

Numerical prediction of the nutrient-limiting growth of *Phragmites Japonica* through soil-plant-atmosphere column

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This paper proposes a new approach for modeling plant growth based on the assumption that required nutrient results from root uptake is needed for optimal growth. Field survey and growth model of *Phragmites japonica* are presented. Growth is considered to be the plant dry matter accumulation and shoot height. This model consists of coupling a transportation of water and nutrient through soil-plant-atmosphere column (SPAC) to crop growth. Nutrient uptake is investigated numerically based on mass flow process. The model was parameterized and calibrated by using observed data collected during one growing season from May to November, 2005. The model was shown to perform well against observed data by 0.93 and 0.87 of efficiency of biomass and height respectively.

Keywords: *Phragmites japonica*, growth model, nutrient uptake, SPAC

1. Introduction

Riparian zones play an important role in shaping stream ecosystems, influencing habitat complexity, biodiversity, energy and nutrient flows (Cooper et al. ¹⁾). Much riparian vegetations have cleared from stream banks or floodplains since activities associated with urbanization, irrigation, navigation, flood mitigation or river engineering (Webb et al. ²⁾). As values of riparian vegetation become better recognized, large amount of resources and improvement have been invested in recovering vegetation bar as part of river rehabilitation program. In recent decades, it has been reported that the number of vegetated bar has been gradually increased.

The development of computation technology, which has enabled to handle very complex and quick-solution mathematical system, has made a big boom in intensifying number of numerical models to simulate crop growth in recent years.

Nutrient and water are indispensable and interrelated components for producing high yields in plant. Nutrient is uptake from soil solution by root as plant food, stored inside their cell and finally incorporated with the energy from sunlight to formulate the matter through the process named photosynthesis. By transpiration, water dissolves nutrients from the soil and transports them up from the roots and throughout the plant, where they serve as raw materials in the growth of new plant tissues. It therefore has established an interaction in vertical column among three parts: soil-plant-atmosphere.

The dynamics growth of macrophyte has been investigated in some researches, as Asaeda et al. ³⁾, Allirand and Gosse ⁴⁾. However, it may be fundamentally flawed due to the lack of consideration of nutrients. Asaeda ³⁾ expressed "...net plant photosynthesis was assumed to be restricted by irradiance, temperature and the age of assimilatory meanwhile nutrient stress was ignored." As plants possess a great capacity to take up nutrients, it is possible that an imbalanced supply of the main nutrients, nitrogen and phosphorous especially, of course adversely affect the metabolism and hence the growth (Romeo et al., ⁵⁾).

On the other hand, water may affect to amount of stored nutrient in plant because of playing an essential part as transporting fluid of nutrient providing to photosynthesis process. Nevertheless, most of recent researches have not pay attention to water as transporting fluid of nutrient. Asaeda ³⁾ pointed the weak points of previous model out and concluded that "...extensive studies are needed to understand the effects of water regime on growth dynamics."

In light of this, despite the recent effort of Kang ⁶⁾ on modification of the growth model in relation to nutrient, it seems to be incomplete since the limitations of nutrient has not been taken into account. Consequently, those have created a gap concerning the plant responses of nutrient limitations to crop production. An improved understanding of nutrient availability- uptake- growth

relationship, therefore, has become essential in developing growth model.

To further address these issues, within this article, we aim to highlight another approach to connect nutrient on crop production. Firstly, the water-nutrient uptake will be integrated in a growth model based on soil -plant-atmosphere column (SPAC). Based on this, the gross photosynthesis formula will be revised. Being of a common perennial reed in Japanese river, *Phragmites japonica* (*P.japonica*) has been chosen in this study.

The objective of this study is to develop a simple and one-dimensional, but basically sound tool that can be used for predicting dry weight and height of plant during growing season.

This paper is divided into three sections: field investigation, model description and the discussion of results. The first section is devoted to the description of the various field works and kinds of data evaluated. While the scheme of the model is presented in second section, the last section contains the analysis of the model performance. The verification of the model will be done on the base of field measurements.

2. Field Investigation

2.1 Site description

The site of study for the macrophyte of *Phragmites japonica* is located at a sandbar 17km from the mouth of the Yahagi river, Japan. Fig.1 shows the distribution of vegetations on the bar. Field measurements have been performed to determine the characteristics of plant growth, nutrient availability and photosynthetic activity among macrophyte population. The collected data are the basis for the development of a numerical model to simulate the plant growth.

2.2 Methods

Two major investigation works were plant and water sampling. Three locations were selected to carry out as shown in Fig.1

To take subsurface water samples, three wells were inserted in soil with 1.2-1.7m of depth. Subsurface water level was measured at each well. Subsurface water samples were taken to analysis concentration of ammonia, nitrite, nitrate, total nitrogen, phosphate and total phosphorous. These samples were measured by the colorimeter analyzer (DR/890, HACH Inc.).

