

Applications of organ-specific growth models; modelling of resource translocation and the role of emergent aquatic plants in element cycles

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Abstract

This paper presents and reviews the conceptual structure of several recently developed organ-specific growth models and discusses their applications, with particular emphasis on material translocation between above- and belowground systems and the role of aquatic plants in element cycles. The efficiency of the element cycling process in wetlands is closely related to the proportional biomass allocation to above- and belowground organs. Therefore, the framework of most macrophyte productivity models is usually similar, with a mass-balance approach consisting of gross production, respiration and mortality losses, and the translocation between organs. The paper delineates how these growth models are linked with decomposition models to evaluate the annual cycle of elements. The model formulating procedure and the material budget and translocation processes of two perennial emergent species, *Typha angustifolia* and *Zizania latifolia*, and the coupling of the validated partitioned growth model with the modules for decomposition based on a modified decomposition coefficient, are further discussed. Furthermore, the effect of differing water depth on the rhizomatous sedge species *Eleocharis sphacelata* was studied based on its responsive adaptation by apportioning additional resources to shoots.

The analysis of latitudinal effects based on the modelling results for *Typha* showed that the annual gross production was larger in lower latitudes; however, the higher temperature therein resulted in larger respiration and mortality losses, which balanced the annual gross production in the equivalent stage. The annual translocation of resources to rhizomes was also larger in lower latitudes. Due to the very slow anaerobic decomposition in water, the amount of litter in the anaerobic substrate accumulated continuously at steady rates.

Management application to determine harvesting timing to remove biomass is discussed for *Phragmites australis* and *Typha angustifolia* based on the elucidations of modelling results on the translocation of resources for spring growth of new shoots and the subsequent exhaustion of rhizome stocks. The model results of *E. sphacelata* depicted that gross production of the plant stand increases with water depth until about 0.5 m, as water availability supports plant production and survival. Thereafter, the maximum production decreases rapidly with increasing water depth because the shoots are increasingly inundated by water, thus restricting the shoot surface area that is capable of photosynthetic production.

These applications highlight the efficiency of employing modelling as a tool to develop management schemes of aquatic macrophytes as well as to obtain insight into the mechanisms involved, as an alternative to cumbersome empirical approaches, such as field observations or pilot investigations.

Keywords: Decomposition; Gross production; Management applications; Material translocation; Partitioned growth models; Perennial macrophytes

Introduction

With their large biomass, aquatic perennial macrophytes have an important role in the cycles of carbon, nutrients, and hazardous chemicals in wetlands, as they uptake nutrients from the belowground surroundings and carbon from the aboveground environment and translocate these in between the organs inside the plant body. Aquatic macrophytes primarily produce organic matter in the aboveground tissues by absorbing carbon from the atmosphere or water, and simultaneously uptake nutrients or other elements from the water or the interstitial water in the sediment, then allocate the photosynthetic products into both above- and belowground systems to produce organs and to stock as resources. When the aboveground tissues die, they are accumulated on the sediment, and are then slowly re-mineralized in subsequent decomposition processes. The efficiency of element cycles, therefore, depends on the annual primary production rate in the aboveground organs and the rate of translocation between the above- and belowground systems. However, these processes are highly seasonal, extremely species-specific and dependent on the environmental conditions.

In order to develop management schemes of aquatic macrophytes as well as to obtain insight into the mechanisms involved, from a scientific point of view, mathematical models are often very useful as, once developed, they do not require much efforts in evaluating various viable options and alternatives, compared to empirical schemes, for example, field observations or pilot macrophyte experiments. The entire framework of these models depends on the type of the application; for analyzing the nutrient cycles in the eutrophicated water and algal blooming, the macrophyte model is incorporated with the modules of water dynamics and nutrients, and phytoplankton production (Asaeda et al., 2001; Best et al., 2001), while for understanding of hazardous element cycles in the subsurface, the modules of the groundwater below the lake bottom and the exchange across the bottom may become the important unit of the scheme, and for the efficient harvesting of nuisance weeds, re-growth under various environments and treatments are the main target (Asaeda et al., 2000). For gaining insight into the mechanism of adaptation to differing water depths by apportioning biomass to above- and belowground organs, sub-modules for light attenuation and water clarity are coupled with the main program structure (Asaeda et al., 2006). In spite of such a wide range of applications, however, the growth and decomposition processes of macrophytes are the main processes used to model the entire scheme.

Compared with submerged macrophytes, which have relatively smaller root systems, emergent macrophytes have a higher efficiency in the element cycle not only because of their higher productivity but also due to their distinctive resource translocation between the shoot and rhizome systems, which are particularly large. Their roots penetrate deeper into the sediment, thus they can pump up the elements from deeper ground. The greater ability of emergent macrophytes to achieve rhizosphere ventilation through stems may also contribute to a higher efficiency of element cycles.

Therefore, in the evaluation of element cycles in wetlands, particularly in the case

of emergent macrophytes, models incorporating above- and belowground systems are essential. This paper describes and reviews the basic structure of several recently developed emergent macrophyte models and their applications, with particular emphasis on the element cycles and material translocation between above- and belowground systems.

1. Development of the dynamic growth model

Macrophyte productivity models are usually similar in that they follow a mass-balance approach, such that a change in standing crop over time is a function of the rate of biomass production through gross photosynthesis and biomass losses due to respiration and mortality. However, most models differ according to the environmental factors modeled, which influence growth rates and/or the algorithms used to describe these relationships.

Macrophyte growth models are designed to quantify photosynthesis and respiration through a segmented column of water or macrophyte canopy to account for the vertical distribution of macrophyte biomass and the influence related to the underwater light penetration and concentrations of available nutrients and dissolved gasses.

Some examples of partitioned growth models of macrophytes and their applications are presented in Table 1. Submerged macrophyte models have been developed since the 1980s, probably because they often caused nuisance by blocking flow channels. However, although macrophytes were one of the key members of lake restoration, macrophyte models were not commonly used in lake or reservoir restoration compared with the widely used phytoplankton models.

Emergent macrophyte models are relatively less common in spite of the plants' higher efficiency in the element cycles in wetlands. This is likely because the macrophyte models were not considered as a tool to quantitatively study element cycles to date.

