

Latitudinal Characteristics of Below- and Above-ground Biomass of *Typha*: a Modelling Approach

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- **Background and Aims** The latitudinal differences in the growth characteristics of *Typha* are largely unknown, although a number of studies have pointed out the effects of climate on the growth and productivity of *Typha*. Therefore, a dynamic growth model was developed for *Typha* to examine the effects of latitudinal changes in temperature and radiation on partitioning of the total biomass during the growing season into rhizomes, roots, flowering and vegetative shoots, and inflorescences.
- **Methods** After validating the model with data from growth studies of *Typha* found in past literature, it was used to investigate the dynamics of above- and below-ground biomasses at three latitudes: 30°, 40° and 50°.
- **Key Results** Regardless of the initial rhizome biomass, both above- and below-ground biomass values converged to a latitude-specific equilibrium produced by the balance between the total production and respiration and mortality losses. Above-ground biomass was high from 10° to 35° latitude with sufficient radiation, despite high metabolic losses; however, it decreased markedly at higher latitudes due to a low photosynthetic rate. Below-ground biomass, on the other hand, increased with latitude up to 40° due to decreasing metabolic losses, and then markedly decreased at higher latitudes. Above-ground biomass was enhanced with an increasing number of cohorts regardless of latitude. However, although more cohorts resulted in a larger below-ground biomass at low latitudes, the largest below-ground biomass was provided by a smaller number of cohorts at high latitudes. This difference is due to low production rates of late-season cohorts in high latitudes, compared with consumption for shooting and establishing foliage.
- **Conclusions** The model could be used to predict the potential growth of *Typha* in given conditions over a wide range of latitudes and is useful for practical applications such as wetland management or wastewater treatment systems using *Typha*.

Key words: Equilibrium seasonal biomass, latitudinal effect, modelling, resource translocation, rhizome system, *Typha*.

INTRODUCTION

Typha is a genus of rhizomatous perennial macrophytes that occur in seepage areas, swamps and billabongs over a wide latitudinal range. Although sometimes considered a weed, *Typha* spp. are now attracting attention for their usefulness in various engineering fields such as lake restoration and sewage treatment (Newman *et al.*, 1996; Coveney *et al.*, 2002).

Rhizomes of *Typha* are tightly linked to above-ground organs through material allocation between organs: spring transport of rhizome materials to form new shoots, mobilization of photosynthates and above-ground tissue to the rhizomes at senescence (McNaughton, 1966; Garver *et al.*, 1988), and the formation of lateral shoots and inflorescences on the newly formed rhizomes (Gustafson, 1976; Fiala, 1978). The material allocation between organs, therefore, affects the growth of *Typha* as well as its vegetative and sexual reproduction (Linde *et al.*, 1976; Grace and Wetzel, 1981a).

The ecology of *Typha* is well-known, with several studies on phenology (Fiala, 1978; Dickerman and Wetzel, 1985), production rate (Mason and Bryant, 1975; Roberts and

Ganf, 1986; Hill, 1987; Grace, 1988), competitive superiority (McNaughton, 1966; Grace and Wetzel, 1982, 1988; Weihe and Neely, 1997) and gas transportation into the below-ground biomass (Sale and Orr, 1986; Tornbjerg *et al.*, 1994). Most of these studies, however, were based on empirical analyses, and focused on a particular phenomenon under limited conditions rather than taking a whole-plant perspective under a wide range of environmental conditions. This makes it difficult to generalize and to understand within-plant integration and how this might vary in response to environmental drivers such as temperature and solar radiation.

In contrast, a mechanistic growth model can synthesize quantitative information about physiological processes and thus provide estimates of ecological, physiological or morphological responses that may otherwise be hard to measure (Asaeda and Karunaratne, 2000; Best *et al.*, 2001). Therefore, there are a variety of fields where a growth model can be effectively used to help to understand growth responses, and it is especially useful when various kinds of quantities or hard-to-measure data sets are required, or when estimates of material budgets are needed.

Typha grows in cold, temperate and tropical climates, and its productive and morphological characteristics vary

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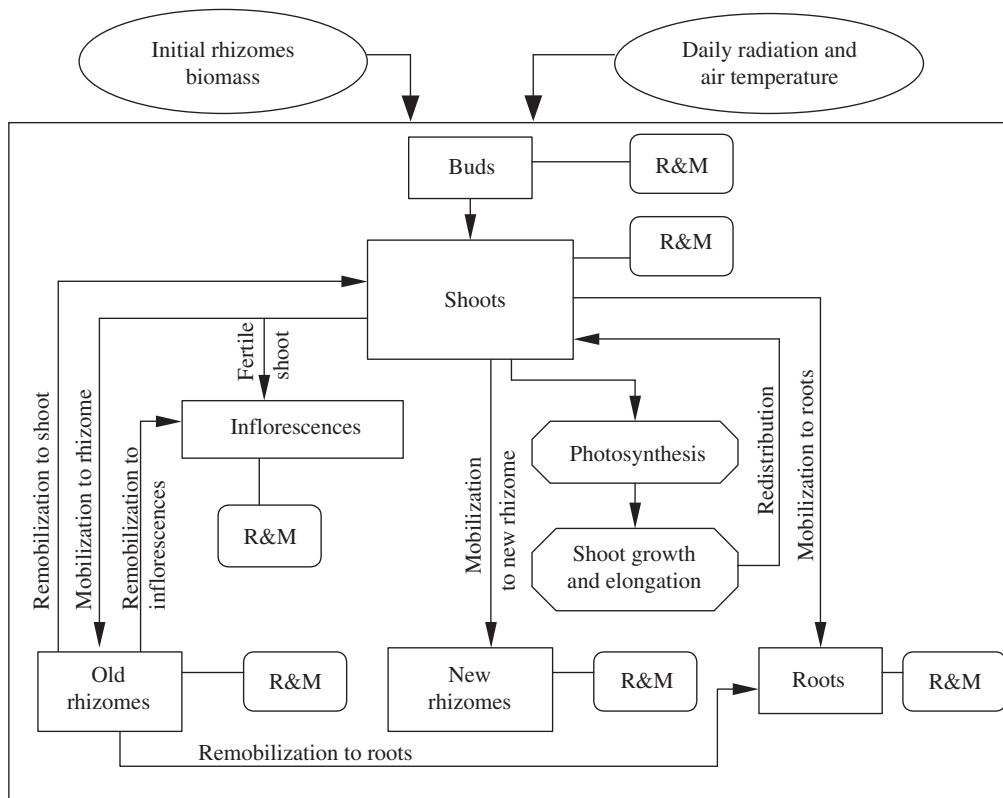


FIG. 1. Flow diagram for the model. R&M is respiration and mortality loss.

accordingly (McNaughton, 1966). There is an inverse relationship between maximum above-ground biomass and latitude (Roberts, 1981). This can be partly attributed to latitudinal differences in photosynthetic rates (Knapp and Yavitt, 1995) and respiration and mortality losses, and partly to climatic differences in resource translocation to below-ground organs (McNaughton, 1966). Many interactive factors mean, however, that relatively little has been understood regarding integrated responses. Dynamic analyses are of paramount importance in understanding these interactive complex systems.

Owing to difficulties in obtaining synchronized observations on the interaction between above- and below-ground biomasses in different latitudes, the latitudinal differences in growth characteristics of emergent rhizomatous plants have been largely unknown, although a number of studies have been conducted independently for species such as *Typha* and *Phragmites*. To study the interaction between above- and below-ground components of these plants, it is essential to understand the mechanism of material allocation to each organ, for which mechanistic modelling based on the material conservation is useful.

This study, therefore, aims to develop and calibrate a whole-plant dynamic growth model for one such macrophyte, *Typha* spp., and to use it to examine the effects of latitude-related factors on material translocation between shoots and rhizomes, and on above- and below-ground biomasses.