Plant sampling was conducted every two weeks. The numbers of stems at a height of approximately 10 cm above ground were counted by using 50 cm×50 cm of quadrat. Aboveground biomass of *P. japonica* was also sampled in quadrat by using hedge clipper. Each sample was dried at 105°C in 12 hours to determine total, leaf and stem dry mass. The stem diameters were also recorded together with the lengths in five individuals on quadrat. Whole plants were harvested every two months and then fractioned into roots, stems and leaves to calculate the portion biomass of each organ. Porometer (LCi, ADC Bioscientific Ltd.) was used to investigate

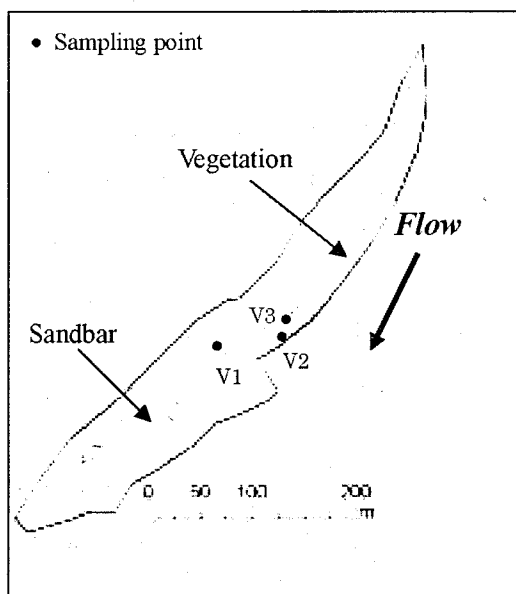


Fig. 1 Locations of sampling.

transpiration, photosynthetic active radiation (PAR) and light attenuate coefficient among plant community.

3. Model Description

It is well known that the supply of water and nutrient from soil to plant is of fundamental importance to the growth of green plants. The process of nutrient uptake refers to the water transfer from soil solution by plant root. Afterwards, absorbed water is released out of plant to atmosphere through transpiration. Meanwhile some nutrients eventually contribute to produce matter by photosynthesis process. The part concept of plant growth model is thus based on the idea of soil-plant-atmosphere column.

The net growth of each fraction overtime can be the result of photosynthesis, respiration and mortality, as expressed by

$$\frac{dB}{dt} = P - R - M \quad (1)$$

where B, P, R, M are biomass, gross photosynthesis rate, respiration rate and mortality rate (g/m²/day).

Therefore, the structure of model is divided into three parts: production, mortality and respiration. The diagram of the model is shown in Fig.2.

3.1 Gross photosynthesis

The total amount of growth for a given time interval depends largely on photosynthesis process (Wang and Engel, ⁷⁾). Transpiration and root uptake are attached in photosynthesis process, because they directly affect to amount nutrient absorb which contributes in photosynthetic production through control of leaf water potential.

Of all the mineral elements required by photosynthesis, nitrogen is needed in the greatest amount and most significantly affect to the growth of *Phragmites*

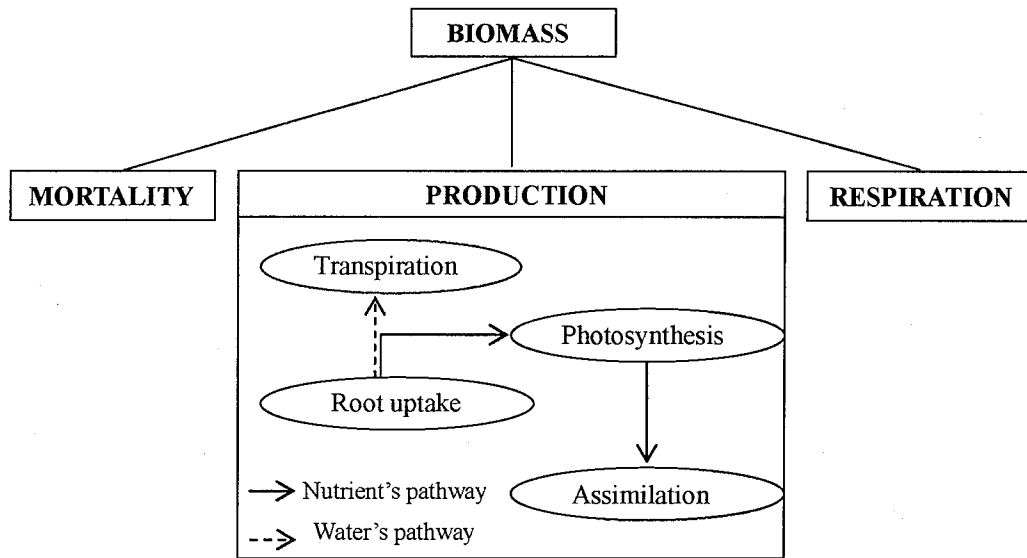


Fig. 2 A diagram of growth model.

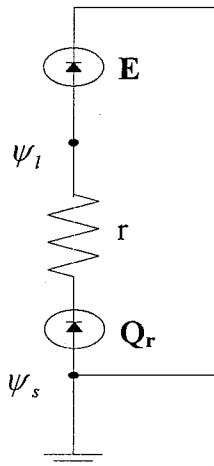


Fig. 3 Electrical analogue scheme of water movement within the plant.

spp than phosphorus (Romero et al., ⁵⁾). The ratio of nitrogen and phosphorus (N:P) has been widely used as an indicator factor to determine which nutrient may limit growth. Romero ⁵⁾ also claimed N:P ratio in nutrient source in range of 4 and 14 on weigh basis (equivalent of 10 and 33 on molar basic) produce a maximized growth. Koerselman and Meuleman ⁸⁾, furthermore, strengthened that the N:P ratio less than 14 should indicate nitrogen limitation on community level. In the present study, the N:P ratio in subsurface water varied between 1 and 13, which would be indicative of nitrogen limitation according to the relationship above.