1.1. Structure of partitioned growth models

The net growth of macrophytes is defined as the algebraic summation of the processes of photosynthetic production (P_r), respiration (R_e), and mortality (D_e). However, if the budgets in some specific organs are focused, then the translocation to and from other organs (T_t) is also incorporated. Therefore,

$$\frac{dB}{dt} = P_r - R_e - D_e - T_t \quad (1)$$

The photosynthetic production, alternatively given by the integrated biomass from the top of the canopy or water transparency, is generally described as a function of light intensity ($L(I_i)$), nutrients ($H(N)$), temperature ($S(T)$), and age ($A(t)$), such that

$$P_r(i) = p_{\max} L(I_i) \cdot H_u(N) \cdot S_e(T) \cdot A(t) \quad (2)$$

where p_{\max} is the maximum photosynthetic rate and I_i is the light intensity at level i . Although the half-saturation constant is a function of temperature (Johnson et al., 1974), and thus not straightforward, the dependence on irradiance is widely described by the Michaelis-Menten equation in Eq. (3) (Ondok and Pokorny, 1987; Davis and McDonnell, 1997; Santamaria and Hootsman, 1997; Asaeda and Karunaratne, 2000), or by the hyperbolic tangent equation (Zimmerman et al., 1994) in Eq. (4).

$$L(I_i) = \frac{I_i}{K_{0.5} + I_i} \quad (3)$$

$$L(I_i) = I(I_i) \tanh(I_i / K) \quad (4)$$

The dependency on temperature is often expressed by Q_{10} concept assuming the power function of temperature; however, it is further discussed by Johnson et al. (1974) and Santamaria and van Vierssen (1997). They proposed the product of the Arrhenius reaction and the concentration of the active conformers of enzyme according to the following expression:

$$k = A \frac{1}{1 + \kappa} \exp(-E_s / RT) \quad (5)$$

where k is the reaction rate, A is an integration constant, E_s is the activation energy of the reaction (in J), R is the gas constant, T is the absolute temperature, and K is the equilibrium constant responsible for the enzyme conformational change.

Dark respiration loss is assumed to be proportional to the biomass as well as dependent on temperature (Eq. (6)); however, the total mortality loss depends on the environmental events or factors other than the regular mortality loss (Eq. (7)). Therefore,

$$R_e = R_m \theta^{T-T_0} \cdot B \quad (6)$$

$$D_e = D \cdot f(t) \cdot B \quad (7)$$

where R_m is the maximum respiration rate, θ is the Arrhenius constant, T_0 is the reference temperature, $f(t)$ is the mortality rate. These processes are schematically represented in Fig. 1a and b (Asaeda et al., 2002, 2005).

1.2. Material translocation

Element transport across the ground surface by plants depends mainly on resource translocation inside the plant. Above- and belowground material translocation is highly seasonal and dependent on environmental conditions. However, as the translocation rates are obtained by following extremely strenuous, time-consuming experimental and monitoring procedures, such as seasonal observation of the above- and belowground biomass as well as the dead biomass and the respiration loss, the available data are limited, especially for uncommon species. Alternatively, the observed seasonal variations in above- and belowground biomasses can be satisfactorily used to elaborate the underlying processes of net production and translocation of resources in between the plant organs.

Figure 2 shows the annual patterns of carbon budgets of *Typha angustifolia* and *Zizania latifolia* monoculture populations at Akigase Park (35°51'N, 139°39'E) and Hasuda (35°59'N, 139°39'E) in Saitama, near Tokyo. The overall carbon budgets are expressed in terms of the rate of processes of net production in the aboveground biomass and translocation of carbohydrates between the above- and belowground systems, where the downward translocation is defined as positive and belowground respiration is indicated as negative.

The initial shoot formation was based entirely on the upward translocation of rhizome materials; however, this source of resources was gradually replaced by products of photosynthesis during the latter's period. At the beginning of March, the upward translocation supported entirely the aboveground growth, but it declined constantly with time and completely ceased by the end of May or early June, for both species. The downward translocation constantly increased until early July in association with the increasing photosynthesis rate, followed by a slight decline until the end of August, and vigorously accelerates thereafter. *Zizania latifolia*, in particular, showed an extreme self-thinning of primal shoots from the end of May, despite a large number of shoots emerging in March and April, which also contributed to subsequent nutrient

release. The formation of secondary shoots was much less significant than primary shoots; therefore, from the middle of September, there was only a small cache of carbohydrates in the aboveground system and most of the products of photosynthesis were mobilized downwards. As such, the translocation rate is highly seasonal and species-specific, thus, normally, empirical efforts are required, though some sinusoidal relations are also proposed (Morris and Lajtha, 1986).

1.3. *Decomposition process*

The decomposition rate of litter in the air above the water surface is usually much lower than that of submerged litter (Polunin, 1984). In the water, although the decomposition rate is relatively higher, it is greatly dependent on type of tissues and their location. Initially, litter decomposes rapidly, quickly losing its weight by leaching for several days, and subsequently the decomposition slows down (Polunin, 1984). An experimental study on leaching of *Phragmites australis* leaves showed that 80% of the weight loss in the initial 20 days is attributable to leaching and the total loss due to leaching from leaves is about five times greater than that of stalks (Polunin, 1984). Taking these facts into consideration, the widely proposed decomposition coefficient $\mu_{j,x,y}$ is therefore modified (Asaeda et al., 2002), such that

$$\mu_{j,x,y} = L_{j-i} \theta_d^{T_j-10} \varphi(y) \frac{\exp(-(j-i-1)\lambda_x(y)) - \exp(-(j-i)\lambda_x(y))}{\exp(-(j-i-1)\lambda_x(y))} \quad (8)$$

where θ_d is the temperature effect on decomposition from the Arrhenius equation. Polunin's study (1984) implies that with leaf litter decomposition in water, θ_d is 1.07 for water temperature below 16°C (Q_{10} is 2) and is 1.02 for temperatures higher than 16°C (Q_{10} equals 1.1); the same values were used also for stalk litter. Here, i is the starting day of the decay, while j is the day being considered in the calculation; $\mu_{j,x,y}$ is the exponential decomposition rate of material x ($x=1$ or 2 for leaves or stalks, respectively), on the j^{th} day in the oxygen condition of y (aerobic/anaerobic); T is the daily average water temperature (°C). For simplicity, the constant value of 5 (per day) was used in L_{j-i} during the first 20 days ($j-i \leq 20$), and was fixed as 1 (per day) thereafter.