MATERIALS AND METHODS

Model description

The growth of a plant can be described by formulating a bio-energetic budget for each organ (Titus *et al.*, 1975). This approach has already been used for aquatic plants of different growth forms such as submerged (Asaeda and Bon, 1997; Best *et al.*, 2001) and emergent macrophytes, including *Phragmites australis* (Asaeda and Karunaratne, 2000). In the present study, biomasses of above-ground (for flowering ramets, leaves and inflorescences; for non-flowering ramets, leaves and non-flowering secondary forming ramets) and below-ground organs (roots, 2-year-old rhizomes, 1-year-old rhizomes and new rhizomes) were separately quantified as dry weight per square metre to account for energy gain and loss of each organ (photosynthetic production, respiration and mortality, and inter-organ movement). These processes are shown schematically in Fig. 1.

Formulation of phenological cycle

The model was developed for two species, *T. latifolia* and *T. angustifolia*, according to their generality. Although there are specific differences between these two species (Tanaka *et al.*, 2004), their plant structure and phenological cycles are quite similar as described below. For simplicity, same values for their plant structure and phenological cycle in the model were assumed. The differences between these two

TABLE 1. Parameters used in the Typha model

Parameter	<i>T. lat.</i>	<i>T. ang.</i>	Units
Maximum photosynthesis rate P_m	0.30 ^a	0.30 ^a	g CO ₂ g ⁻¹ d ⁻¹
Respiration rate of leaves β_{leaf}	0.006 ^b	0.006 ^b	g g ⁻¹ d ⁻¹
Mortality rate of leaves γ_{leaf}	0.0025 ^d	0.0025 ^d	g g ⁻¹ d ⁻¹
Respiration rate of rhizomes and roots $\beta_{rhi.root}$	0.003 ^b	0.003 ^b	g g ⁻¹ d ⁻¹
Mortality rate of rhizomes and roots $\gamma_{leaf.root}$	0.002 ^c	0.002 ^c	g g ⁻¹ d ⁻¹
Half-saturation constant of PAR K_{par}	5.8×10^{6c}	5.8×10^{6c}	$\mu\text{mol m}^{-2} \text{d}^{-1}$
Extinction coefficient of plant ak	0.25 ^f	0.25 ^f	—
Half-saturation constant of age K_{age}	90 ^g	90 ^g	Days
Constant for calculation of LAI A_{lai}	0.0226 ^h	0.0101 ^f	—
Constant for calculation of LAI B_{lai}	0.8214 ^h	0.926 ^f	—
Elongation rate of leaves A_{ke}	0.4 ^g	0.52 ^c	—
Fraction of rhizome transferred to AGB α_{rhi}	0.012 ^c	0.012 ^c	—
Fraction of leaf transferred to rhizome ϵ_{leaf}	0.015 ^b	0.026 ^c	—

Key to sources: ^aGartner (1976); ^bGustafson (1976); ^ccalibrated; ^dDickerman and Wetzel (1985); ^eKnapp and Yavitt (1995); ^fDykyjova (1971); ^gMcNaughton (1973); ^hWeisner (1993).

species are addressed in specific parameters such as the difference in leaf structure, inter-organ resource allocation rate, photosynthetic and respiration rates, etc. (also see Table 1).

Field studies of *Typha* show that shoot growth starts in spring but also depends on locality and latitude: *Typha latifolia* starts to grow from day 100 at 43°N (Smith *et al.*, 1988), day 110 at 44°N (McNaughton, 1966) and day 133 at 47°N (Garver *et al.*, 1988); *T. angustifolia* grows from day 60 at 33°N (Hill, 1987), day 120 at 44°N (McNaughton, 1966) and day 133 at 47°N (Garver *et al.*, 1988). Dates are given as Julian days, and dates of southern hemisphere have been converted to northern hemisphere equivalents by shifting 182 d. Based on these values the Julian day (y) when shoot growth is initiated can be given as a function of latitude (x) as follows:

$$y = -0.0011x^3 + 0.1182x^2 - 1.7902x + 58 \quad (r^2 = 0.83) \quad (1)$$

Although new shoots emerge mostly in spring, shoots may continue to emerge throughout the growing season, as recorded for *T. latifolia* (Fiala, 1978; Dickerman and Wetzel, 1985) and for *T. angustifolia* (Fiala, 1978). Fiala (1978) and Dickerman and Wetzel (1985) reported three pulses of shoot emergence: in spring, in July–August and in September, although these were not always distinct and were related to shoot density and standing shoot biomass (Dickerman and Wetzel, 1985). This study assumed three cohorts, unless otherwise stated. The first cohort grows from buds formed during the previous autumn and starts to grow in spring, the second cohort grows 60 d after the first cohort

has been initiated and the third cohort emerges 60 d after the second (Gustafson, 1976; Dickerman and Wetzel, 1985).

Translocation of photosynthetic assimilates to the rhizome system is marked by the rhizome biomass beginning to recover in spring and by the reduction of above-ground biomass in autumn, respectively, although the increase of reserves in rhizomes is often affected by the later cohort formation (Linde *et al.*, 1976; Fiala, 1978). Photosynthetic assimilates start to be allocated to the rhizome system after above-ground shoots start to grow and manufacture carbohydrates (Linde *et al.*, 1976). Based on a comparison of photosynthetic assimilates and the increase in rhizome biomass observed by Gustafson (1976), it was assumed that 40 % of the photosynthates are allocated to the rhizome system of *Typha latifolia*. Similarly, the photosynthate allocation was estimated to be at approx. 40 % for *Typha angustifolia* (Garver *et al.*, 1988). The translocation of resources to rhizomes started after the shoots were sufficiently developed, when the photosynthetic assimilates dominated the utilization of carbon reserves from rhizome (Linde *et al.*, 1976).

Maximum above-ground biomass was reached around day 120 at 47°N (Garver *et al.*, 1988), day 130 and day 140 at 43°N (Dickerman and Wetzel, 1985; Smith *et al.*, 1988) for *T. latifolia*; day 120 at 47°N (Garver *et al.*, 1988) and day 145 at 33°N (Hill, 1987) for *T. angustifolia* after shoot growth started. The emergence of inflorescence (day z) was assumed to be a function of the latitude (x) and the day (Julian day) when the first cohort began to grow (y) (McNaughton, 1966).

$$z = y - 0.762x + 82 \quad (r^2 = 0.73) \quad (2)$$

Governing equations

The net growth of each fraction of a plant is the result of photosynthesis, respiration and mortality losses, and translocation between organs, as follows.

$$dB/dt = G - R - D + Tr \quad (3)$$

where B , G , R , D and Tr are biomass, gross photosynthesis rate, respiration rate, mortality rate and inter-organ translocation, respectively. Therefore, given dry weight in grams and stratifying the above-ground organs into 1-cm-thick horizontal layers, the following equations describe the material budget for each organ or layer of *Typha*.

For rhizomes:

$$\frac{dB_{rhi}(n)}{dt} = -R_{rhi} - D_{rhi} - Rhif.m(n) + k(n) \times \left[\sum_{l=1}^{l_{max}} \epsilon_{fl.nf.se} b_{fl.nf.se}(l) + \sum_{l=1}^{l_{max}} \epsilon_{ph} G_{fl.nf.se}(l) \right] \quad (4)$$

For roots:

$$dB_{root}/dt = -R_{root} - D_{root} + Rhif.F_{root} \quad (5)$$

For leaves of flowering, non-flowering and secondary shoots at the l -th layer:

$$\begin{aligned} [db_{fl,nf,se}(l)]/dt = & G_{fl,nf,se}(l) - R_{fl,nf,se}(l) - D_{fl,nf,se}(l) \\ & + Rhif : f_{fl,nf,se}(l) - \varepsilon_{fl,nf,se} b_{fl,nf,se}(l) \\ & - \varepsilon_{ph} G_{fl,nf,se}(l) \end{aligned} \quad (6)$$

For inflorescences at the l -th layer (only for flowering ramets):

$$[db_{flo}(l)]/dt = -R_{flo}(l) - D_{flo}(l) + Rhif : f_{flo}(l) \quad (7)$$

The subscripts rhi, fl, nf, se, root and flo indicate rhizomes, leaves of flowering shoots, first cohort non-flowering shoots, shoots from the second cohort, roots and inflorescences, respectively. $b_a(l)$ denotes the biomass of the l -th layer of each plant organ, and $B_a (= \sum_{l=1}^{l=\max} b_a(l))$ is the total biomass. $Rhif$ is the daily upward translocation from rhizomes to the above-ground organs. F_a is the fraction of rhizome reserves allocated to above-ground organs and roots, satisfying $F_{fl} + F_{nf} + F_{flo} + F_{root} + F_{se} = 1$. The allocation to the l -th layer of the above-ground organs is proportional to the existing biomass in that layer ($f_{fl,nf,flo,se}(l) = F_{fl,nf,flo,se} b_{fl,nf,flo,se}(l) / B_{fl,nf,flo,se}$); ε_a is the rate of allocation to rhizomes from organs a , and ε_{ph} is the photosynthesis assimilates assigned to the rhizome system.

