. Res. 35, 901-912.

Frenette, J.J., Demers, S., Legendre, L., Dodson, J., 1993. Lack of agreement among models for estimating the photosynthetic parameters. Limnol. Oceanogr. 38, 679-687.

Garbey, C., 2000. Les proliférations de Renoncule peltée dans le Massif vosgien : répartition, biomasse et traits biologiques de l'espèce. Unpublished Master thesis, University of Metz, Metz.

Garbey, C., Thiébaut, G., Muller, S., 2004. Morphological plasticity of a spreading aquatic macrophyte, *Ranunculus peltatus*, in response to environment variables. Plant Ecol. 173, 125-137.

Garbey, C., Thiébaut, G., Muller, S., in press. Experimental study of *Ranunculus peltatus* plastic responses to four environmental parameters. Hydrobiol.

Hootsmans, M.J.M., 1994. A growth analysis model for *Potamogeton pectinatus* L. In Van Vierssen, W., Hootsmans, M., Vermaat, J.E. (Eds). Lake Veluwe. A macrophyte-dominated system under eutrophication stress. Kluwer Academix Publishers, The Netherlands. Dordrecht, pp. 250-286.

Hootsmans, M.J.M., Vermaat, J.E., 1994. Light-response curves of *Potamogeton pectinatus* L. as a function of plant age and irradiance level during growth. In Van Vierssen, W., Hootsmans, M.J.M., Vermaat, J.E. (Eds). Lake Veluwe, a Macrophyte-dominated System under Eutrophication Stress. Kluwer Academic Publishers, Dordrecht, pp. 62-117.

Jassby, A.D., Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21, 540-547.

Kirk, J. T. O., 1994. Light and photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge, U. K.

Lorenzen, B., Brix, H., Mendelssohn, I.A., McKee, K.L., Miao, S.L., 2001. Growth, biomass allocation and nutrient use efficiency in *Cladium jamaicense* and *Typha domingensis* as affected by phosphorus and oxygen availability. Aquat. bot. 70, 117-133.

Maberly, S.C., 1985. Photosynthesis by *Fontinalis antipyretica* I. Interaction between photon irradiance, concentration of carbon dioxide and temperature. New phytol. 100, 127-140.

Madsen, T.V., Maberly, S.C., 1991. Diurnal variation in light and carbon limitation of photosynthesis by two species of submerged freshwater macrophyte with a differential ability to use bicarbonate. Freshwat. Biol. 26, 175-187.

MacBride, G.B., 1992. Simple calculation of daily photosynthesis by means of five photosynthesis-light equations. Limnol. Oceanogr. 37, 1796-1808.

MacCree, K.J., 1970. An equation for the respiration of white clover plants grown under controlled conditions. In Stelik, I. (Ed.). Prediction and measurement of photosynthetic productivity. Pudoc, Wageningen, pp. 221-229.

Murphy, K.J., Hootsmans, M.J.M., 2002. Predictive modelling of aquatic community attributes: biomass, biodiversity, biointegrity and biomonitoring. Acta Limnol. Bras. 14, 43-60.

Pearcy, R.W., Yang, W., 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. Oecologia 108, 1-12.

Pilon, J., Santamaria, L., 2001. Seasonal acclimation in the photosynthetic and respiratory temperature responses of three submerged freshwater macrophyte species. New phytol. 151, 659-670.

Pilon, J., Santamaria, L., 2002. Clonal variation in morphological and physiological responses to irradiance and photoperiod for the aquatic angiosperm *Potamogeton pectinatus*. J. Ecol. 90, 859-870.

Raghothama, K.G., 1999. Phosphate acquisition. Ann. Rev. Plant Physiol. Plant Mol. Biol. 50, 665-693.

Sand-Jensen, K., 1983. Photosynthetic carbon sources of stream macrophytes. J. Exp. Bot. 34, 198-210.

Santamaria, L., Van Vierssen, W., 1997. Photosynthetic temperature responses of fresh- and brackish-water macrophytes : a review. Aquat. bot., 58, 135-150.

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

Spence, D.H.N., Chrystal, J., 1970. Photosynthesis and zonation of freshwater macrophytes. I. Depth distribution and shade tolerance. New phytol. 69, 205-215.

Thornley, J.H.M., Johnson, I.R., 1990. Temperature effects on plant and crop processes. Plant and crop modelling, A mathematical approach to plant and crop physiology. Oxford: Oxford University Press.

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

Van, T.K., Wheeler, G.S., Center, T.D., 1999. Competition between *Hydrilla verticillata* and *Vallisneria americana* as influenced by soil fertility. Aquat. bot. 62, 225-233.

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

Water Agency, 1999. Etude et modélisation du phytobentos dans les différents types de rivières du bassin Rhin-Meuse. 73p.

Westlake, D. F., 1973. Aquatic macrophytes in rivers. A review. Pol. Arch. Hydrobiol. 20, 31-40.