Moreover, Liebig's Law of the Minimum states that yield is proportional to the amount of the most limiting nutrient. From above reasons, in among nitrogen and phosphorous, it may be inferred that nitrogen affects the yields more than other. Therefore, to simplify the model, only nitrogen is mentioned, even though phosphorus is also important for plant growth. As plant roots use dissolve inorganic nutrient only and nitrogen is the most limiting factor of production, inorganic nitrogen, hence, is considered in this model.

(1) Water/nutrient transport

The pathway of nitrogen absorption and translocation to leaves by photosynthesis and the way of water uptake by transpiration are important for plant growth. Most of plant nitrogen are supplied by mass flow of water, however a part is supplied by diffusion (Barber and Peterson, ⁹⁾). For simplicity, this article only considered the flow of nitrogen to the root system as convective (mass flow). Mass flow involves the movement of nutrients along with the water that is being absorbed by plant root. Then, the amount of nutrient being transported by mass flow is given by the product of the volume of water absorbed and the concentration of the nutrient in the soil solution.

In SPAC, the movement of nutrient through the soil solution towards the plant in the mass flow is caused by driving force. Conceptually, water transport in the plant is induced by the gradient in total water potential between the soil and the leaves. That kind of movement is mathematically described based on an analogy of electric circuit by Ohm's Law which is shown in Fig.3.

The total root uptake is calculated as:

$$Q_r = \frac{\psi_s - \psi_l}{r} \quad (2)$$

where Q_r denotes root water uptake ($\text{g/m}^2/\text{s}$), r describes the overall resistance ($\text{m}^3/\text{s/g}$), ψ_s is defined as soil water potential (m) and ψ_l is leaf water potential (m).

The total root resistance is obtained by:

$$r = \frac{r_o}{\int_0^l b_r(z) dz \times srl} \quad (3)$$

in which r_o is expressed as resistance per unit length of root ($\text{m}^2/\text{s/g}$), b_r denotes root biomass per unit of root's length (g/m), l defines length of root (m) and srl is

specific root length (m/g). The specific root length is assumed to be constant.

The total amount of water lose through transpiration over the height is depicted by (Kanda, ¹⁰) as follow

$$E = k_H \times u \times sla \times (W_s - W) \int_0^h b_l(z) dz \quad (4)$$

where E is transpiration rate ($\text{g/m}^2/\text{s}$), h displays the height of plant (m), k_H denotes exchange coefficient of vapor (dimensionless), u describes wind speed (m/s), sla manifests specific leaf area (m^2/g), b_l depicts leaf biomass per unit of plant's height (g/m), and $(W_s - W)$ is the difference of water vapor concentration between leaf air spaces and the air outside the leaf (g/m^3). The specific leaf area (sla) is assumed to be constant during the period of modeling.

However, Kanda ¹⁰ proposed that the rate exchange of vapor (k_H) is given by the combination effect of photosynthesis active radiation-PAR (I), maximum vapor exchange (k_{Hmax} , $\text{m}^{1/2}/\text{s}^{1/2}$) and leaf water potential (ψ_l)

$$k_H = u^{-\frac{1}{2}} k_{Hmax} [f_1(I) f_2(\psi_l)]^{\frac{2}{3}} \quad (5)$$

From this equation, $f_1(I)$ and $f_2(\psi_l)$ are functions indicating the dependence of PAR and the leaf water potential on k_H as calculated by:

$$f_1(I) = \frac{I}{c_0 + c_2 I} + c_3 \quad (6)$$

Furthermore, the following Lambert-Beer's law may approximated the distribution of PAR in plant community:

$$I = I_0 e^{-kz} \quad (7)$$

where I_0 , I are PAR at the top surface of community and PAR passing through the leaf surface (W/m^2), k : the light extinction coefficient within the community ($1/\text{m}$), z : depth from the top surface of the plant community (m).

Then, the above equation (6) can be rewritten as

$$f_1(I) = \frac{e^{-kz}}{c_1 + c_2 e^{-kz}} + c_3 \quad (8)$$

$$f_2(\psi_l) = e^{-c_6 \theta_s \left(\frac{\psi_b}{\psi_{ml}} \right)^{\frac{1}{b}}} \quad (9)$$

$$\psi_l = \psi_{ml} + \int_0^h z \times dz \quad (10)$$

where c_0 , c_1 , c_2 , c_3 and c_6 are numerical constants, θ_s shows saturated volumetric water content of soil in root zone (m^3/m^3), ψ_b denotes air-entry suction head (m), ψ_{ml} :

leaf matric water potential (m) and b displays empirical specific parameter (dimensionless).