Second and third cohort shoots normally do not form inflorescences in the year (Fiala, 1978), therefore, the total leaf biomass for non-flowering shoots is the sum of non-flowering shoots of the first cohort plus second and third cohort shoots. $k(n)$ and $m(n)$ are fractions of the biomass translocated to and from n -year-old rhizome segments ($\sum_{n=1}^{n=n_{\max}} k(n) = 1$ and $\sum_{n=1}^{n=n_{\max}} m(n) = 1$).

Gross photosynthesis rate

$G(l)$ is the gross photosynthetic rate in the l -th layer, which is proportional to the l -th layer biomass and is a function of the amount of limiting resources. The rate of photosynthesis for *Typha* was estimated by multiplying the Michaelis–Menten equations of restrictive factors such as photosynthetically active radiation (PAR) and plant age (Asaeda and Karunaratne, 2000). Effects of temperature and nutrients on the photosynthetic rate have been reported by McNaughton (1973), Cary and Weerts (1984), Ulrich and Burton (1988) and Grace (1988).

Then,

$$G_a(l) = k_{co} P_m K_{NP} \frac{PAR(l)}{K_{PAR} + PAR(l)} \times \frac{K_{age}}{K_{age} + Age} \theta^{-|T-T_o|} b_a(l) \quad (8)$$

where P_m is the maximum photosynthesis rate ($\text{g CO}_2 \text{ g}^{-1} \text{ d}^{-1}$); age is the age of the leaf after the emergence of the cohort (day); k_{co} is the conversion constant from oxygen to ash-free dry weight ($\text{g g}^{-1} \text{ CO}_2$); $PAR(l)$ is the daily averaged active radiation ($\mu\text{mol m}^{-2} \text{ d}^{-1}$) at the l -th layer; K_{PAR} , and K_{age} are the half-saturation constants of PAR ($\mu\text{mol m}^{-2} \text{ d}^{-1}$) and the effect of age (days) on the rate of photosynthesis, respectively. K_{NP} is the constant of the availability of nutrients, where $K_{NP} = 1$ when nutrients

are sufficient but decreases due to the shortage of nutrients (Cary and Weerts, 1984; Ulrich and Burton, 1988). θ is the temperature constant (1.09). T and T_o are mean daily temperature and optimum temperature, respectively. $b_a(l)$ is the leaf biomass of the l -th layer. The photorespiration was assumed to be proportional to the photosynthesis rate (Erdei *et al.*, 2001), and therefore was included in the maximum photosynthesis rate, which is estimated from measured data (McNaughton, 1973; Gartner, 1976). The gross photosynthesis rate reaches the maximum value in the range of optimum temperature and is lower if the temperature is outside this range.

PAR and temperature

The instantaneous rate of photosynthesis changes throughout a day with changes in solar radiation (Gartner, 1976; Gustafson, 1976). In this study, a daily integrated rate of photosynthesis was simulated rather than using hourly values, because of lack of input data.

The above-ground organs were divided into 1-cm-thick horizontal layers, for which the dry matter budget and the elongation rate were calculated. The intensity of the PAR, about 40–45 % of the total global radiation (Dykyjova, 1971), can be obtained for each level using the Lambert–Beer Law, $I_{PAR}(i) = I_{PAR} e^{-ak.Fi}$, where I_{PAR} is the PAR intensity and $I_{PAR}(i)$ is the PAR intensity within the stand at the i -th layer, which is determined by the cumulative leaf area index from the top, $Fi (= \sum_{j=1}^{j=i} LAI(j))$ (Ondok, 1973) and the extinction of light coefficient, ak , depending on the leaf angle and clustering of leaves (Ondok, 1973). The relationship between leaf biomass and leaf area index (LAI) of *Phragmites australis* was established by Asaeda and Karunaratne (2000) in the form of a power function ($r^2 = 0.92$) based on measurements for *Phragmites australis* in southern Moravia. For *Typha* spp., a similar relationship was used: $LAI(i) = A_{lai} [B_{leaf}(i)]^{B_{lai}}$, where A_{lai} and B_{lai} are the constants characterizing the leaf structure. These were estimated by regression analysis using data in Weisner (1993) ($r^2 = 0.85$) and Dykyjova (1971) ($r^2 = 0.91$), and are shown in Table 1 for each species.

The daily global radiation at the surface was modelled as a function of latitude on a fine day as proposed by Brock (1981):

$$S = (1 + \eta) S_o / \exp[A / \cos(z_e)] \quad (9)$$

where S is the solar radiation (Wm^{-2}); z_e is the solar zenith angle (degrees); η , S_o and A are the proportion of diffused-direct solar radiation, the average clear-sky radiation ($\text{MJ m}^{-2} \text{ h}^{-1}$) and the atmospheric extinction coefficient (air mass^{-1}), respectively (Brock, 1981).

The solar zenith angle is expressed by

$$z_e = \cos^{-1}(\sin\Phi_o \sin\delta_o + \cos\Phi_o \cos\delta_o \cos\varepsilon_o) \quad (10)$$

where Φ_o is the latitude of the place for which the computation is done, δ_o is the declination angle of the sun (degrees) and given by

$$\delta_o = 23.4 \sin[0.986(284 + J\text{day})] \quad (11)$$

where Jday is the Julian day. ϵ_o is the hour angle from which the solar noon (degrees) was computed as:

$$\epsilon_o = \arccos\{-[\tan(\Phi_o) \tan(\delta_o)]\} \quad (12)$$

The seasonal variation of air temperature, T , depends on the local geographical conditions; it was approximated by a sinusoidal function of latitude-dependent average temperature, T_{ave} , and Julian day (Tsuboi, 1974);

$$T_{ave} = 27.1 - 44.9 \sin^2(\Phi_o - 6.5) \quad (13)$$

$$T = T_{amp} \sin[2\pi \cdot (Jday - 80 - Jday_o)/365] + T_{ave} + T_{const} \quad (14)$$

where T_{amp} is the amplitude of the temperature from average maximum and minimum temperatures at the site, T_{ave} , $Jday_o$ is the time lag between temperature and radiation peaks and T_{const} is the difference between the observed average temperature and the estimated temperature (Tsuboi, 1974).

Daily respiration, mortality losses and upward translocation

The daily respiration, mortality and upward translocation rates from the rhizome system are proportional to biomass and mean daily temperature:

$$R_a = \beta_a \theta^{T-20} B_a; D_a = \gamma_a \theta^{T-20} B_a; Rhif = \alpha_a \theta^{T-20} B_a \quad (15)$$

where β_a , and γ_a are the specific rates of respiration and mortality at 20 °C, respectively, α_a is the specific rate of upward translocation from rhizomes, θ is the temperature constant (1.09), T is mean daily temperature and subscript a represents the plant organ, such as shoot, flower, etc.

Bud formation, shoot sprouting and litter effects

The increase in the above-ground biomass is allocated to the elongation of ramets and the growth of shoots and peduncles in the same layer. For the sake of simplicity, therefore, the concept of critical layer biomass is introduced: starting the elongation once the biomass in the layer exceeds a critical biomass (Asaeda and Karunaratne, 2000).