Wrigth, R.M., McDonnell, A.J., 1986. Macrophyte growth in shallow streams : biomass model. J. Env. Eng. 112, 967-982.

Zimmerman, R.C., Cabello-Pasini, A., Alberte, R.S., 1994. Modelling daily production of aquatic macrophytes from irradiance measurements: a comparative analysis. Mar. Ecol. Progress Series 114, 185-196.

Figure captions

Figure 1. – Description of *R. peltatus* architecture and biomass splitting between the canopy (S) and the rest of the water column (H-S).

Figure 2. – Biomass production (photosynthesis) and loss (respiration, washout and senescence) in function of time for sites A, C and E.

Figure 3. – Biomass produced using three different ways of formulating plant architecture. The simulations were made for sites A, C and E.

Figure 4. – Impact of variations of 1°C in temperature, of 10cms in water depth, of 10% in shading percentage, of 10µg/l in nutrient concentration and of 0.2m/s in current velocity on biomass production for sites A, C and E.

Figure 5. – Temporal relative sensitivity of the model to a 2% variation in physiological parameters for sites A, C and E. See Tab. 2 for constant legend.

Figure 6. – Simulation of the benefits of plasticity for populations of *R. peltatus* in response to seasonal change of water temperature in sites A, C and E.

Figure 7. – Simulation of the benefits of plasticity for populations of *R. peltatus* in response to stresses in (a) light availability; (b) nutrient availability – in site A.

Figure 1

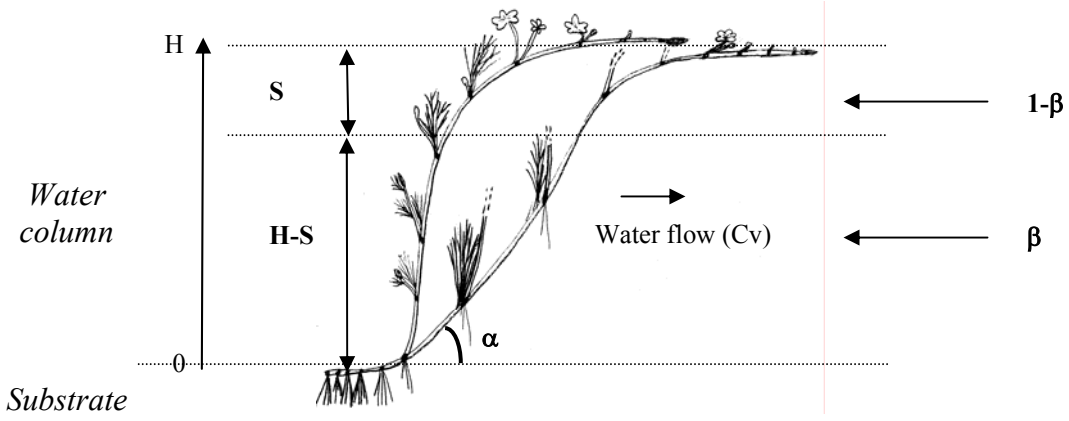
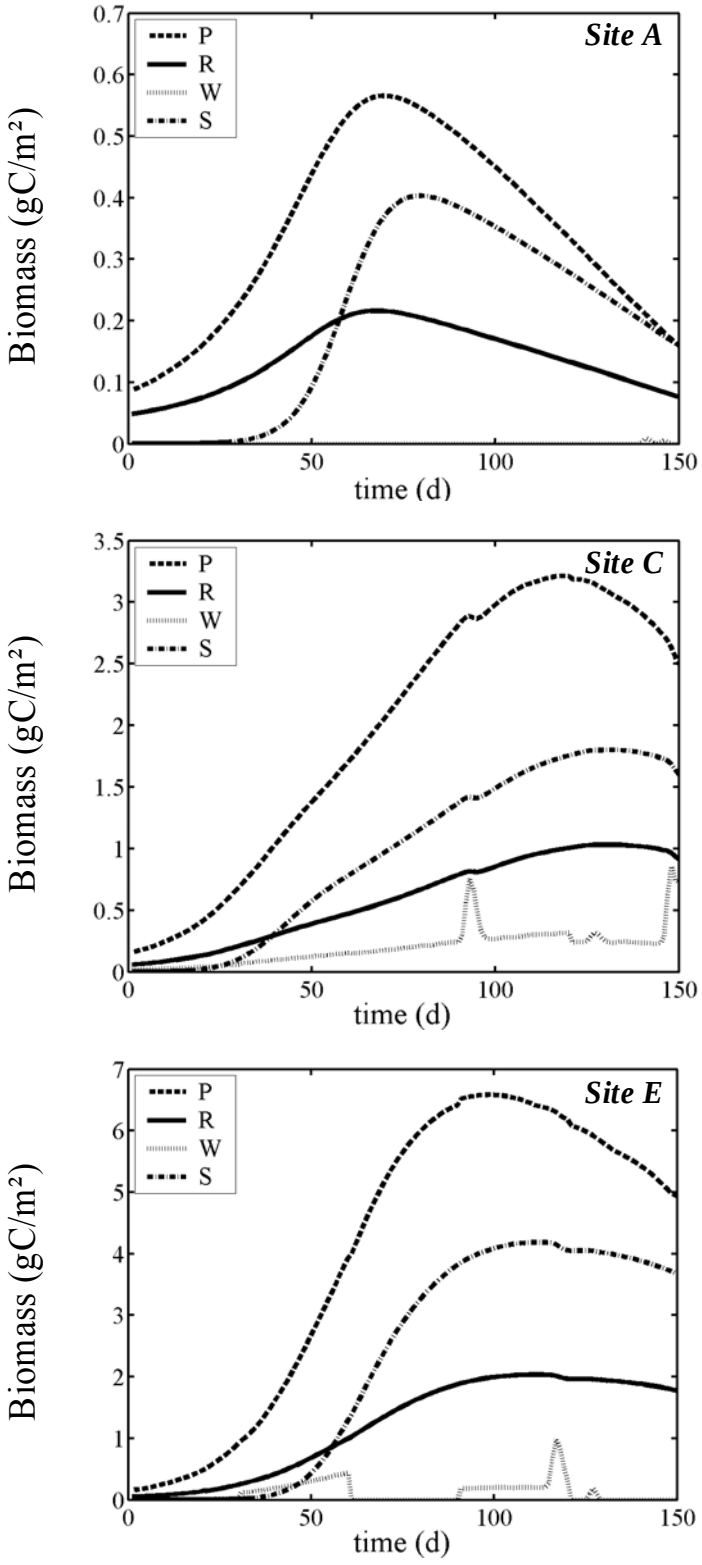