1.4. *The depth of root penetration*

The depth of penetration of roots into the sediment for the purpose of water and nutrient uptake is extremely site specific. In water-logged areas, the maximum penetrable depth can be approximately estimated by considering the ability of oxygen transport into the rhizome system (Vretare and Weisner, 2000), while Weisner and Strand (1996) further elaborate the methodology as it applies to *Phragmites australis*.

1.5. *Effect of water depth*

In emergent species, both above- and belowground biomasses consume resources by way of respiration; however, only the aboveground biomass is engaged in production by way of photosynthesis. In formulating a similar growth model for *Eleocharis sphacelata*, it was assumed that the water is opaque and no sunlight was able to penetrate into the submerged portion of the plant, thus, photosynthesis in the submerged portions was neglected. As the shoot diameter is relatively constant from the bottom of the shoot to the apical part, the shoot biomass, equivalent to the ratio of the aerial height to the total height, was assumed to engage in photosynthesis (Asaeda et al., 2006).

1.6. *Validation of the model*

As most of the parameters are determined empirically, validation of the model with several experimental datasets, under different environmental conditions, is of particular

importance. Results from sample simulations were compared with field data to validate results of two species; for *T. angustifolia*, data from 18 sites at latitudes from 30°N to 56°N were used (Garver, et al., 1988), while for *E. sphacelata* two data sets from Goulburn (34° 44' S and 149° 44' E) and Ourimbah ((33° 21' S and 151° 22' E) sites in Australia were used (Asaeda et al., 2006). The level of agreement between the calculated results and field data were compared by correlation coefficients (r), which showed that although simulated results were slightly different from the observations for some sites, in general, there was good agreement for all sites of the two species.

2. Applications of the model

2.1. Application to the latitudinal effects on the above- and belowground biomass

Material translocation is highly dependent on the above- and belowground biomass ratio, as a large belowground biomass is a result of significant translocation of photosynthetic products. However, empirical results indicate that the above- and belowground biomass ratio is generally determined by the climates of the habitat as the belowground system is an important medium for hibernation.

Figure 3 shows the variation of above- and belowground biomasses for *Typha* spp. over a period of six consecutive years depending on the initial rhizome biomass and assuming no flowering or nutrient limitations. Regardless of the initial rhizome biomass, the annual maximum above- and belowground biomasses converged to within 5% of equilibrium values in 3, 4 and 5 years for three test latitudes, respectively. These maximum values were 2920 g·m⁻² for aboveground (AGB) and 2680 g·m⁻² for belowground (BGB) at 30°, 2690 g·m⁻² for AGB and 3300 g·m⁻² for BGB at 40°, and 1910 g·m⁻² for AGB and 3020 g·m⁻² for BGB at 50°.

Aboveground biomass started to increase earlier at lower latitudes as described by an empirical latitude-starting time relationship, while simulation results indicated that the aboveground biomass reached its maximum value earlier, at higher latitudes. Dying-off of the aboveground biomass occurred only slightly earlier at higher latitudes, thus, the aboveground biomass existed for seven months at 30°, six months at 40°, and five months at 50°.

With a longer growing season, higher solar radiation, and higher temperatures, the annual gross production was larger in lower latitudes, resulting in 9960 g·m⁻² at 30°, 7360 g·m⁻² at 40°, and 3730 g·m⁻² at 50°. However, in lower latitudes, higher temperatures also led to larger respiration and mortality losses, which balanced the annual gross production in the equivalent stage. Therefore, the magnitude of the seasonal cycle of the whole macrophyte net production was larger in lower latitudes, yet the annual integration of the net production was always zero in the equilibrium stage, regardless of latitude.

The starting time of translocation was almost two months earlier in 30° than in 50°; however, the ending time was only one month later at 50° than at 30°. Therefore, the duration of downward translocation was one month longer at 30° than at 50°. With a larger net production and a longer period of downward translocation, the annual translocation of resources to rhizomes was larger in lower latitudes: 3340 g·m⁻², 2800 g·m⁻², and 1850 g·m⁻² at 30°, 40° and 50°, respectively. Concurrently, the amount of rhizomes increased from 950 to 2680 g·m⁻² at 30°, from 1460 to 3300 g·m⁻² at 40°, and from 1720 to 3020 g·m⁻² at 50° (Fig. 3). Therefore, respiration and mortality losses of rhizomes during the translocation period accounted for about 50% of the total translocated at 30°, declining to 30% at 50°. The resources stored in the rhizome system were consumed by early spring shoot formation, and respiration and mortality losses in

the belowground organs throughout the year. In the equilibrium stage, the annual translocation into rhizomes, whether positive or negative, balanced with the respiration and the mortality losses in the rhizome system.

2.2. Applications to element cycles in the growth and decomposition processes

The carbon and nutrient uptake during the growth of macrophytes and the subsequent release due to decomposition is one of the major processes of element cycles in wetlands. Emergent or floating leaved macrophytes take up nutrients completely from belowground, then release a portion of the material into the overlying water. However, the process is extremely seasonal and dependent on environmental conditions.

Figure 4 illustrates the results of the application of the model to the element cycles in the decomposition processes of *Phragmites australis* in Neusiedlersee, Austria. Figure 4(a, b) shows the biomass of standing dead stalks and litter decomposing aerobically and anaerobically. The dead standing biomass increased gradually in the first three years as new shoots were produced and dead ones collapsed rather slowly. Thus, the amount of litter decomposing in the aerobic layer increased during the first several years. Later, litter production was offset by decomposition and transferred to the anaerobic layer. If litter remained in the aerobic layer for longer, a greater duration was necessary to achieve steady state and the amount of litter in the aerobic layer became increasingly larger. Due to the very slow anaerobic decomposition rate, the amount of litter in the anaerobic substrate constantly accumulated. If litter remained longer in the aerobic layer, the accumulation of anaerobic substrate was delayed, reducing the amount transferred to the substrate. Figure 4(c, d) shows the nitrogen and phosphorous stocks of the litter in the anaerobic layer. The steady accumulation rates were about $8.52 \text{ g N m}^{-2}\cdot\text{y}^{-1}$ and $0.89 \text{ g P m}^{-2}\cdot\text{y}^{-1}$ if decomposition was aerobic for six months, and about $5.82 \text{ g N m}^{-2}\cdot\text{y}^{-1}$ and $0.64 \text{ g P m}^{-2}\cdot\text{y}^{-1}$ for 24 months.