Most of buds are formed from the terminals of the fresh rhizomes (Linde *et al.*, 1976) at the expense of their resources, therefore, the critical layer biomass for buds, B_{cri} ($\text{g m}^{-2} \text{ layer}^{-1}$) seems reasonably related to the existing fresh rhizome biomass as well as mean daily temperature (Asaeda and Karunaratne, 2000):

$$B_{cri} = a_{kz} \theta^{T-20} B_{rh}^{2/3} \quad (16)$$

when the amount of material mobilized from the fresh rhizomes exceeds the critical biomass of the layer, the buds will emerge from the first layer, extending into the next layer and subject to further elongation processes. a_{kz} is a parameter to account for bud formation ($= 0.0049$) for both *T. latifolia* and *T. angustifolia*, which was estimated from Asaeda and Karunaratne (2000).

The sprouting and initial growth of shoots are influenced by the existence of litter by way of delaying the emergence

of shoots and limiting the light that supports the initial growth of shoots. However, the parameters used in the model and the observation of the initial growth in the field studies used for the calibration are based on experiments without removing litter. Therefore, the effect of litter on the emergence and the initial growth of shoots is considered to be included in the model.

Model execution

For each simulation, the input data were average climate data (daily solar radiation and air temperature) and the initial (i.e. spring) rhizome biomass at each site. If climate data were not available for the site, then site latitude was used instead to estimate daily solar radiation (Eqn 9) and air temperature (Eqn 14). If no initial rhizome biomass was reported, a series of simulations was conducted using different initial values, and the value that provides the best fit of the above-ground biomass to the observation was then used. Parameters required for the model were taken from published papers or were calibrated based on specific published data for each species (Table 1). Then all parameters other than the constant of the availability of nutrients, K_{NP} , were fixed for each species during simulation processes, and the biomass variation patterns, such as increasing trend, peak time and decreasing trend were compared with the observed data. The value of K_{NP} was assumed to be site-specific and was calibrated to match the observed biomass in each simulation (Table 2).

Growth equations for each layer and organ were solved simultaneously using the fourth order Runge–Kutta method (Press *et al.*, 1992). The model simulated the seasonal variation of the biomass of plant organs (i.e. flowering shoots, non-flowering shoots, inflorescences, roots and rhizomes) as well as variations of total production and respiration in cases of first, second and third cohorts for latitudes from 10° to 60°. Values for each *Typha* species are shown in Table 1. After validating the model with field data from previous studies of two *Typha* species, the model was used to explore the response of *Typha* at three latitudes (30°, 40° and 50°) central to its wider distribution, due to the availability of data sets.

Sensitivities of coefficients

A sensitivity analysis was carried out to investigate the influence of several important parameters on the results by changing them $\pm 30\%$ (Table 3). The most sensitive parameters were coefficients related to the gross production (the maximum photosynthesis rate P_m , half saturation constant of PAR), the respiration and mortality losses of shoots and rhizomes and the translocation from shoots to rhizomes (ϵ_{leaf}). A 30% increase in the maximum photosynthetic rate resulted in a 35% change in above-ground biomass and a 32% change in below-ground biomass, while a 30% increase of half-saturation constant of PAR reduced the below-ground biomass by 10%. A 30% increase in the respiration and mortality losses of shoots and rhizomes and in the allocation rate to rhizomes resulted, respectively, in the 19% and 21% reduction and the 17% enhancement of the below-ground biomass. By comparison, only less than 10% of change was brought about by a 30% change in other parameters.

TABLE 2. Datasets utilized for model validation

Site	Species	Latitude	K_{NP}	Flo. (%)	r	Reference
Florida, USA	<i>T. lat.</i>	30N	0.8	–	AGB: 0.95 BGB: 0.92	Reddy and Portier (1987)
Carolina, USA	<i>T. lat.</i>	33N	0.55	0	AGB: 0.96	Boyd and Hess (1970)
Texas, USA	<i>T. ang.</i>	33N	1.0	70	AGB: 0.95 BGB: 0.76	Hill (1987)
Oklahoma, USA	<i>T. lat.</i>	35N	0.65	–	AGB: 0.89	Penfound (1956)
New Jersey, USA	<i>T. lat.</i>	40N	0.7	–	AGB: 0.92 BGB: 0.88	Jervis (1969)
Michigan, USA	<i>T. lat.</i>	42N	0.7	0	AGB: 0.91	Dickerman and Wetzel (1985)
Michigan, USA	<i>T. lat.</i>	42N	0.7	–	AGB: 0.85	Grace and Wetzel (1981b)
Michigan, USA	<i>T. ang.</i>	42N	0.7	–	AGB: 0.87	Grace and Wetzel (1981b)
Michigan, USA	<i>T. lat.</i>	42N	0.65	0	AGB: 0.95	Ulrich and Burton (1985)
Wisconsin, USA	<i>T. lat.</i>	43N	0.7	–	AGB: 0.94	Klopatek and Stearns (1978)
Wisconsin, USA	<i>T. lat.</i>	43N	0.7	<5	AGB: 0.92 BGB: 0.84	Smith <i>et al.</i> (1988) Gustafson (1976)
Oregon, USA	<i>T. lat.</i>	44N	0.7	–	AGB: 0.79	McNaughton (1966)
	<i>T. ang.</i>				BGB: 0.82	
Minnesota, USA	<i>T. lat.</i>	47N	0.65	0	AGB: 0.94 BGB: 0.91	Garver <i>et al.</i> (1988)
Minnesota, USA	<i>T. ang.</i>	47N	0.65	0	AGB: 0.92 BGB: 0.95	Garver <i>et al.</i> (1988)
Moravia, Czech	<i>T. ang.</i>	49N	1.0	–	AGB: 0.93	Kvet <i>et al.</i> (1969)
Norfolk, England	<i>T. ang.</i>	52N	0.8	–	AGB: 0.94	Mason and Bryant (1975)
Masurian, Poland	<i>T. ang.</i>	53N	0.7	–	AGB: 0.88	Kufel (1991)
Alberta, Canada	<i>T. lat.</i>	56N	1.0	15	AGB: 0.96	Lieffers (1983)

r , Correlation coefficient; Flo. (%), percentage of flowering ramets in all ramets; K_{NP} , the constant of the availability of nutrients at the site; AGB, above-ground biomass; BGB, below-ground biomass.

TABLE 3. Sensitivity of parameters

Parameter	Variation (%)	AGB (%)	BGB (%)
Maximum photosynthesis rate	+30	+35	+32
	–30	–37	–35
Respiration and mortality rate of leaves	+30	–14	–19
	–30	+12	+17
Respiration and mortality rate of rhizomes	+30	–9	–21
	–30	+8	+19
Half-saturation constant of PAR	+30	–11	–10
	–30	+15	+15
Fraction of leaf transferred to rhizome	+30	–5	+17
	–30	+5	–22
Fraction of rhizome transferred to AGB	+30	+6	–5
	–30	–4	+7

AGB, above-ground biomass; BGB, below-ground biomass.

RESULTS

Validation of the model

The model was validated for two species, *T. latifolia* and *T. angustifolia*, using 18 data sets for sites located at latitudes between 30°N to 56°N (Table 2). Results from three sample simulations, compared with field data, are shown in Fig. 2A–C. In Fig. 2A, the population, which initiated from seedlings in the first year, was still in the developing stage (Garver *et al.*, 1988), therefore the biomass gradually increased until it reaches equilibrium values (see below). In Fig. 2B, the earlier emergence of shoots in the second year enabled a larger production of shoots compared with that in the first year. Despite a higher above-ground production in the second year, the population in this simulation was considered to be in an equilibrium stage because the difference of biomasses between 2 years was not significant

(Hill, 1987). The observed below-ground biomass was unexpectedly constant throughout the second year (Hill, 1987), resulting in a low fitness between the calculated and observed below-ground biomass (Table 2). Figure 2C shows a satisfactory agreement between calculated results and observed data for both above- and below-ground biomass.

The level of agreement between the calculated results and field data (Table 2), as given by correlation coefficients (r) showed that, although simulated results were slightly different from the observations, there was an acceptable agreement for all the sites for the numerical experiments described below.

Long-term growth dynamics in terms of latitude

Figure 3 shows the variation of above- and below-ground biomasses, depending on initial rhizome biomass, assuming no flowering and no nutrient limitations ($K_{NP} = 1$). Regardless of the initial rhizome biomass, the annual maximum above- and below-ground 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 above ground (AGB) and 2680 g m^{–2} for below ground (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°.