Figure 2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R
W
S
Biomass (gC/m²)
time (d)
Site C
P
R
W
S
Biomass (gC/m²)
time (d)
Site E
P
R
W
S
Biomass (gC/m²)
time (d)

Figure 3.

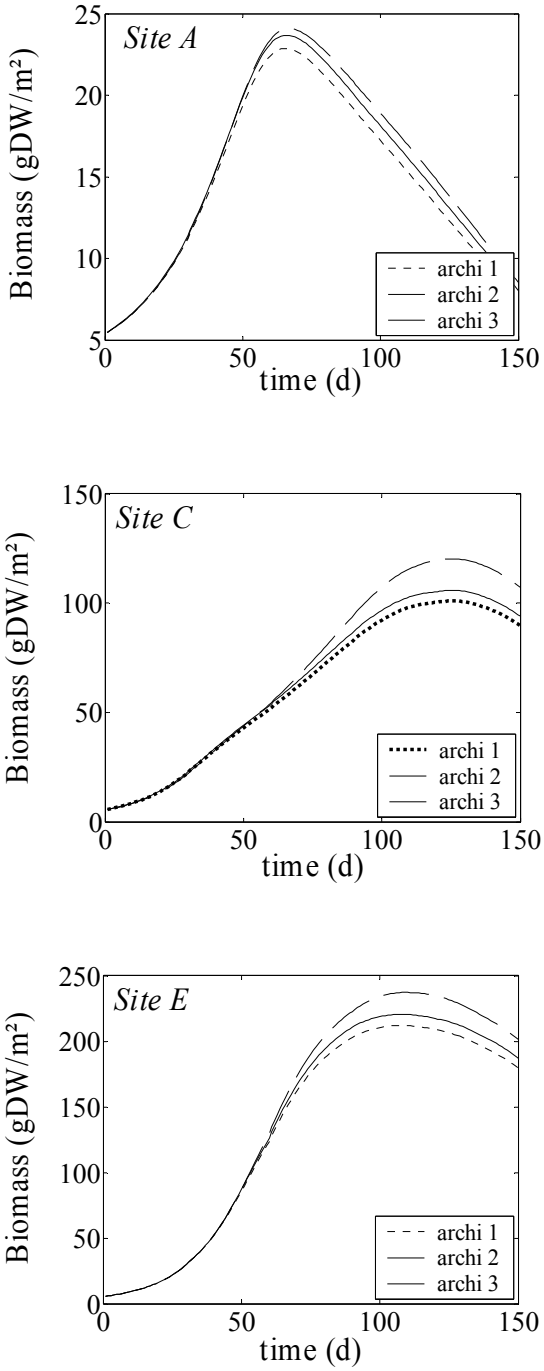

Site A
Biomass (gDW/m²)
time (d)
archi 1
archi 2
archi 3
Site C
Biomass (gDW/m²)
time (d)
archi 1
archi 2
archi 3
Site E
Biomass (gDW/m²)
time (d)
archi 1
archi 2
archi 3