The calculated rate of oxygen consumption during decomposition gradually increased in spring along with the rising temperatures, but with low oxygen concentration, it decreased to less than $1.0 \text{ g O}_2 \text{ m}^{-2}\cdot\text{d}^{-1}$ in November. Oxygen consumption remained low during winter due to the low water temperature. If litter remained longer in the aerobic layer, this led to higher oxygen consumption from April to September, but the difference was less in winter.

Figure 5(a, b) shows nitrogen and phosphorous release from decomposing litter and uptake by growing reed. Due to the initial accumulation of litter, its release of nutrients increased during the first few years. The release rates were high from April to September, with slight variations being caused by fluctuations in dissolved oxygen. Subsequently, the release of nitrogen and phosphorous declined because of low oxygen concentration and low temperatures during winter. With longer time spent in the aerobic layer, nutrient release increased: the release rates for 24 months of aerobic decomposition were almost twice as large as for six months. Nutrient uptake was independent of the decomposition process. Therefore, though in all cases annual uptake was more than four times higher than the release by decomposition, the difference was minimized by the longer period of litter being kept in the aerobic layer; the annual net uptake was $0.052 \text{ g N m}^{-2}\cdot\text{d}^{-1}$ and $0.006 \text{ g P m}^{-2}\cdot\text{d}^{-1}$ for 6 months of aerobic decomposition, and $0.045 \text{ g N m}^{-2}\cdot\text{d}^{-1}$ and $0.005 \text{ g P m}^{-2}\cdot\text{d}^{-1}$ for 24 months.

Table 2 shows the annual accumulation of organic sediment and the amount of nutrients trapped and stored in the anaerobic layer, based on the time during which the litter decomposed aerobically. Following the stabilization of the annual growth, 7% of the annual production was translocated to the belowground biomass, while the remaining 93% entered the decay process. Depending on the period of aerobic

decomposition, between 33% and 48% of the production decomposed, whereas the remaining two thirds to one half were stored in the anaerobic substrate.

The simulation showed that reed growth and litter production was substantially higher than decomposition under both, aerobic and anaerobic conditions. This resulted in a substantial accumulation of nutrients in the anaerobic layer.

Accumulation of organic sediment and an anaerobic substrate is typical for wetlands dominated by emergent macrophytes, such as *Phragmites*, *Typha*, and *Eleocharis* (Asaeda and Karunaratne, 2000; Asaeda et al., 2002, 2005; Rajapakse et al., 2006). The model simulation results (Asaeda et al., 2002) have shown that the shift from aerobic to anaerobic decomposition and the oxygen concentrations in the water-litter-sediment interface are important variables in determining the sediment and nutrient deposition rates and should receive more attention in the future. Knowledge concerning the potential of absorbing nutrients and the factors controlling this process is important when considering the efficiency of reed stands for treating wastewater and the effect on water quality of natural lakes. However, as vast amounts of nutrients are stored in the sediment, damage to the littoral vegetation and the oxidation of the sediment can release these nutrients, causing substantial eutrophication.

2.3. Application to determine harvesting timing to remove biomass

The rationale behind cutting plants, as a potential control mechanism, stems from the fact that it will retard the subsequent growth and development of the stand (Asaeda and Karunaratne, 2000) because reserves produced during the season are removed by cutting the aerial part of the plant, thus reducing its vigor (Marks et al., 1994). Based on the results of a cutting experiment, Granéli et al. (1992) delineated that the removal of shoot biomass of *Phragmites australis* in population management applications should be based on the available carbohydrate reserves in the rhizomatous organs, depending on whether the requirement is to suppress the growth of the population in the next season or to ensure healthy survival of the stands throughout. It has been noted that harvesting of the aboveground biomass in late summer after the rhizome energy reserves had already been replenished did not seriously affect the population's performance in the following season (Husak, 1978), while the harvest of shoot tissues when the rhizome reserves were lowest, in general towards the end of the heterotrophic growth period, was more effective in reducing and impeding growth (Karunaratne et al., 2004).

Moreover, strong decline of plant beds after several years of lush growth has been observed in many European countries for *Phragmites* (Van der Putten et al., 1997) and in Australia for *Eleocharis* (Rajapakse et al., 2006), and in some instances, these declines have been related to the high production and accumulation of nutrient-rich detritus (Čížková et al., 1996; Rajapakse et al., 2006). Mowing of plant beds has been proposed as a countermeasure (Ostendorp, 1995; Rajapakse et al., 2006), and the findings of model simulations can be employed in effectively identifying the optimal timing for shoot harvesting to minimize detrimental influence on the plant stands in subsequent seasons (Asaeda and Karunaratne, 2000; Asaeda et al., 2005; Asaeda et al., 2006). In addition, long-term removal of nutrients from aquatic ecosystems using plants can also be predicted by such models (Asaeda et al., 2000; Tanaka et al., 2004).

2.4. Application to investigate the effect of water depth on growth dynamics

As an application of the growth model formulated for *E. sphacelata* and subsequently calibrated using data from two shallow and deep water populations, respectively, the annual gross production, translocation, and respiration and mortality losses of the plant stand were calculated as a function of water depth (Fig. 6a). The gross production of the

plant stand ($\text{g}\cdot\text{m}^{-2}$) increased with water depth until about 0.5 m, as water availability supported plant production and survival. Thereafter, the maximum production decreased rapidly with increasing water depth because the shoots were increasingly inundated by water, thus restricting the plant area that is capable of photosynthetic production. This result corresponds with simplified assumptions of this model; the maximum biomass, hence the total biomass of the stand should increase with water depth up to a certain critical depth, and then decrease rapidly thereafter. The percentage of downward translocation is higher in order to support the high upward translocation at the start of the growing season in shallower depths, and then decreases with increasing water depth, leading to a lower belowground biomass in deep water, while the total respiration and mortality losses vary correspondingly. The model predicts that the above- to belowground biomass ratio increases with water depth (Fig. 6b), which corresponds to field observations reported previously (Sorrell et al., 2002).