Most of water uptake by root is used for transpiration. It, therefore, is possible to assume the transpiration is equal to the root uptake.

$$Q_r = E \quad (11)$$

To run the model, initial values of leaf, stem and root biomass are needed. The set of ultimate formulas to solve the amount of water being uptake is equation (2), (4) and (11). The leaf water potential (ψ_l) firstly is defined from these equations by iteration process. The amount of water Q_r is finally specified by equation (2).

(2) Photosynthesis

Since the demand of nutrient varies depending on the growth period, the uptake rate of nitrogen within the plant is regarded as a kinetic process. This kinetic which mostly used for the description of enzyme-catalyzed reactions is described by Michaelis-Menten equation.

Michaelis-Menten kinetics is often used to relate solution concentration of particular nitrogen to uptake (Romero et.al, ⁵) and Tlylova-Munzarova et al., ¹¹) and it also can be included in determination photosynthesis rate (Aseada ³).

Aseada ³) and Kang ⁶) proposed the photosynthesis model without consideration of nutrient uptake limitation. In this study, the gross photosynthesis rate is corrected by revising the classical photosynthesis model. That is a first attempt to drive the contribution of nitrogen to material production.

$$P = P_m \times \frac{Q_r \times N_s}{K_u + Q_r \times N_s} \quad (12)$$

As a rule, ion uptake by plant roots has features of saturation kinetics that can be seen by the last expression in accordance with the Michaelis-Menten. P , P_m denotes the photosynthesis and maximum photosynthesis rate ($\text{g/m}^2/\text{d}$); K_u is half saturation coefficient of amount of nutrient uptake ($\text{gN/m}^2/\text{d}$). N_s express nitrogen concentration in soil solution (mg/L)

3.2 Respiration

A part of the biomass is exerted for respiration to provide energy for maintaining the existing plant components. The respiration rate which are computed by Hootsmans as proportional to their biomass and specific rate (Asaada, ³) described as the set of following equations

$$R_l = \varepsilon \int_0^h b_l(z) dz \quad (13)$$

$$R_{st} = \varepsilon \int_0^h b_{st}(z) dz \quad (14)$$

$$R_r = \varepsilon \int_0^l b_r(z) dz \quad (15)$$

where R_b , R_{st} and R_r denote respiration of leaf, stem and root respectively ($\text{g/m}^2/\text{day}$). ε is the specific rate of respiration. b_b , b_{st} refer the biomass of leaf and stem per unit stem's height. b_r is the root biomass per unit root's length.

The depth of root (l) is depicted by combination of the total root biomass and root density (ρ_r , g/m^3) as follow

$$l = \frac{\int_0^l b_r(z) dz}{\rho_r} \quad (16)$$

3.3 Mortality

The mortality refers the loss of biomass to carry out essential physiological processes. It is also calculated in the same way of respiration.

$$M_l = \delta \int_0^h b_l(z) dz \quad (17)$$

$$M_{st} = \delta \int_0^h b_{st}(z) dz \quad (18)$$

$$M_r = \delta \int_0^l b_r(z) dz \quad (19)$$

M_b , M_{st} and M_r are mortality rate of leaf, stem and root ($\text{g/m}^2/\text{day}$). δ manifests the specific rate of mortality.

3.4 Biomass partitioning

During the vegetative growth period, *P.japonica* has three components namely leaf, stem and root. The distributed biomass ratio of each organ is supposed to be constant over the plant height or root length.

$$B_l = \int_0^h b_l(z) dz = b_l \int_0^h dz \quad (20)$$

$$B_{st} = \int_0^h b_{st}(z) dz = b_{st} \int_0^h dz \quad (21)$$

$$B_r = \int_0^l b_r(z) dz = b_r \int_0^l dz \quad (22)$$

Assimilate partitioning is the process by which assimilates available for growth are partitioned over the different components according to various partitioning coefficients.

$$P_l = \alpha_l P, P_{st} = \alpha_{st} P, P_r = \alpha_r P \quad (23)$$

$$P = P_l + P_{st} + P_r \quad (24)$$

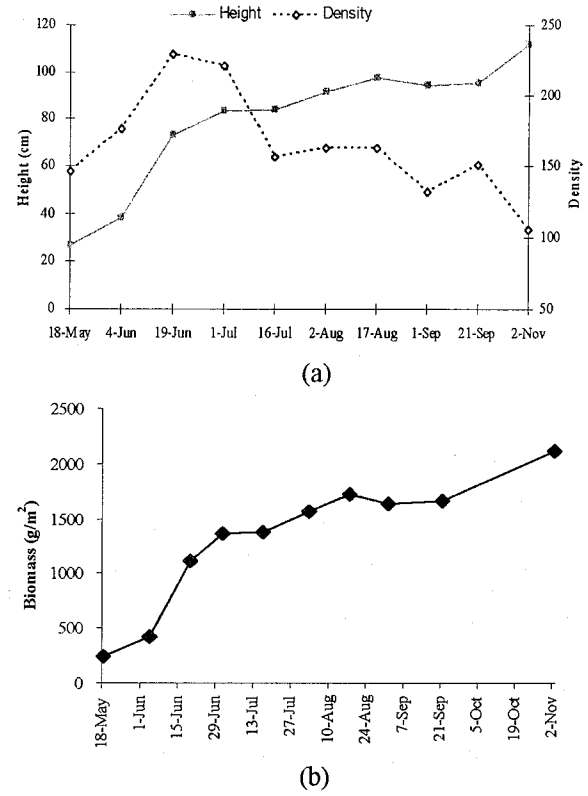


Fig. 4 Plant's growth expresses in (a) Mean height and population density (b) Mean above ground biomass.