Figure 4

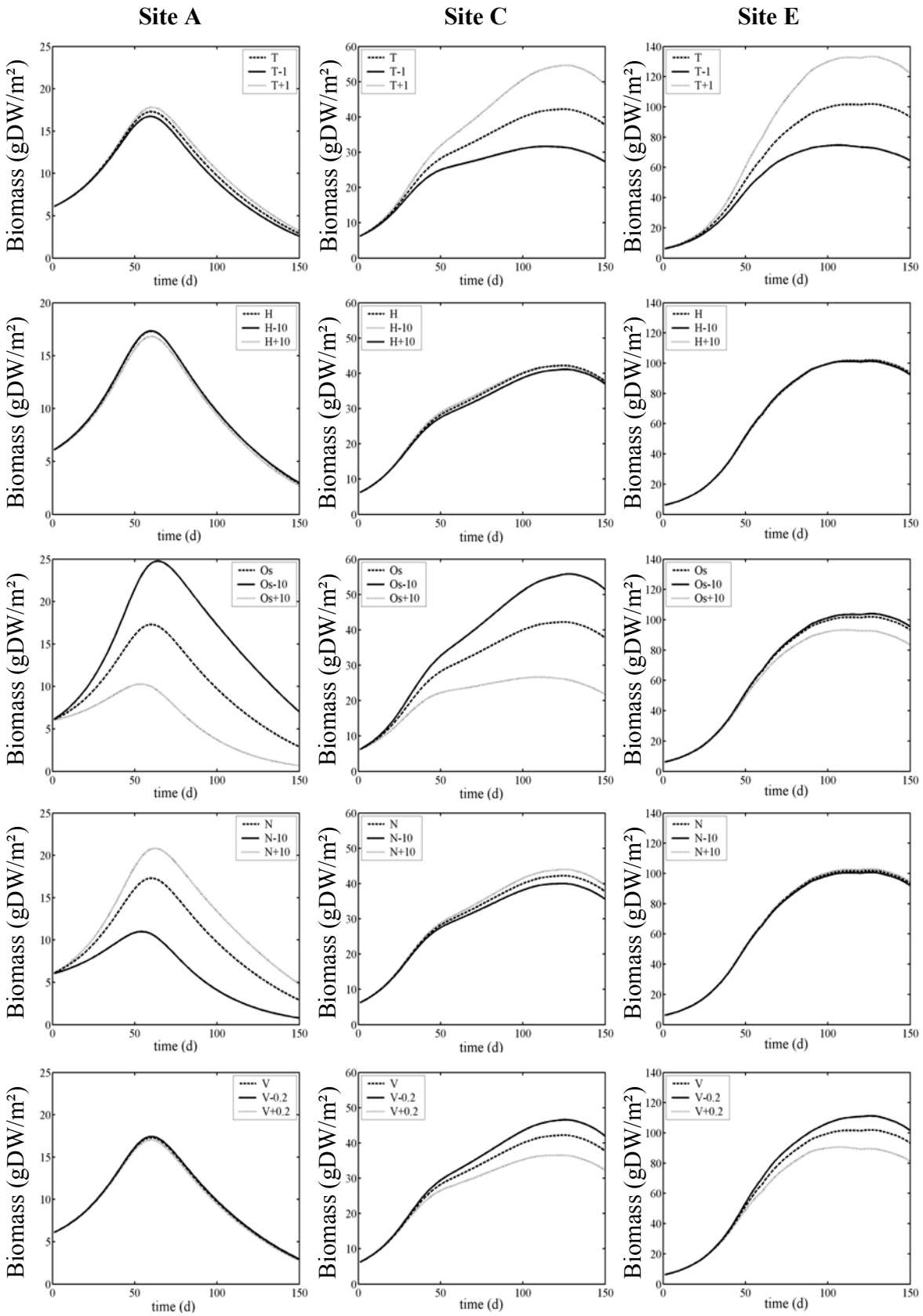