An increase in shoot height and additional biomass allocations to shoot growth are required in deep water in order to maintain a similar above-water biomass for photosynthesis at all depths. This is due to the limiting effect of carbon dioxide availability on underwater photosynthesis in emergent plants. The limited carbon supply in relation to the overall plant size with increasing depth often leads to lower total growth and biomass in deeper water than in shallower water (Sorrell et al., 2002; Asaeda et al., 2006). It is assumed that the limited capability to aerate the deepwater rhizomes through gaseous exchange by shoots might also limit the growth of belowground organs (Sorrell et al., 2002).

3. Conclusive remarks

These applications highlight the efficiency of employing modelling as a tool to develop management schemes of aquatic macrophytes as well as to obtain insight into the mechanisms involved to serve as an alternative to cumbersome empirical approaches like field observations or pilot investigations.

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Tables & Figures

Tables

Table 1. Partitioned growth models of macrophytes and their purpose or applications

	Purpose or application	Species	Reference
Submerged macrophytes	Effect of eutrophication on abundance	<i>Potamogeton pectinatus</i>	Hootsman, 1994
	Responses to environmental and climatic changes	<i>Hydrilla verticillata</i>	Best and Boyd, 1996
	Nutrient cycle	<i>Potamogeton pectinatus</i>	Asaeda and Bon, 1997
	Biomass partitioning based on phenological stage	<i>Elodea canadensis</i> , <i>Potamogeton crispus</i>	Davis and McDonnel, 1997
	Responses to environmental and climatic changes	<i>Myriophyllum spicatum</i>	Best and Boyd, 1999
	Nutrient cycle and harvesting effects	<i>Potamogeton pectinatus</i>	Asaeda et al., 2000
	Responses to environmental changes	<i>Submerged macrophytes</i>	Best et al., 2001
	Responses to environmental changes	<i>Zostera marina</i>	Zharova et al., 2001
	Competition with phytoplankton	<i>Potamogeton pectinatus</i>	Asaeda et al., 2001
	Competition between macrophytes	<i>Chara aspera</i> , <i>Potamogeton pectinatus</i>	Nes et al., 2003
	Biomass, nitrogen quotas, epiphytes and model assessment	<i>Zostera noltii</i>	Plus et al., 2003
Emergent macrophytes	Growth modelling and model assessment	<i>Phragmites australis</i>	Asaeda and Karunaratne, 2000
	Competition between <i>Typha</i> spp.	<i>Typha</i> spp.	Tanaka et al., 2004
	Growth modelling and model assessment	<i>Phragmites australis</i>	Soetart et al., 2004

Table 2. Annual nutrient release and litter production of *Phragmites australis* as described by a growth and decomposition model (Asaeda et al., 2002)

Aerobic period (months)	Nitrogen release rate (g m ⁻² per year)	Phosphorous release rate (g m ⁻² per year)	Existing litter in aerobic layer (g m ⁻²)	Litter accretion rate in aerobic layer (g m ⁻² per year)
6	6.15	0.52	500	800
12	7.12	0.61	800	700
24	7.88	0.75	1500	450

Figures

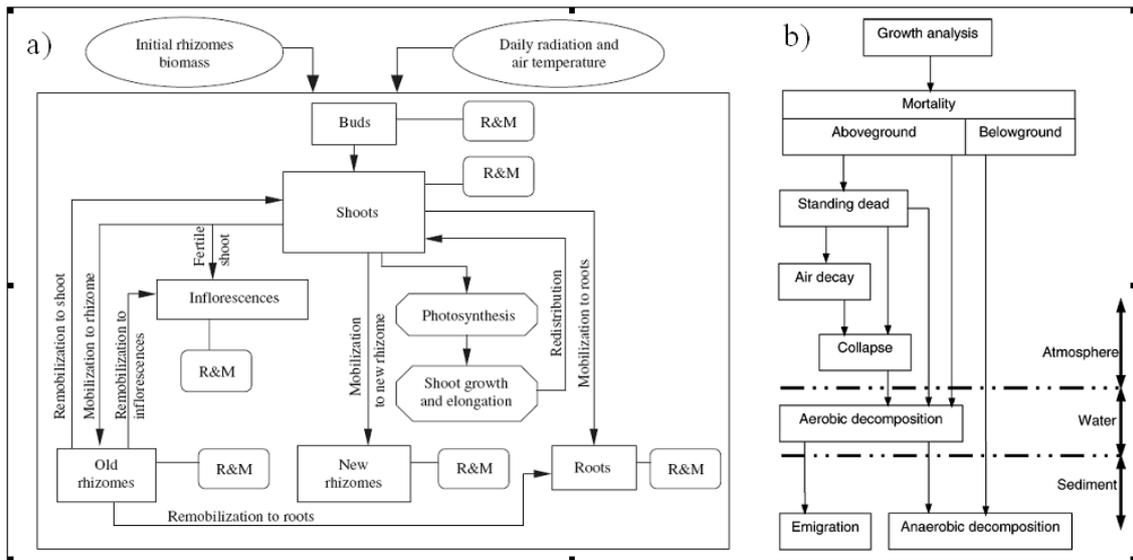


Fig. 1. Schematic depiction of the modelling procedure for a) the growth model (Asaeda et al., 2005) b) the decomposition model of *Phragmites australis* (Asaeda et al., 2002). R&M stands for respiration and mortality loss.