In these formulas, α_l , α_{st} and α_r refer to fractions of total gross photosynthesis allocated to leaves, stems and roots respectively. However, because of difficulties in determining partition of photosynthesis production to other organ, material-allocation rate is assumed as a dry weight-partitioning ratio. The calculation of the net growth in each organ shows following results:

$$\frac{dB_l}{dt} = P_l - R_l - M_l \quad (25)$$

$$\frac{dB_{st}}{dt} = P_{st} - R_{st} - M_{st} \quad (26)$$

$$\frac{dB_r}{dt} = P_r - R_r - M_r \quad (27)$$

4. Results and Discussion

4.1 Field Investigation

Fig.4 shows the mean height and density of *P.japonica* community which markedly increase until July 2005 and gradually reach maximum at the end of growing season in November 2005. Population density nevertheless reaches the maximum value (240 individuals/m²) in the end of June and decrease afterward to 105 individuals/m² in November.

The relationship between plant height and stem biomass is shown in Fig.5. A logarithmic regression equation has provided the best fit with $r^2 = 0.8758$.

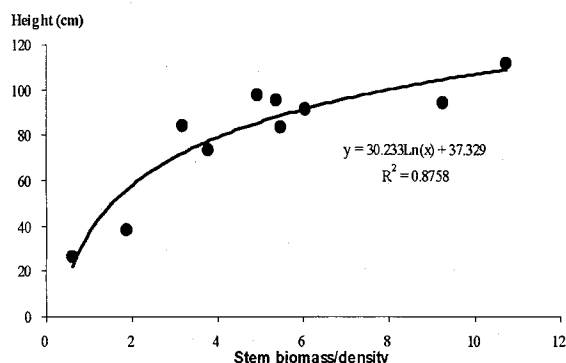


Fig.5 Means of individual height and stem biomass.

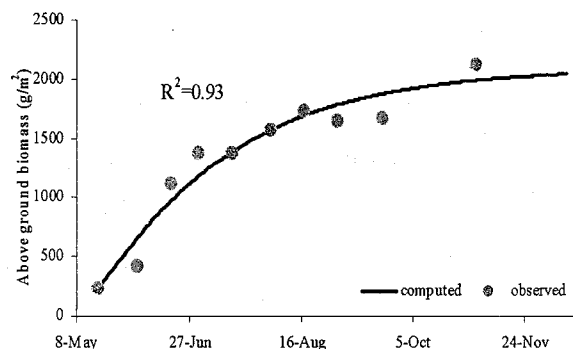
Therefore, it can be concluded that they correlate quite well. This information is used in model to estimate height of plant based on stem biomass. Because the purpose of this study is to figure out the crop growth, however, the other results of field observations which are needed, are summarized in Table 1.

4.2 Numerical Simulation

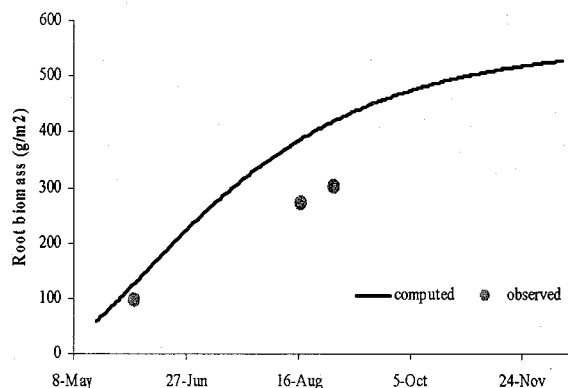
Simulation was conducted by using the collected data and the initial determined values. The model was calibrated to define the unknown variables; to compare between resulted and the observed data in changes of plant biomass and height during the growing season.

After screening several articles on crop growth modeling, four variables still remain non-inspected and need to be quantified including the maximum photosynthesis rate (P_{max}), the half saturation coefficient of amount of nutrient uptake (K_u), the specific respiration rate (ϵ), and the maximum vapor exchange (k_{Hmax}).

Following the equations (4) and (5), it is obvious that transpiration directly impact on k_{Hmax} . The first step of calibration was to adjust the maximum vapor exchange (k_{Hmax}) to match computed with observed transpiration. The transpiration at noon varied from 1.0×10^6 to 4.0×10^6 g/m²/day which was obtained from June to October 2005. is used as reference. The leaf water potential, ψ_l is an output of the soil-plant-atmosphere column as given in set of equation (2), (4) and (11). If $|\psi_l| > |\psi_{lc}|$ (ψ_l : leaf water potential, ψ_{lc} : critical leaf water potential), transpiration may reduce considerably (Braud et al., ¹²).



(a)



(b)

Fig. 6 Comparison between observed and computed aboveground (a) and (b) root biomass.