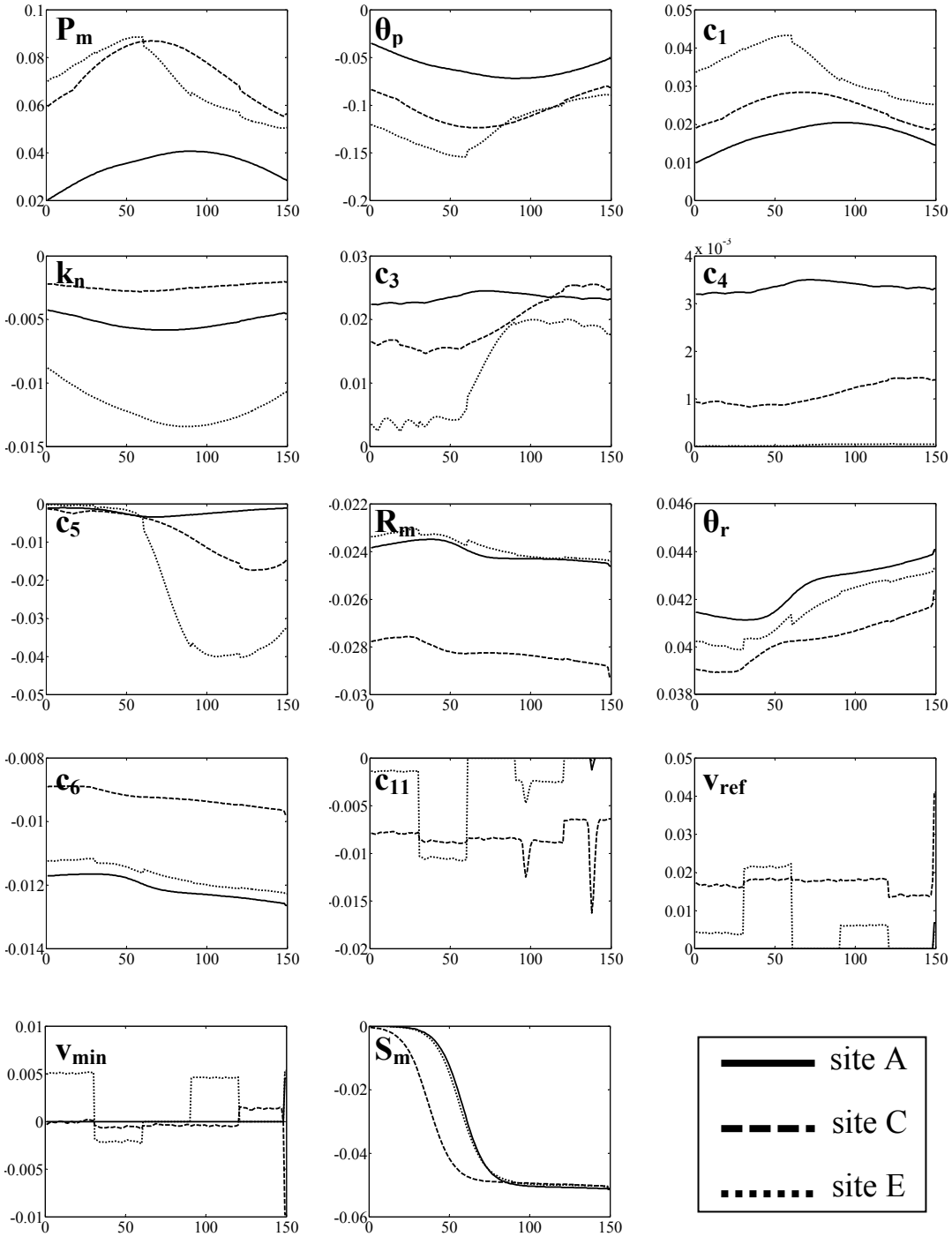