Above-ground biomass started to increase earlier at lower latitudes as described by the empirical latitude–starting time relationship (eqn 1: day 80 at 30°, day 105 at 40° and day 126 at 50°), and simulation results indicated that the above-ground biomass reached its maximum earlier at higher latitudes: day 220 at 30°, day 240 at 40° and day 250 at 50° (Fig. 3). Die-off of the above-ground biomass occurred only slightly earlier at lower latitudes, thus, the above-ground

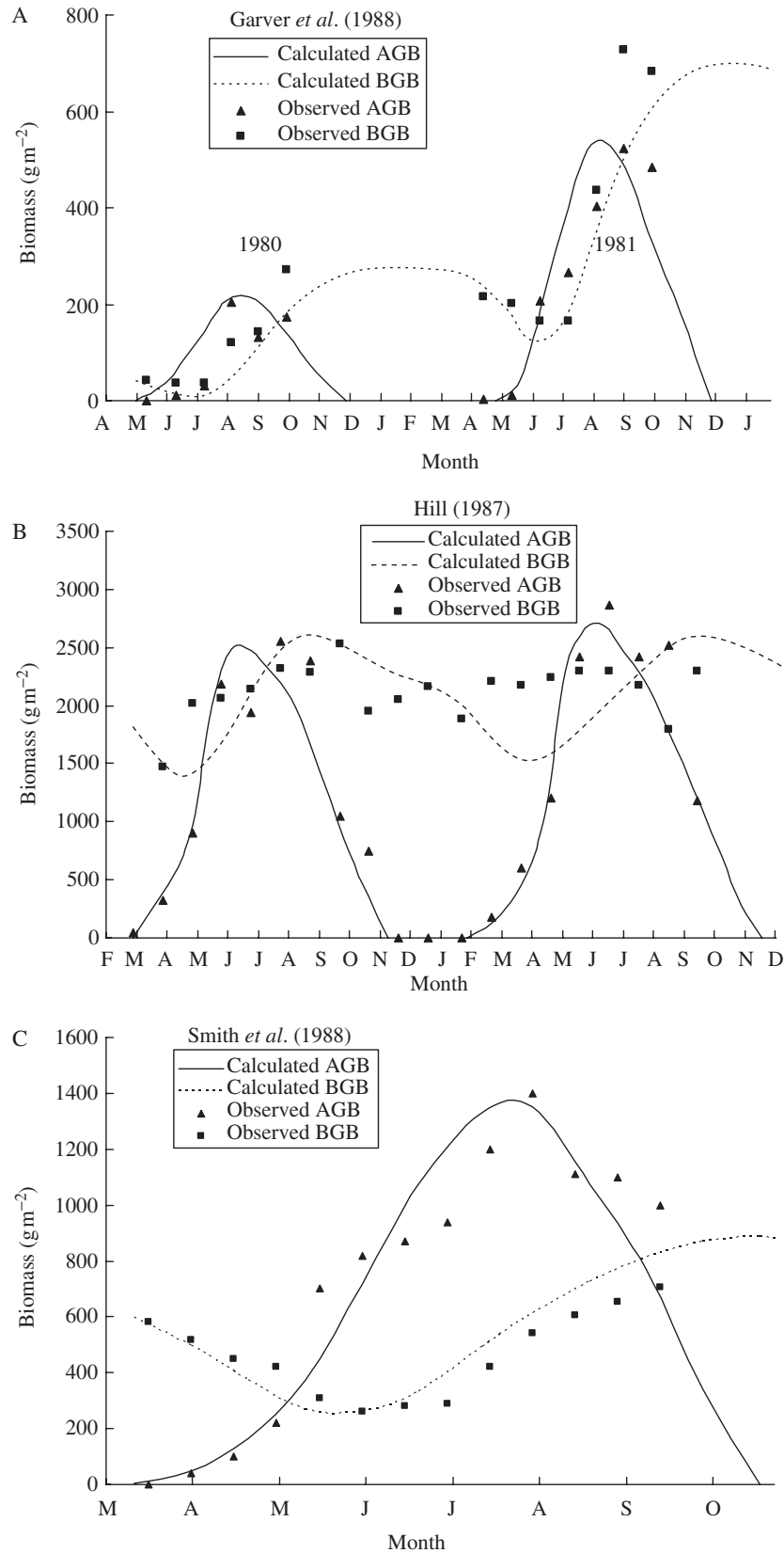


FIG. 2. (A) Simulated results for *T. angustifolia* compared with observed data at 47°N (Garver et al., 1988). (B) Simulated results for *T. angustifolia* compared with observed data at 33°N (Hill, 1987). (C) Simulated results for *T. latifolia* compared with observed data at 43°N (Smith et al., 1988). AGB, above-ground biomass; BGB, below-ground biomass.

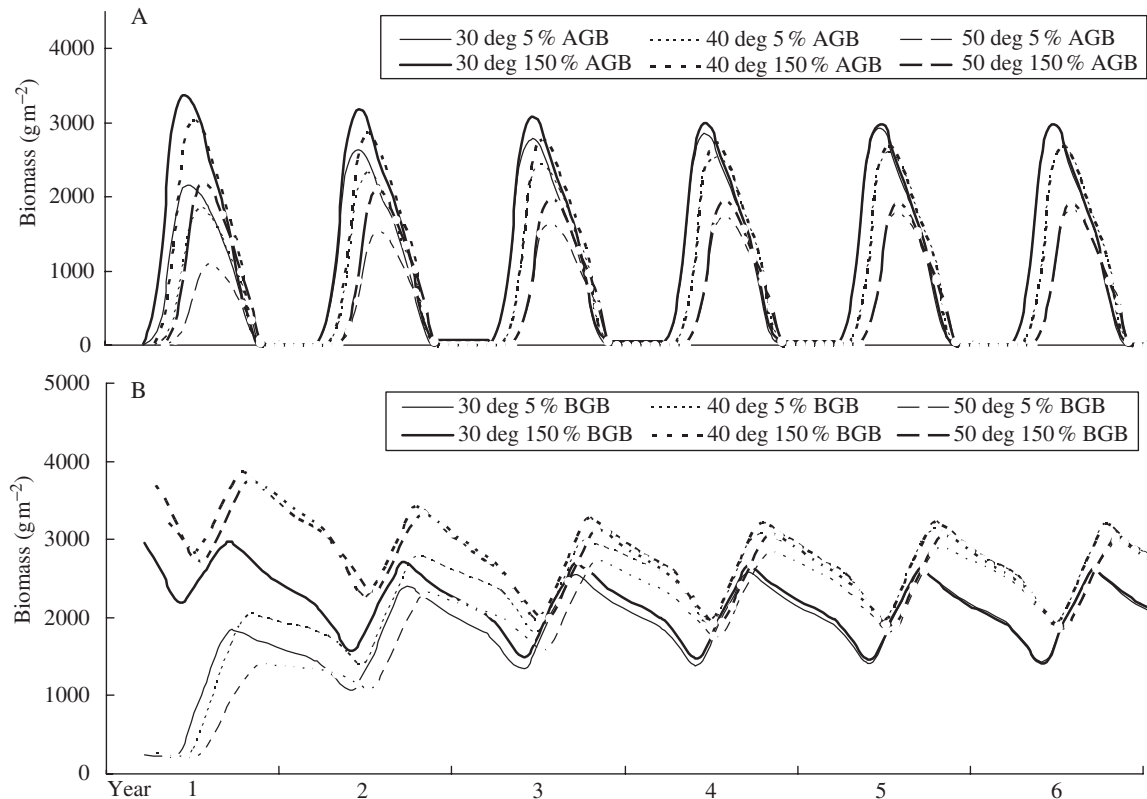


FIG. 3. Variations in (A) above-ground biomass (AGB) and (B) below-ground biomass (BGB) modelled over 6 years as a function of initial rhizome biomass (150 % and 5 % of equilibrium values).

biomass existed 7 months at 30°, 6 months at 40° and 5.5 months at 50°.