Typically, ψ_{lc} may vary between -100m and -150m of water (Friend, ¹³). For this reason, the leaf water potential was carefully observed during model running time.

Three remaining parameters (P_{max} , K_u and ϵ) which are in needs of determination were calibrated independently to fit the observed values of aboveground biomass and plant's height. The simulation started at 18, May and had been done for 249 days, covering the full period of field investigation. The values of the parameters used in model simulation are listed in Table 2. The correlation coefficient was employed to quantify the deviation of computed and measured results.

The simulated values of both aboveground biomass and height followed the observed values well untill 150 days (from May to October). The comparison between

Table 1: Summary results of field observations.

No	Parameters	Symbol	Mean value	Unit
1	Density	n	164	Individual/m ²
2	Total nitrogen concentration in soil solution	N_s	2	mg/L
3	Canopy light extinction coefficient	k	0.5	
4	Specific leaf area	sla	0.087	m ² /g
5	Specific root length	slr	200	m/g
6	Root density	ρ_r	1043	g/m ³
7	Partitioning coefficient of leaf	α_l	0.32	
8	Partitioning coefficient of stem	α_{st}	0.44	
9	Partitioning coefficient of root	α_r	0.24	

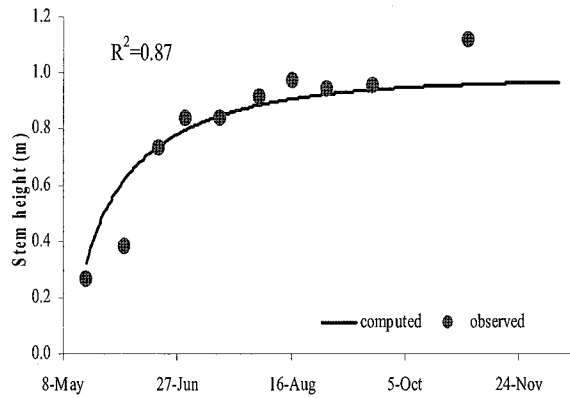


Fig.7 Comparison height of stem between observation and computation.

measured and computed results of aboveground biomass and stem height during the growing season shows very good agreement with the correlation coefficients 0.93 and 0.87, respectively as depicted in Fig.6(a) and Fig.7.

The difference between the last computed and observed values on 2nd November may result from changes in the numbers of stems. The illustrations of leaf and stem biomass are not showed as they have the same trend curve like the aboveground biomass. However, the root biomass as expressed in Fig.6 (b) is slightly underestimated. Although the observation of root

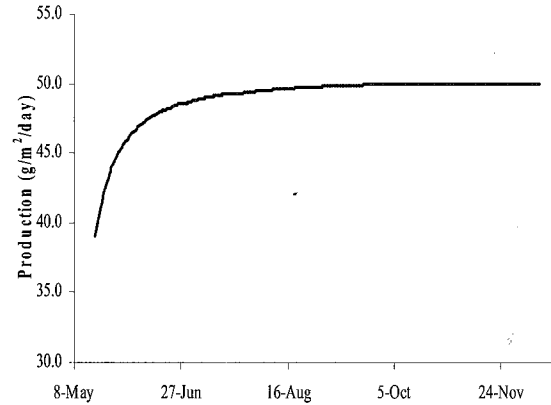


Fig. 8 Dry matter production.

biomass was not abundantly conducted, the observed ratio of leaf biomass to shoot biomass decrease from 1.04 (in May) to 0.45 (in November) may imply that the partitioning coefficient of root may change during the growth period. Aseada ¹⁴⁾ claimed that a translocating materials of photosynthesis production from aboveground to belowground organ was not invariable but depending on both rhizome age and the season.

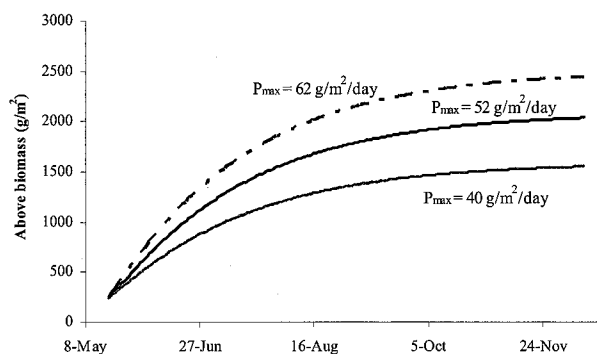
Fig.8 shows 39 ~ 50 g/m²/day of dry matter is produced by photosynthesis process. The results also display that the magnitude of leaf water potential is still in a critical status (around -42.5 ~ -34.1 m) and the transpiration rate varies from $1.5 \times 10^5 \sim 1.24 \times 10^6$ gH₂O/m²/day.

Table 2: Values of parameters used in the simulation.