Site A
Site C
Site E
Biomass (gDW/m²)
time (d)
T
T-1
T+1
H
H-10
H+10
Os
Os-10
Os+10
N
N-10
N+10
V
V-0.2
V+0.2

Figure 5


P_m
θ_p
c_1
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c_3
c_4
x 10^-5
c_5
R_m
θ_r
c_6
c_{11}
v_{ref}
v_{min}
S_m
site A
site C
site E

Figure 6

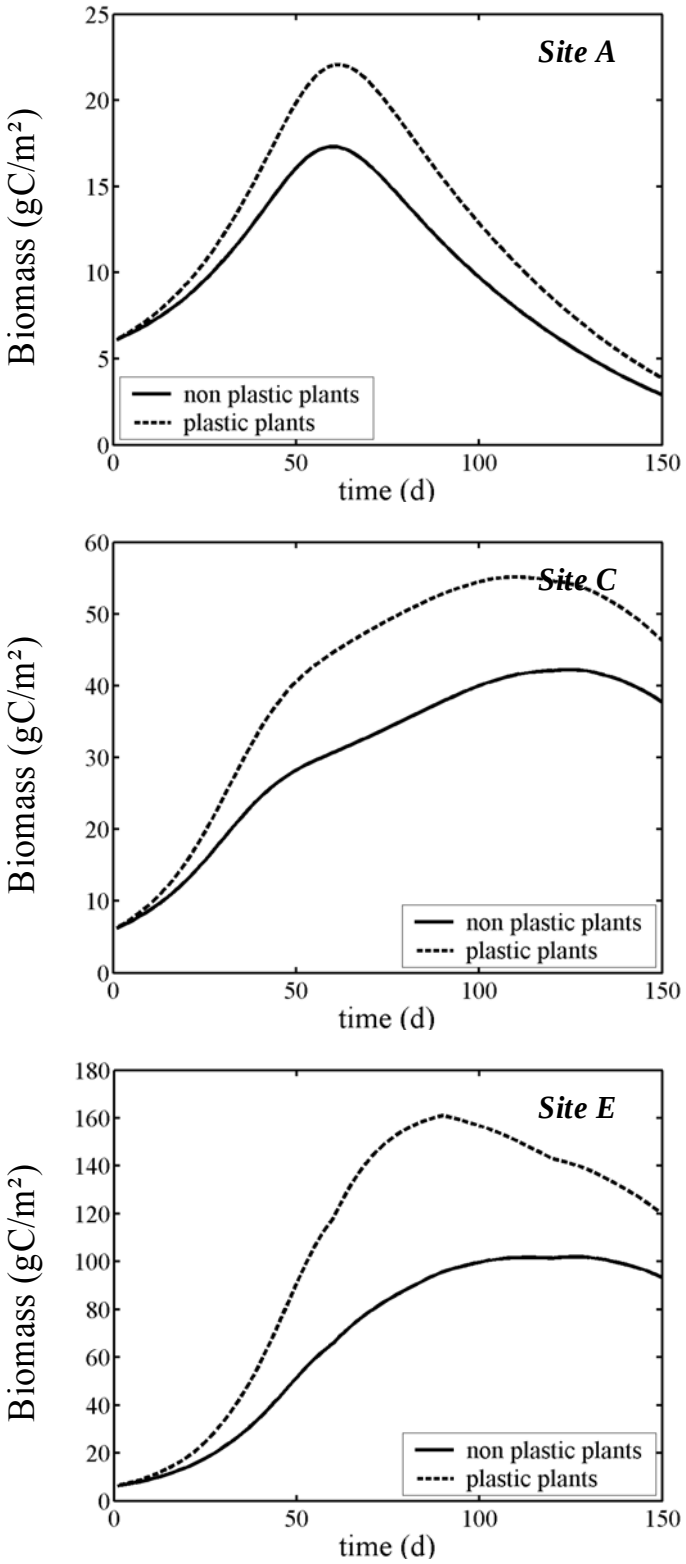
Site A
Biomass (gC/m²)
time (d)
non plastic plants
plastic plants
Site C
Biomass (gC/m²)
time (d)
non plastic plants
plastic plants
Site E
Biomass (gC/m²)
time (d)
non plastic plants
plastic plants

Figure 7

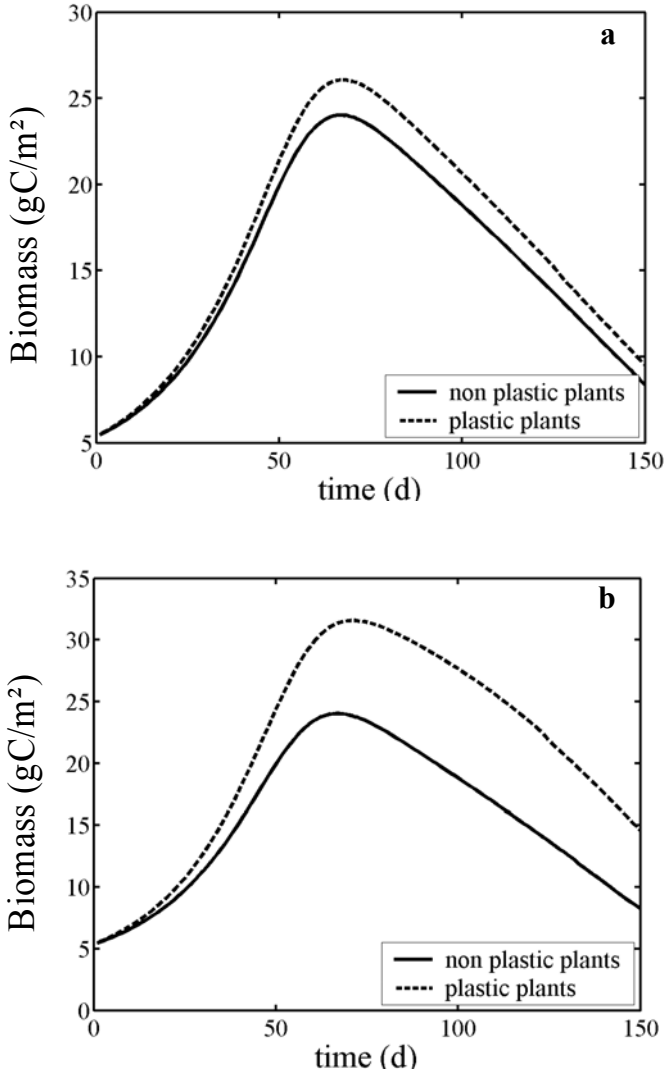
a
b
Biomass (gC/m²)
time (d)
non plastic plants
plastic plants
0
5
10
15
20
25
30
35
50
100
150

Table 1. – Synthesis of the different mathematical formulation for photosynthesis, respiration, washout, senescence and plant architecture