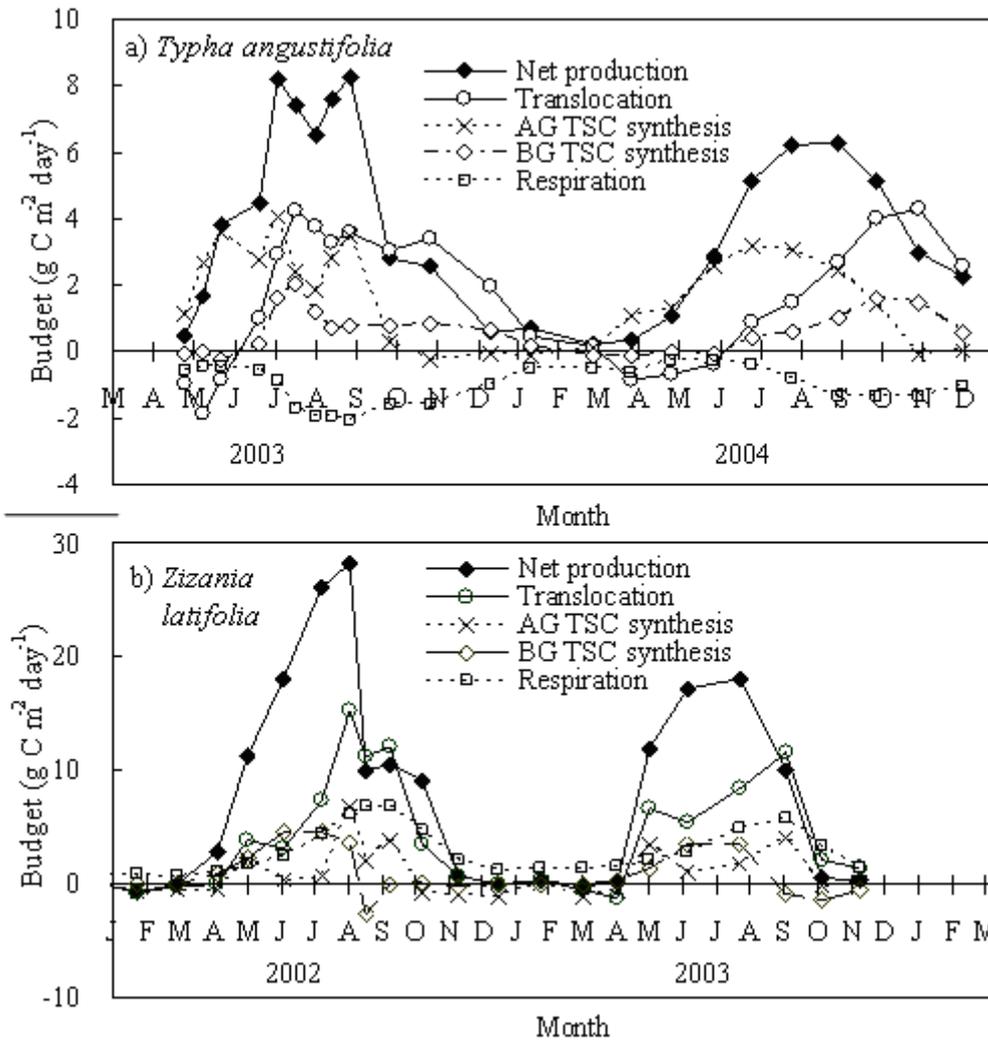


Fig. 2. Annual variation patterns of carbon budgets of a) *Typha angustifolia* and b) *Zizania latifolia* obtained at Akigase Park and Hasuda in Saitama, Japan.

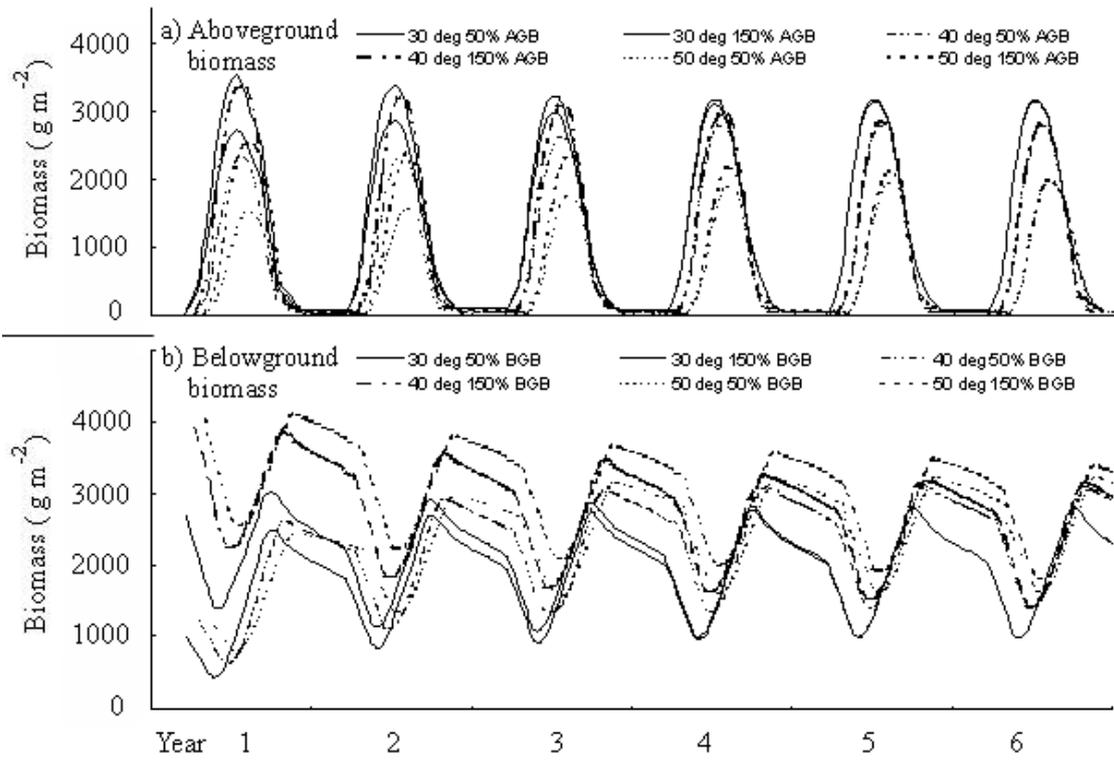
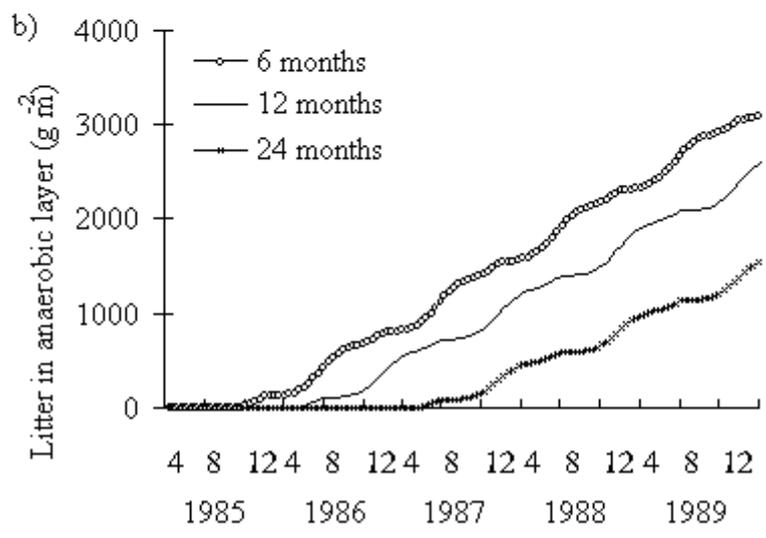
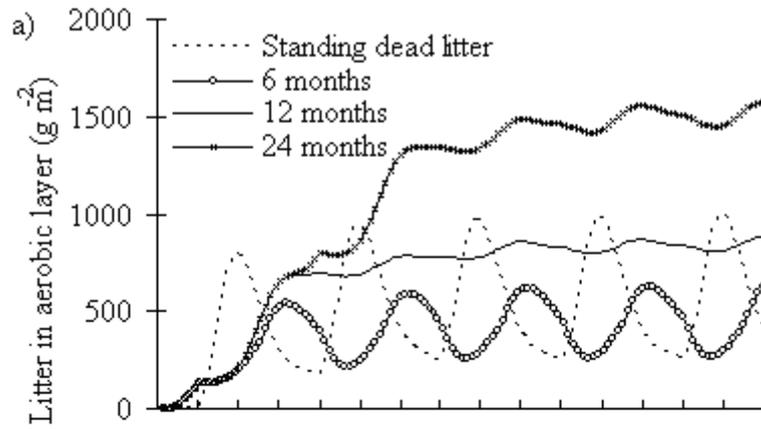