Gross production was restricted to the growing season, which corresponded to the existence of living above-ground biomass; however, respiration and mortality losses continued over 1 year. The respiration loss was larger during summer with the larger above-ground biomass and higher temperature. In contrast, the mortality loss became larger in late autumn due to the senescence of shoots. As a result of these patterns, net production, which is the surplus of gross production over losses due to respiration and mortality, peaked slightly earlier than the gross production, then rapidly decreased during summer, became negative in early autumn and reached the lowest value in late autumn (Fig. 4).

With the longer growing season, higher solar radiation and higher temperature, the annual gross production was larger in lower latitudes: $9960\ g\ m^{-2}$ at 30°, $7360\ g\ m^{-2}$ at 40° and $3730\ g\ m^{-2}$ at 50°. However, in lower latitudes, higher temperature also resulted in 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 plant net production was larger in lower latitudes; however, the annual integration of net production was always zero in the equilibrium stage regardless of latitude.

The translocation of resources to rhizomes started after the shoots were sufficiently developed, and then ended with all shoots dying off. The starting time of translocation was

almost 2 months earlier in 30° than in 50°; however, the ending time was only 1 month later at 50° than at 30°. Therefore, the period of the downward translocation was 1 month longer at 30° than at 50°. With the larger net production and the 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. At the same time, the amount of rhizomes increased from 950 to $2680\ g\ m^{-2}$ at 30°, from 1460 to 3300 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°, and this was reduced 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 below-ground organs throughout the year. In the equilibrium stage, translocation to rhizomes, whether positive or negative, throughout a year balanced with the respiration and the mortality losses in the rhizome system.

The upward translocation of rhizome resources to form new shoots in spring showed a higher ratio to the gross production in higher latitudes: 0.07 at 30°, 0.11 at 40° and 0.21 at 50° because of the lower gross production in the growing season and the relatively large rhizome biomass. Correspondingly, the downward translocation afterwards also showed a higher ratio to the gross production in higher latitudes: 0.33 at 30°, 0.38 at 40° and 0.49 at 50°.

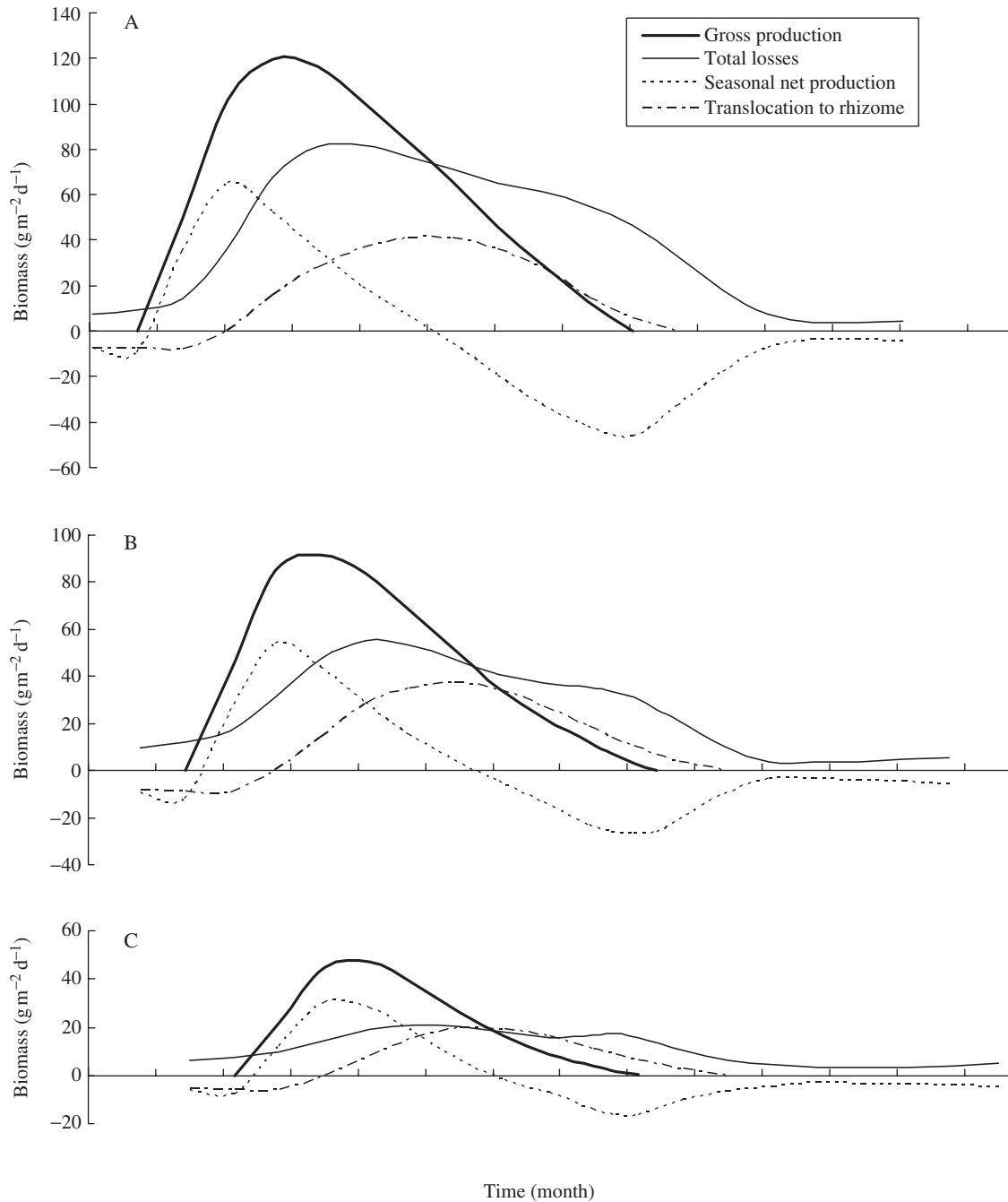


FIG. 4. Seasonal cycle of gross production, total losses due to respiration and mortality, translocation and net production in the equilibrium stage ($\text{g m}^{-2} \text{d}^{-1}$): (A) at latitude 30° ; (B) at latitude 40° ; (C) at latitude 50° .

Figure 5A and B show the simulated equivalent values for above- and below-ground maximum biomasses of *T. latifolia* at latitudes from 10° to 60° , assuming that growth was restricted only by solar radiation and temperature. Level of nutrient availability considerably regulated the above- and below-ground biomasses (Cary and Weerts, 1984; Ulrich and Burton, 1988), therefore, the results of $K_{\text{NP}} = 1$ and 0.7 have been presented. These figures also include observed biomasses of *Typha* [extracted from Vymazal (1995) and others listed in Table 2] for comparison. The value of K_{NP}

was estimated by simulated results of the entire growth pattern of the plant in each site as shown in Table 2. The plotted values are shown separately as $K_{\text{NP}} \leq 0.7$ and $0.7 < K_{\text{NP}} \leq 1$.

Some observed populations lasted only several years after the previous disturbance or after starting growth from seedlings, therefore, these populations seemingly have been in developing (or recovering) stages. In such instances, the biomasses are smaller than the values for the equilibrium populations (Robert and Ganf, 1986; Garver