Mathematical formulation	Number referenced in text
Photosynthesis	
$P = B_v(t) \int_0^{24} \rho(to,t,\tau)\, dto = \int_0^{24} Pmf(\theta)\; g(N)\; k(I)\; dto$	1
$f(\theta) = \exp\left[-\left(\frac{(\theta(t) - \theta p)}{c_1}\right)^2\right]$	1.1.1
$f(\theta) = \; c_2^{\,[\theta(t) - \theta p]}$	1.1.2
$g(N) = \left(\frac{N}{k_N + N}\right)$	1.2.
$k(I) = \int_0^H b(z)\, \tanh\,(c_3\; I(to,t)\; dz$	1.3.1
$k(I) = \int_0^H b(z)\, (1 - \exp(-c_3\; I(to,t)))\; dz$	1.3.2
$k(I) = \int_0^H b(z)\, \frac{I(to,t)}{k_i + I(to,t)}\; dz$	1.3.3
$I(to,t) = Io\;(to,t)\left[1 - \frac{Os}{100}\,(1 - c_4)\right] x\, \left[\exp\left(-\left(Ot + c_5\; b(z)\right) z\right)\right]$	1.4
Respiration	
$R = l(\theta)\; m(P,B)$	2
$l(\theta) = \exp\left[-\left(\frac{(\theta(t) - \theta r)}{c_6}\right)^2\right]$	2.1.1
$l(\theta) = \; c_7^{\,[\theta(t) - \theta r]}$	2.1.2
$m(P,B) = Rm\; B$	2.2.1
$m(P,B) = Rm\; B + Rp\; P$	2.2.2
Washout	
$W = \; w(v(\tau,t))\; B(t)$	3
$w(v) = (\; c_8 + c_9\; v^2)\; \times c_{10} \times B^2$	3.1.1
For $v < v_{\min}$, $w(v,t) = 0$ and for $v \geq v_{\min}$, $w(v) = c_{11} \times \frac{(v - v_{ref})}{(v_{ref} - v_{\min})}$	3.1.2
$v(\tau,t) = v_o(t)\,(1 + v_1(t))$	3.2

$$v_1 = 1 + c_{12}\left(w_2 - \frac{1}{2}\right) + F\left[c_{12}\ x\ \left[p(t \in (1\Lambda\ 30)) < w_3(\tau)\ \right] x\ w_4\right]$$

Senescence

$$S = s(P,B) = a_o(t)\ B = \ Sm\ \frac{\left(1 + \tanh\left(\frac{dt_f\left(t - t^*\right)}{T}\right)\right)}{\left(1 + \tanh\left(\frac{dt_f\left(T - t^*\right)}{T}\right)\right)} \qquad 4$$

Plant individual architecture

$$b(z) = \frac{1}{H}\ B \qquad 5.1$$

$$b(z) = \frac{1}{0.1}\ B \qquad 5.2$$

$b(z) = \dfrac{\beta}{\left(H - S\right)}\ B$ into the zone below the canopy (z $\in$[S;H]) 5.3

$b(z) = \dfrac{\left(1 - \beta\right)}{S}\ B$ in the canopy (z $\in$[0;S])

with $\alpha = \dfrac{\pi}{2}\left[1 - \tanh\left(C_o v(\tau)\right)\right]$ and $\beta = \min\left(\dfrac{\left(H - S\right)}{\sin\left(\alpha\right) L}, 1\right)$

Table 2. – Physiological parameters entering the models

Physiological parameters	Symbol	Ref. formula	Unit	Selected value	References
Maximum photosynthesis rate	P_m	1.	h^{-1}	0.011	[11]; [3]; [9]
Optimal temperature for photosynthesis	θp	1.1.1 & 1.1.2	°C	19.7	[3]
Temperature sensibility for photosynthesis	c_1	1.1.1	°C	16	[11]; [3]
Multiplying coef. for temperature formulation in photosynthesis	c_2	1.1.2		1.2	[9]
Half-phosphorus saturation constant	k_N	1.2	µg/l	4.7	[11]; [1]; [2] [3]; [4]; [6]
Light use efficiency slope from the function P/I	c_3	1.3.1 & 1.3.2	$h^{-1}/\mu E.m^{-2}s^{-1}$	7.8×10^{-6}	[6]
Half- light saturation constant	k_i	1.3.3	$\mu E.m^{-2}s^{-1}$	100	[10]
Above-ground vegetation extinction coefficient	c_4	1.4		0.1	[6]
R. peltatus specific light extinction coefficient	c_5	1.4	m^2/gC	0.04	[11]; [1]; [2] [6]; [12]
Maximum respiration rate	R_m	2.2.1	d^{-1}	0.04	[11]; [5]
Optimal respiration temperature	θr	2.1.1 & 2.1.2	°C	19.7	[11]; [6]; [8]
Temperature sensibility for respiration	c_6	2.1.1	°C	16	[6]
Multiplying coef. for temperature formulation in respiration	c_7	2.1.2		1.08	[11]; [12]
c_8	c_8	3.1.1		0.685	[6]
c_9	c_9	3.1.1	$m^2.s^{-2}$	0.0015	[6]
c_{10}	c_{10}	3.1.1	d^{-1}	0.002	[6]
Reference current velocity (data set 1)	v_{ref}	3.1.2	m/s	0.31	[6]
Minimum current velocity beyond there is no washout (data set 1)	v_{min}	3.1.2	m/s	0.1	[6]
Washout rate corresponding to the reference current velocity (data set 1)	c_{11}	3.1.2	d^{-1}	0.023	[6]
Reference current velocity (data set 2)	v_{ref}	3.1.2	m/s	1.2	[11]