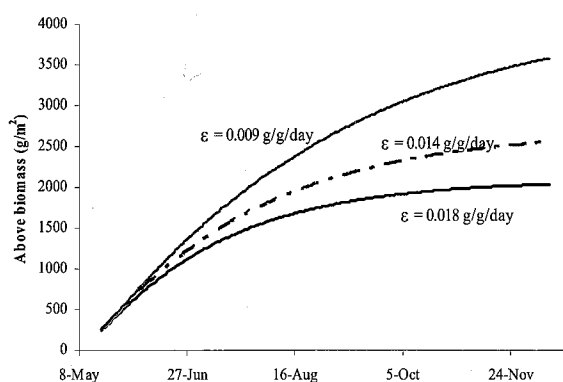
Descriptions	Symbol	Literature value	Assign value	Unit	Reference
Canopy light extinction coefficient	k	0.5	0.5		b,f
Soil water potential	ψ_s	-50	-50	J/kg	d
Air entry suction head	ψ_b	-10	-10	J/kg	d
Saturated volumetric	θ_s	0.4 ~ 0.5	0.5	m ³ /m ³	d,e
Nutrient concentration in soil solution	N_s		2	mg/L	f
empirical parameter	b	5 ~ 7	7		d
Resistance to water flux per unit length of root	r_o	2.5×10^{10}	2.5×10^{10}	m ³ /kg/s	a
Specific leaf area	sla		0.087	m ² /g	f
Specific root length	rl		200	m/g	f
Wind speed	u	2	2	m/s	
Maximum vapor exchange	k_{Hmax}		5	(s/m) ^{-1/2}	g
Saturation concentration of water vapor in leaf	W_s	25	25	g/m ³	d
Concentration of water vapor in air	W	16	16	g/m ³	d
Respiration rate	ε	0.007	0.018	g/g/day	c, g, i
Mortality rate	δ	0.00015	0.00015	g/g/day	c, i
Root density	ρ_r		1043	g/m ³	f
Partitioning coefficient of leaf	α_l		0.32		f
Partitioning coefficient of stem	α_{st}		0.44		f
Partitioning coefficient of root	α_r		0.24		f
Maximum photosynthesis rate	P_{max}		52	g/m ² /day	g
Half saturation coefficient of amount of nutrient uptake	K_u		0.1×10^6	gN/m ² /day	g

Sources of articles:

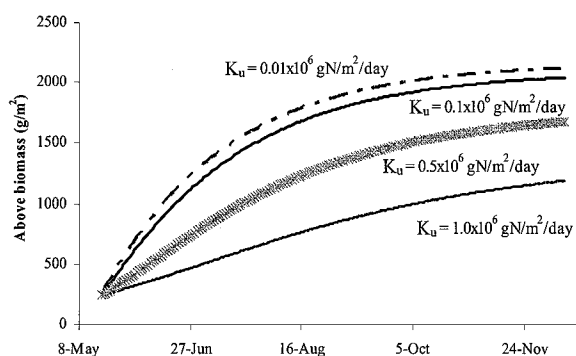
^a Campell ¹⁵⁾, ^b Running and Gower ¹⁶⁾, ^c Asaeda et al. ³⁾, ^d Friend ¹³⁾, ^e Braud et al. ¹²⁾, ^f Field investigation, ^g Model calibration, ^h Kang et al. ⁶⁾, ⁱ Karunnaratne et al. ¹⁷⁾.



(a)



(b)



(c)

Fig. 9 Sensitive analysis with (a) maximum photosynthesis rate P_{max} (b) respiration rate ϵ and (c) half saturation of amount of nutrient uptake K_u .

In terms of both growth characteristic and demand of nutrient uptake, one can recognize two stages during the growth period: the raising and constant rate stage. The raising stage, in which, the environmental conditions are optimal, *P.japonica* produces materials at the maximum rate. In the constant rate stage, at the end of the growing season, *P.japonica* attains the dynamic equilibrium condition on growing. Instead of continuing gaining more weight, *P.japonica* executes a transformation of physiology such as panicle emergence, translocation of dry matter to store at belowground organ for the following growing season. It is apparent that the gross production and the metabolic losses finally converge both of biomass and height curve to achieve the equilibrium of *P.japonica*'s growing (Fig. 6 and Fig. 8).

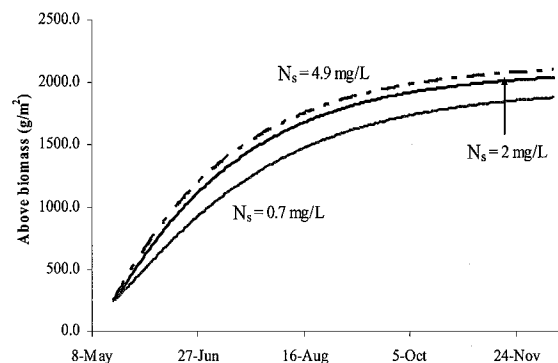


Fig. 10 Variations in aboveground biomass at three levels of nitrogen concentration.

A sensitivity analysis was performed to investigate the influence of the parameters on the results. The analysis of growth was conducted by varying the measured values of each parameter independently. For each test, only the value of the studied parameter was modified, whereas the remaining parameters and input variables were maintained at their supposed values.