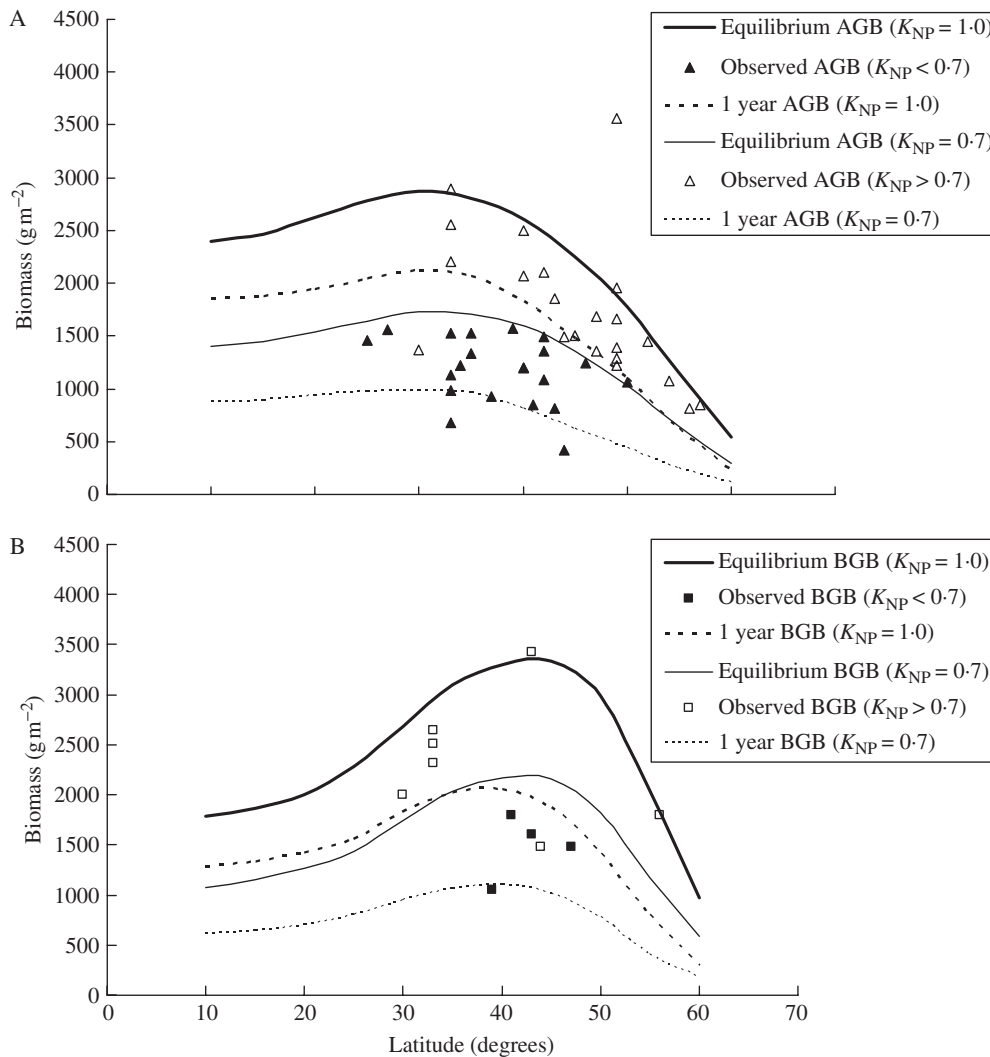


FIG. 5. Maximum biomasses for *T. latifolia* modelled for $K_{NP} = 1$ and 0.7 at latitudes 10–60, with observed data from a range of sources (see text): (A) above-ground biomass (AGB); (B) below-ground biomass (BGB).

et al., 1988). Figure 5A and B shows the simulated biomasses of both 1-year-old population from seedling and the population in the equilibrium stage. For both $K_{NP} \leq 0.7$ and $0.7 < K_{NP} \leq 1$ populations, most of the observed data are plotted between relations of 1-year-old and equilibrium populations.

Biomasses in the equilibrium stage show an inconsistent variation of above- and below-ground biomass along the latitudinal gradient. Above-ground biomass was fairly constant across low latitudes, up to about 35° (Fig. 5A). Below-ground biomass, however, increased steadily up to 45° before markedly decreasing at higher latitudes (Fig. 5B). Above-ground biomass was larger than below-ground biomass at low latitudes, and gradually decreased at latitudes greater than 35°.

Relationship between latitude and number of cohorts

Table 4 shows the annual maximum above and below-ground biomasses, the gross production, and the upward and

downward resource translocation as a function of the number of cohorts at three latitudes. At each latitude, above-ground biomass increased with the number of cohorts. In contrast, below-ground biomass showed a more complex, inverse relationship. At 30°, maximum above-ground biomass was highest with three cohorts; however, at 40° the highest value was obtained with a two-cohort system and at 50° with a single cohort.

Regardless of latitude, total growth production was enhanced by increasing the number of cohorts. Accordingly, the downward translocation was larger with more cohorts; however, the increment rate due to increasing cohort number was smaller in higher latitudes: a three-cohort system increased the downward translocation by 28% at 30°, but by only 11% at 50° compared with that of one-cohort system. The upward translocation to form shoots also increased with increasing number of cohorts, although at a relatively lower rate than that of the downward translocation: changing a single-cohort to a three-cohort system increased the upward translocation by 70% at 30°, 77% at 40° and 83% at 50°.

TABLE 4. Maximum above- and below-ground biomass ($g\ m^{-2}\ d.\ wt$) as a function of number of cohorts

Latitude	No. of cohorts	AGB	BGB	Gross production	Upward translocation	Downward translocation
30	1	2540	2390	8490	450	2820
	2	2920	2680	9960	650	3340
	3	3080	2750	10610	760	3610
40	1	2420	3100	6380	540	2330
	2	2690	3300	7360	800	2800
	3	2780	3160	7470	960	2890
50	1	1760	3110	3600	490	1720
	2	1910	3020	3730	770	1850
	3	1960	2980	3810	880	1920

AGB, above-ground biomass; BGB, below-ground biomass.

The difference in the variable rate of translocation due to the increasing number of cohorts caused the complex behaviour in the below-ground biomass.

DISCUSSION

In this study, a mechanistic growth model for *Typha* spp. based on the conservation of biomass was developed, and the computed results matched the observed data to a satisfactory level. Subsequently, the model was applied to the latitudinal growth behavioural differences to elucidate the interaction between the above- and the below-ground systems during the growth process and to study how the number of cohorts affected the above- and the below-ground interaction.

Seasonal patterns of above- and below-ground production

The growth of shoots, incorporated with the rhizome biomass initially, is later supported by photosynthesis production and depends on the above-ground biomass as well as local environmental conditions such as climate, substrates and nutrient availability. If other resources are abundant, then the solar radiation and temperature are the principal factors regulating shoot growth, which then affects the rhizome growth in the year through the downward translocation of photosynthates and the above-ground reserves (McNaughton, 1966; Gustafson, 1976; Asaeda and Karunaratne, 2000). Therefore, the long-term growth of shoots and rhizomes, which is different from the annual growth depending on both the local climate and the initial rhizome biomass, are dependent only on the climate at each site (Fig. 3).

Above-ground biomass during the growing season is increased by the surplus of the sum of the initial upward translocation of rhizome reserves and the later photosynthetic gross production over the respiration and mortality losses. The annual gross production and the losses depend on climate and the above-ground biomass, while the initial upward translocation to form shoots is influenced by the below-ground biomass, having been enhanced as a result of the downward translocation in the previous year. Thus, for each latitude, the maximum above-ground biomass is

determined by the early spring rhizome biomass, whereas during the latter part of the season, the net production depends on the climate. Above-ground biomass then increases rhizome biomass through translocating resources remaining after respiration and mortality losses.

Unlike metabolic losses, which are more or less proportional to total biomass, gross production undergoes various restrictions such as mutual shading, and hence does not simply increase in accordance with the above-ground biomass (Gustafson, 1976). Therefore, annual losses, which are smaller than gross production when the above-ground biomass is small, exceed annual gross production with a large above-ground biomass (Fig. 4).

If the initial rhizome biomass is small, then the above-ground biomass is correspondingly small, which, however, provides a gross annual production that is larger than the losses. Net production in a year, therefore, increases rhizome biomass, which in turn will increase the above-ground biomass in the subsequent growing season (Robert and Ganf, 1986; Garver *et al.*, 1988). Even if an initial rhizome biomass that is too large, on the other hand, produces a large above-ground biomass, losses associated with a large total biomass exceed the gross production, resulting in a decrease in the rhizome biomass and a smaller amount of reserves available for shoot growth in the following year; this in turn reduces the above-ground biomass (Fig. 3).

Equilibrium seasonal pattern

Through the net production in a year, the early spring below-ground biomass in the next year gradually shifts toward a potential value, followed by the above-ground biomass, the gross production and the metabolic losses, finally converging to their equilibrium values or seasonal patterns, where the annual gross production balances the annual metabolic losses.