Fig. 3. The a) above- and b) belowground biomass variations modeled over 6 years based on initial rhizome biomass for different latitudes (10° to 60°) for *Typha angustifolia* (150% and 50% of equilibrium values) (Asaeda et al., 2005).



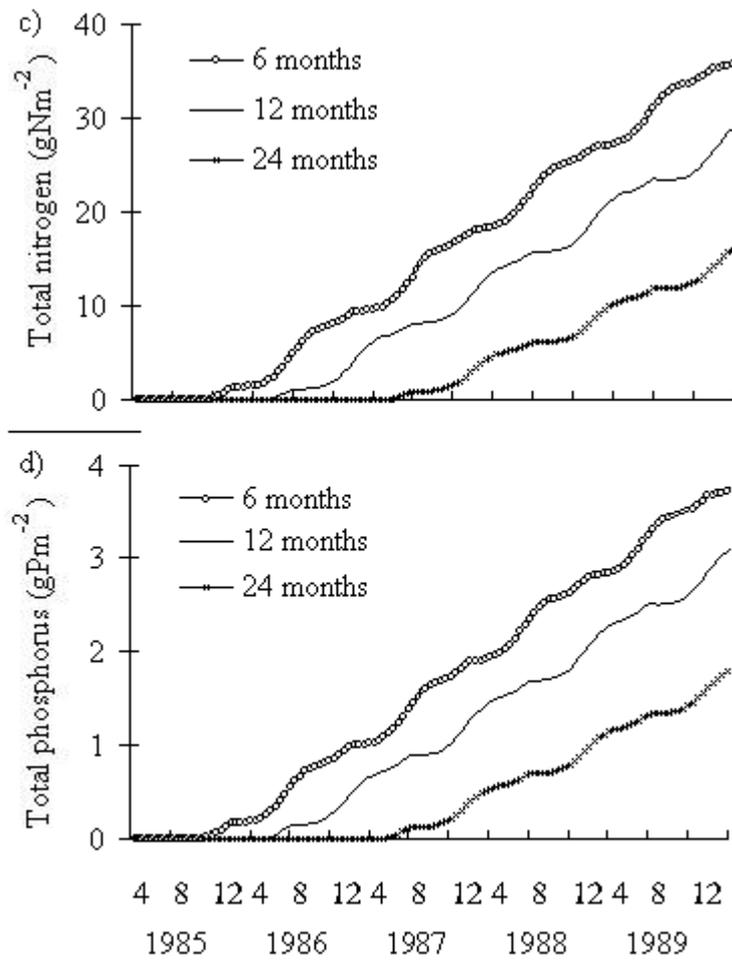


Fig. 4. The modeled biomass of dead standing stalks and litter of *Phragmites australis* decomposing, a) aerobically and b) anaerobically (Asaeda et al., 2002), and the modeled c) total nitrogen and d) total phosphorous stocks in the anaerobic layer of a reed (*Phragmites australis*) marsh (Asaeda et al., 2002).