Among all the tested parameters, sensitivity analysis results showed that model outputs were only sensitive to variations of the maximum photosynthesis rate, the specific respiration rate and the half saturation of amount of nutrient uptake. It was found that the maximum photosynthesis rate (P_{max}) and the specific respiration rate (ϵ) are the most sensitive on growth magnitude as illustrated in Fig. 9 (a) and (b) whilst half saturation of amount of nutrient uptake affects the shape of growth curve given in Fig. 9 (c).

Fig. 9 (a) shows that the profiles of growth for each test run was almost identical. Any change in maximum photosynthesis rate would be directly impact on the amount of dry matter to be produced. As indicated in the literature, the specific respiration rate is proposed around value of 0.007 g/g/day. The choice of the specific respiration rate (ϵ) in this model however, is also significant since *P.japonica* may possess different respiration characteristic to another *Phragmites spp.* The curve trends from Fig. 9 (b) express the meaning of ϵ to achieve the equilibrium status of plant growth characteristic. The bigger the values of ϵ , the earlier the equilibrium stage will be reached. For this reason, respiration is an unavoidable part in developing the dry matter accumulation of *P.japonica*.

Different from P_{max} and ϵ , the variation of K_u may or may not vary on both magnitude and shape of growth curve depending on value of K_u . It is obvious that the shape and magnitude would not be fluctuated if value of K_u smaller than 0.1×10^6 . Conversely, rising up K_u would make the curve change differently than previous one.

To test the interactive effects of nitrogen concentration (N) in root solution on growth, three levels of concentration including minimum, maximum and mean values (0.7, 4.9 and 2 mg/L, respectively) are examined. Fig. 10 shows that the nitrogen level significantly affects the growth rate of plant. The rate is being lowest at minimum N, higher at intermediate and

highest at maximum N. Nevertheless, the biomass at the maximum value of concentration was slightly greater than that at average value. The biggest difference between biomass of maximum and minimum N was 288.8 g/m² in comparison to 74.6g/m² of intermediate and maximal N.

To evaluate the influences of root partitioning coefficient on model performance, three values of root partitioning coefficient were tested ($\alpha_r=0.12, 0.2, 0.24$). In order to achieve mass conservation whilst changing root-partitioning coefficient, values of leaf and shoot partitioning coefficient were set at 0.36, 0.33, 0.31 and 0.52, 0.47, 0.45 respectively based on 0.7 of the mean ratio of leaf and shoot biomass. The results showed that root biomass curve fitted well with observation at 0.12 of root-partitioning coefficient. These curves of leaf, shoot biomass and stem height however displayed very good agreement with observation until beginning of August but shows moderately good fitting from August to November by the overall correlation coefficients of 0.5, 0.67, and 0.55 respectively. It may support the hypothesis that the partitioning coefficient of root may change during the growth period. The bigger the values of root-partitioning coefficient, the higher the degree of accuracy in aboveground biomass and height will be obtained.

It is possible to indicate that the growth rate has been strongly related to nitrogen concentration in root solution less than 2 mg/L, however a higher level of N has an inconsiderable effect. The half saturation coefficient of amount of nutrient uptake may be a main agent in order to adjust the amount of nutrient demand or constraint the ability productivity through equation (12).

5. Conclusion

Although many attempts have been made to develop a growth model of macrophyte, the effect of nutrient uptake on growth still has not been considered. In order to achieve more capability, this study presents a new approach in developing a crop growth model. Conceptually, to deal with nitrogen uptake on growth, the soil-plant-atmosphere column should be applied.

Growth performance of perennial stands of *P. japonica* was investigated during 6 months. Temporal variations of biomass and height as well as population density have shown growing traits. Stem biomass and height exhibited the logarithmic pattern of relationship.

A model has been formulated to reproduce the growth of *P. japonica*. Agreement between simulated and measured data provides a modeling efficiency of 0.93 and 0.87 for aboveground biomass and height. The curve also manifests a good trend of equilibrium stage. This indicates that this model has reached the ability to predict not only aboveground biomass but also plant height during the growing season. Better results could be obtained by adjusting the three most sensitive parameters included maximum photosynthesis rate, specific respiration rate and half saturation coefficient of amount of nutrient uptake.

The results also suggest that the nitrogen level in root solution less than 2 mg/L controls the rate of plant growth but higher N has not significantly affected.

Moreover, it should be pointed out that the fluctuation of maximum vapor exchange influences transpiration. To produce good reliable results, consequently, transpiration should be observed as much as possible.

Nonetheless, to obtain a better understanding and more precise results, it is suggested that the model should be further improved. Firstly, as pointed out before, this model only considers mass flow uptake but in reality, as plant solution concentration of many macronutrients may be larger than in soil solution, active uptake must have occurred (Epstein, ¹⁸). Secondly, the conditions under which each trait of uptake process occurs also need to be further investigated. Thirdly, because photosynthesis is a dependent process of surrounding factors, also the temperature needs to be involved. Lastly, by developing and realizing these refinements concerning the effects of soil water regime on uptake capability, the model may become a greater applicability in the result.

The results from this model are able to confirm that the contribution of nutrient is significant for optimal growth. The application of soil-plant-atmosphere column on growth model may bring the effective way to manifest the movement of nutrient from soil into plant. Hopefully, this research will provide credibility valuable information and be a perspective prediction tool regarding reproducing a crop growth model of macrophyte.

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