The time taken to reach the equilibrium seasonal pattern depends on the net production rather than the gross production or the difference between the present and the equilibrium below-ground biomass in early spring. The net production increases or decreases more intensively depending on how far the below-ground biomass is away from its equilibrium value. Therefore, although the rate of convergence is high when the below-ground biomass is very different from its equilibrium value, it gradually slows down as it approaches the equilibrium value. When the below-ground biomass reaches the equilibrium value, then the annual net production becomes zero and the balance between total production and total metabolic losses is maintained at this level by local climate conditions, unless disturbed in some way.

A population is considered to follow the patterns in the equilibrium stage only if it is growing in a stable meteorological cycle for a long time. However, some experimental sites that were examined in this study have not undergone a sufficient period after the previous disturbance. Although there are other restrictions for growth, such as nutrient shortage, effect of the litter layer, etc., the insufficient period for the full development of the stands may be the factor that caused a smaller biomass than the equilibrium values.

This study found that, in the above-ground production, the contribution of resource translocation from rhizomes increased with latitude, with a contribution of 22 % to gross above-ground production at 30°, 30 % at 40° and 40 % at 50°, respectively, indicating larger dependence on resource translocation rather than the later net production in higher latitude populations. Since the net production facilitates the recovery to the equilibrium biomass, if the initial biomass is different from the equilibrium value, then *Typha* populations at high latitudes will take longer to reach the seasonal equilibrium pattern, taking 5 years at 50° compared with 3 and 4 years at 30° and 40°, respectively (Fig. 3). These results suggest that *Typha* at low latitudes may be more resilient than at high latitudes, and that the effect of repeated disturbances such as fire, grazing or harvesting is latitude-specific.

Maximum above- and below-ground biomass ratios

Figure 5B shows that rhizome biomass is larger at high latitudes, at least up to 45°, than in low latitudes.

The curves for 1-year-old and equilibrium conditions provide a range of growth of a *Typha* population under nutrient-unlimited conditions ($K_{NP} = 1$) or under nutrient-limited conditions ($K_{NP} = 0.7$). These curves envelope most of the field data, even though the observed values are affected by various factors, such as experimental errors, developing stage of the stand after the establishment or disturbance, and other restrictions of environmental factors such as nutrient availability or herbivory. Figure 5A and B shows that a 1-year-old population (when $K_{NP} = 1$) has 70 % and 67 % of above- and below-ground biomasses of the equilibrium stage, meanwhile, the decrease of K_{NP} from 1 to 0.7 reduced the equilibrium values by 45 % and 35 % of above- and below-ground biomasses, respectively.

Equilibrium values of both above- and below-ground biomasses essentially depend on photosynthetic gross production and total losses. The simulation indicates that gross production stays high up to about 20° in latitude, then decreases, presumably in association with decreasing radiation and temperature in the growing period. In this study it was found that annual losses decreased rapidly with temperature and were extremely low at high latitudes. Therefore, despite low gross photosynthetic production at high latitudes (Knapp and Yavitt, 1995), *Typha* can maintain a larger rhizome biomass than at low latitudes. As a result, although gross production starts to decrease at about 20° in latitude, above-ground biomass stays high up to 35° (Fig. 5A), and below-ground biomass, with its low metabolic loss in low temperature, actually increases, reaching a maximum at 45° before declining (Fig. 5B).

The ratios of maximum below-ground to maximum above-ground biomass, therefore, varied from 0.75 at 20°, 1.0 at 35° to 1.6 at 50°, which are comparable to 0.95 at 33° (Hill, 1987), 1.4 at 47° (Garver *et al.*, 1988) and 1.5–1.8 at 49° (Dykyjova, 1971). This implication also agrees with the data showing that rhizome proliferation is stimulated by the cool temperatures at high latitudes (McNaughton, 1966; Reddy and Portier, 1987).

Having a large rhizome system at high latitudes makes *Typha* extremely tolerant of environmental disturbances and of damage to above-ground organs, which are more responsive in *Typha* in cold climates (McNaughton, 1966). The amount of reserves in rhizomes utilized in spring for shoots and for establishing the canopy is 35 %, 31 % and 25 % of initial rhizome biomass, respectively, at 30°, 40° and 50° in latitude (data not shown). Thus, the rhizome biomass of a *Typha* population at the latitude of 50° is equivalent of four sets of spring shoots compared with only three at 30°. This is similar to data reported for another emergent macrophyte with a wide latitudinal distribution, *Phragmites australis* (Granelli *et al.*, 1992).

Another advantage of a large rhizome system is that in spring shoots can grow rapidly. This is an advantage at high latitudes due to the relatively short growing season. Being stimulated by rising temperatures in spring, a large rhizome biomass, with a low metabolic cost during winter, enables the early emergence from over-wintering buds and the rapid growth thereafter (Gustafson, 1976; Fiala, 1978; Dickerman and Wetzel, 1985).

No nutrient limitation, which is reasonably true in many cases with *Typha* species as they are eutrophic plants, especially in long-term populations, was assumed in the model, and all calculated processes were generalized upon this assumption. However, the below-ground biomass can increase markedly as nutrients become limited when a *Typha* stand invades highly calcareous wetland sediments (Grace and Wetzel, 1981a). Other studies also indicated that the below-ground to above-ground biomass ratio increases with decreasing fertility (Cary and Weerts, 1984; Ulrich and Burton, 1988). This effect of nutrient availability on the growth dynamics of *Typha* needs further study.

Effect of the number of cohorts

This study shows that as the number of cohorts increases, both above- and below-ground biomasses also increase at low latitudes, but at high latitudes, rhizome biomass decreases. More cohorts extend the period of active growth and delay the time when maximum above-ground biomass is reached (Dickerman and Wetzel, 1985); however, the contribution of later cohorts is latitude-specific (McNaughton, 1966). The first cohort, subject to increasing solar radiation and rising temperature in spring, grows rapidly from over-wintering buds, then photosynthesizes throughout the summer, translocating enough photosynthates downwards to grow rhizomes after compensating for the expense of the initial growing stage. In contrast, later cohorts (i.e. in autumn) experience lower and decreasing radiation levels and lower temperatures, and are unable to compensate for the expense of the initial shoot growth, which, thus, leads to a reduction in rhizome biomass at high latitudes (Table 4). The shorter growing season is suggested to be a reason for the immature growth of later cohorts at high latitudes compared with that at low latitudes (McNaughton, 1966). Having multiple cohorts, therefore, seems to be disadvantageous for a rhizomatous plant such as *Typha* at high latitudes.

Despite this disadvantage for rhizomes at high latitudes, above-ground biomass increases with the number of cohorts

regardless of latitude. The later cohorts contributed only a small part of the total gross production in the year: 20 % at 30°, 14 % at 40° and 5 % at 50° (data not shown). However, the later cohorts, which have a higher probability of overwinter survival at higher latitudes (McNaughton, 1966), sometimes can survive through winter and start to grow earlier than newly emerging shoots due to rising temperatures in spring (Dickerman and Wetzel, 1985). The overwintering shoots, which are mostly immature shoots remaining from the later cohort, were reported to contribute greatly (>50 %) in the total production of population in the subsequent year (Dickerman and Wetzel, 1985). The formation of later cohorts, therefore, provides an advantage over other species in the competition for light (Fiala, 1978; Dickerman and Wetzel, 1985).

Applications of the model

Although developed to explore growth responses of *Typha* as a function of latitude, the model has wider applications because it can predict the growth of populations in any given condition as well as the potential growth of *Typha* over a wide range of latitudes for periods ranging from a single season to several years. At this stage, the model does not consider the effect of nutrient availability on the growth dynamics of *Typha*. To do this would require specific studies, targeting how variations in nutrient availability affect the growth and phenology of *Typha*, and how these responses vary with latitude. This would be useful for wastewater treatment systems using *Typha*, as well as for understanding the effects of climate variation on natural populations. In addition, the structure of the model could easily be adopted for other emergent species which have morphological characteristics similar to *Typha* by appropriately calibrating relevant parameters. Models similar to this can be integrated into comprehensive aquatic ecosystem models in order to understand the interaction of organisms in the aquatic ecosystem.

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