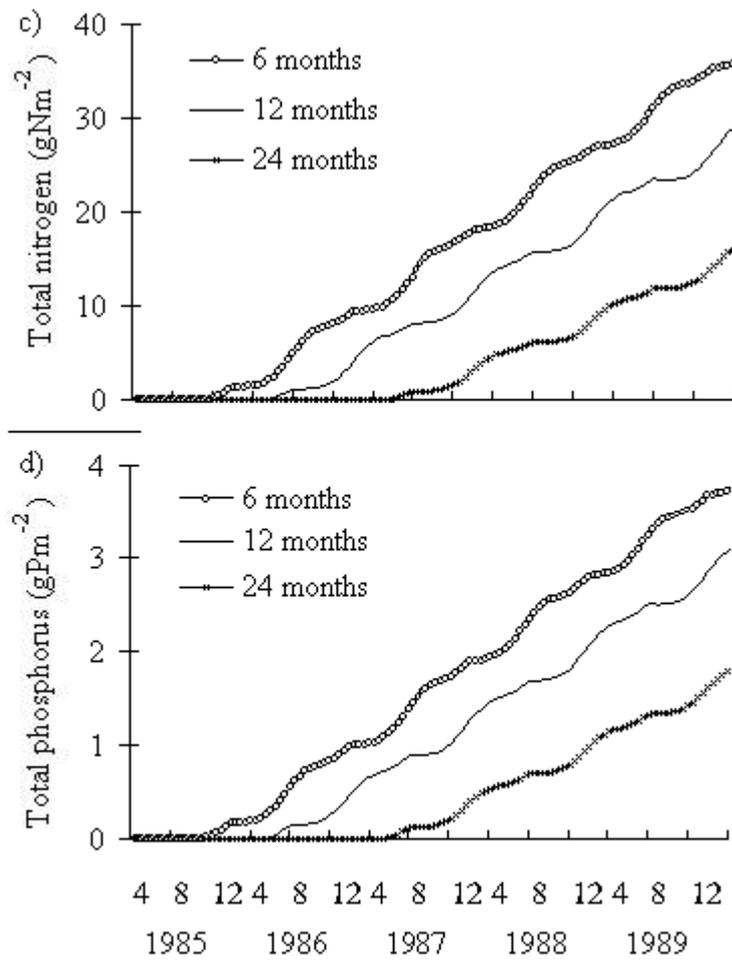


Fig. 5. Simulation of daily release and uptake of a) nitrogen and b) phosphorus inside the reed (*Phragmites australis*) stands. Nutrient release depends on the length of time during which the decomposition of fresh litter remains aerobic. Note the different scales on the y-axis.

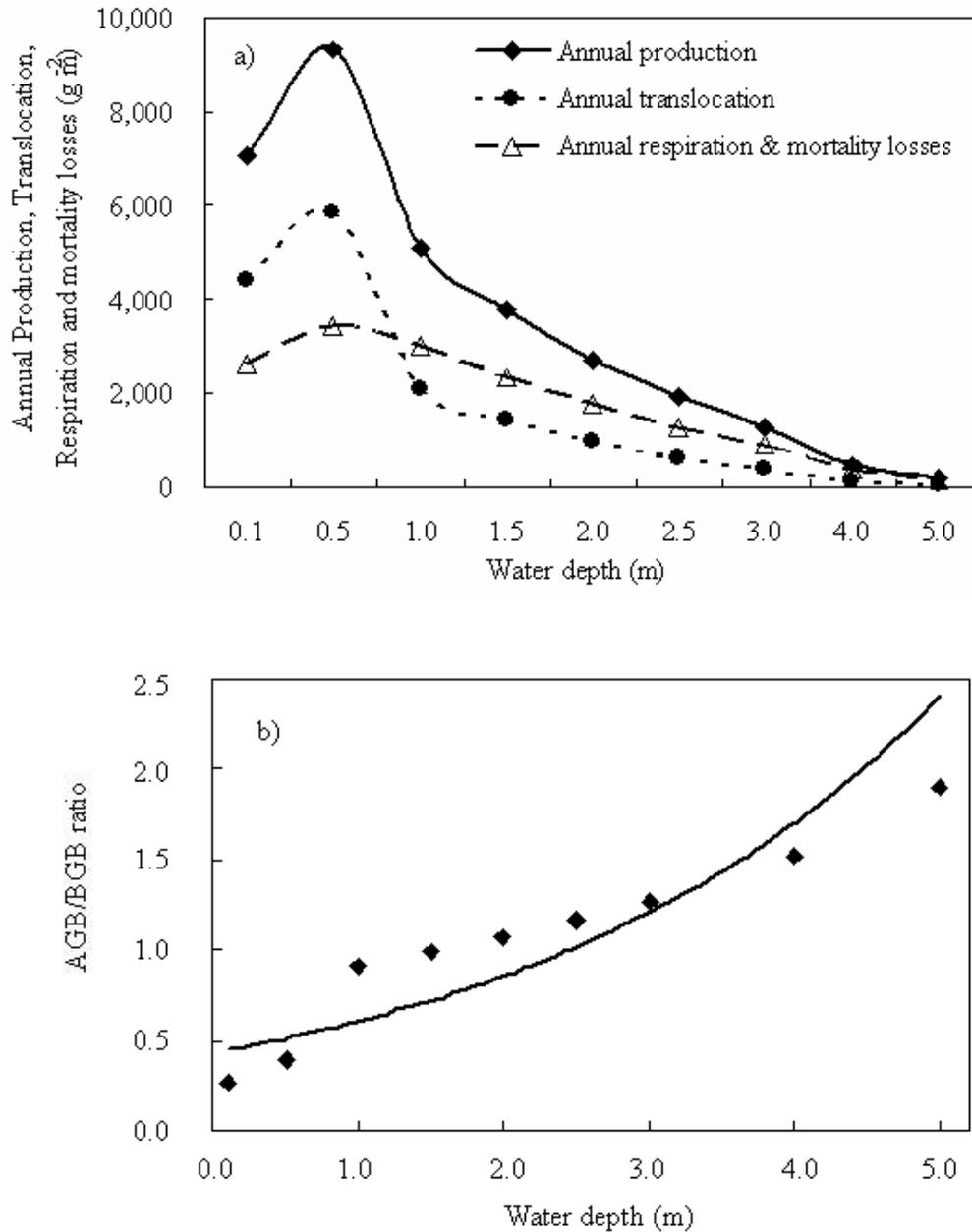


Fig. 6. a) The variation in the annual gross production, translocation, and respiration and mortality losses of *Eleocharis sphacelata* with water depth as predicted by the model results and b) the variation in the above- to belowground biomass ratio as a function of water depth as predicted by the model. The summer time climatic variations of the Goulburn-shallow site were assumed to prevail (Asaeda et al., 2006).