Minimum current velocity beyond there is no washout (data set 2)	v_{min}	3.1.2	m/s	0.5	[11]
Washout rate corresponding to the reference current velocity (data set 2)	c_{11}	3.1.2	d^{-1}	0.01	[11]
Maximum senescence rate	S_m	4	d^{-1}	0.0005	[1]; [2]; [3]; [4]; [7]; [11]

References quoted: [1] Best and Boyd, 1996 ; [2] Best & Boyd, 1999 ; [3] Best and Boyd, 2001 ; [4] Collins and Wlosinski, 1985 ; [5] Dawson et al., 1981; [6] Dufayt, 2000 ; [7] Hootsmans and Vermaat, 1994 ; [8] Sand-Jensen and Madsen, 1991; [9] Van der Bijl et al., 1989 ; [10] Van Dijk and Janse, 1993 ; [11] Water agency, 1999 ; [12] Wright and McDonnell, 1986.

Table 3. - Synthesis of the alternatives described and tested for modelling *R. peltatus* growth.

	Number of possibilities described	**Number of possibilities tested**
Temperature (*)	2	2
Photosynthesis		
- Nutrient	1	1
- Light	4	4
- Plant architecture	3	3
Respiration	2	1
Washout	2	2
Senescence	1	1
Total of models	**96**	**48**

(*): implemented in photosynthesis and respiration functions.

Table 4. – Description of the study sites.

	Site A	**Site B**	**Site C**	**Site D**	**Site E**
Physical parameters					
Width (m)	2.1	2.7	5	18.2	54
Mean water depth (m)	0.25	0.2	0.32	0.45	0.5
Shading by the river bank (%)	62.5	62.5	37.5	2.5	2.5
Mean current velocity (m/s)	0.26	0.32	0.85	0.58	0.48
Minimum temperature (°C)	9	9	11	10	9
Maximum temperature (°C)	15	15	19	16	15
Chemical parameters					
pH	5.8	6.4	7.1	6.9	6.8
$N\text{-}NH_4^+$ (µg/l)	26	40	101	43	51
$P\text{-}PO_4^{3-}$ (µg/l)	18	11	79	26	152
Conductivity ($\mu S.cm^{-1}$)	50	51	28	74	77
ANC (µeq/l)	96	150	523	324	373
Biological parameters					
Date of flowering initiation (*)	58	58	37	47	56
R. peltatus cover percentage in June (%)	5	10	30	50	50

(*): the date of initiation of flowering was calculated as described in section “Global framework”.

Table 5 – Maximum biomass produced (gDW/m²) in function of the model and the site.

	T°C	Light	Washout	A	B	C	D	E
Model 1	1 (*)	1	1	26	46	61	78	140
Model 2	1	2	1	17	28	50	71	127
Model 3	1	3	1	95	158	77	88	168
Model 4	2	1	1	18	30	33	27	63
Model 5	2	2	1	14	21	24	26	58
Model 6	2	3	1	31	65	54	29	72
Model 7	1	1	2	6	10	5	5	10
Model 8	1	2	2	5	6	5	5	9
Model 9	1	3	2	16	42	5	5	11
Model 10	2	1	2	5	7	5	5	6
Model 11	2	2	2	5	5	5	5	6
Model 12	2	3	2	7	11	5	5	6
Model 13	**1**	**1**	**3**	**24**	**45**	**92**	**110**	**223**
Model 14	1	2	3	15	25	63	104	197
Model 15	1	3	3	140	394	449	223	564
Model 16	2	1	3	18	30	17	21	46
Model 17	2	2	3	14	21	15	22	47
Model 18	2	3	3	31	66	22	23	50

(*): For temperature, formula 1 corresponded to the formula noted 1.1.1 and 2.1.1 for respiration; for light, formula 1 corresponded to the formula noted 1.3.1; formula 2 to 1.3.2; formula 3 to 1.3.3; for washout, formula 1 corresponded to the formula noted 3.1.1, formula 2 to the formula 3.1.2 calibrated with data from Dufayt (2000), formula 3 to formula 3.1.2 calibrated with data from the Water Agency (1999). A, B, C, D, E: the five study sites. The selected model is highlighted in bold.