

EFFECTS OF WATER DEPTH ON THE GROWTH OF *Phragmites australis*

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SYNOPSIS

The purpose of this study is to develop a descriptive model to simulate the growth potential of *Phragmites australis* under various climate conditions and water depths. The present model includes such factors as the effects of water depth, reduction in photosynthesis and morphological change of rhizomes. The model represents accurately the seasonal aboveground and belowground biomass variation and maximum penetrative water depth. *Phragmites australis* have to grow over a critical height above the water level during the early growing season so that they can use the stored material of rhizomes. As a result, aboveground and belowground biomasses decrease sharply beyond some water depth. The zone severely influenced by deep water depth varies depending on the initial rhizome biomass. The density ratio of one shoot decreases as the water depth increases, and furthermore the shoot strength also decreases. Morphological change of rhizomes helps to maintain the biomass up to the critical depth. Seasonal variations of water depth affect considerably the production of *Phragmites australis*.

INTRODUCTION

The common reed *Phragmites australis* (Cav.) Trin. ex Steud. is a major component of freshwater bodies in temperate regions throughout the world (1). The importance of the role of its rhizomes in its growth and spread to the surrounding environment has been acknowledged for many years (2). Reeds are used for the non-food commodities, such as pulp and roofing, and for waste treatment plants (3). Also, in river engineering, the belowground structure of *P. australis* plays an important roll in preventing bank erosion (4). The reed community is an extremely important environment for various plants and animals.

To evaluate the effectiveness of *P. australis* in such measures as water quality management, bank protection and ecological protection, it is necessary to investigate quantitatively the primary production and biomass of *P. australis* and its nutrient removal capacity. However, the biomass variations are dependent on various environmental conditions, such as water depth (5), soil and water nutrient content (6,7), salt concentration (6) and seasonal variation of water depth (8,9). Among many environmental factors, it is important to understand the effects of water level management on the

vegetation in the field of engineering. Stark and Dienst (8) investigated lakeside borders of *P. australis* at Lake Constance (Untersee) in Switzerland from 1984 to 1986. In their study they pointed out that the rise in water level in springs is a critical factor. Moreover, Ostendorp (9) examined the relation between the rising curve of water depth and the growth curve of *P. australis*. Rea (10) found that the stabilization of water depth reduces the lower limit of *P. australis*. Moreover, Yamauchi et al. (11) investigated reed decline in the upstream of Nagara River mouth weir and pointed out that the reed diminishes every year from deeper region after the water depth stabilization by the weir. Based on these studies, we have come to understand some fundamental growth dynamics of *P. australis* qualitatively and have established empirical relationships (12); however, biomass has not been fully explained because of a number of interactive factors in natural conditions. Therefore, we do not yet understand quantitatively how the growth of *P. australis* is affected by water depth variations.

As for the methods analyzing plant growth, a number of mathematical models have been proposed by bioenergetic methods (13, 14, 15, 16, 17, 18). Bioenergetic models represent energy transport to and from the plant organs, including photosynthetic production, translocation of photosynthate, respiration and mortality. The bioenergetic methods represent successfully the growth of various plants, including the model of *Potamogeton pectinatus* L. (13, 14) and *P. australis* (15, 16, 17, 18). A model of *P. australis* was proposed by Karunaratne and Asaeda (15) and by Hoffmann et al. (16). The biomass of *P. australis* in shallow water can be calculated in temperate zones and in nutrient-rich and healthy conditions (17). Karunaratne and Asaeda (18) verified this model by using field data gathered from two Scottish lochs.

In consideration of above-mentioned, this paper will focus on examining the dynamics of monospecific stands of *P. australis* under fluctuating water depth by developing the model of Asaeda and Karunaratne (17) and analyze the effects of water depth variation on *P. australis*.

METHODS

Definition of time scale in the life stage of P. australis

Asaeda and Karunaratne (17) introduced the phenology of *P. australis* into the model by time periods of initial growing stage utilizing stored belowground material, photosynthesized growing stage, and senescent season in Julian days in terms of simple mathematical relationships by regression analysis of published observation data.

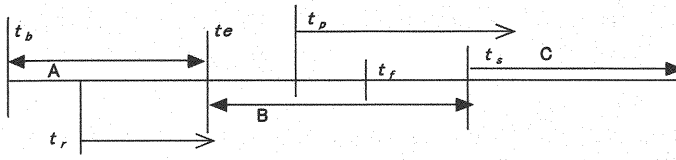
Fig. 1 shows the schema and notations of the time scale in Julians of the life cycle of *P. australis*.

Governing equations

The same governing equations of *P. australis* introduced by Asaeda and Karunaratne (17) were used in this analysis. In this model, biomass per square meter of five organs (shoots, rhizomes, new rhizomes, roots and panicles) was separately formulated to account for the energy gain and loss (photosynthetic production, respiration and mortality, inter-organ transport to and from the plant organs), that is, spring energy flow to form new shoots, translocation in the senescent season, and at the time of florescence. The characteristics and life cycles of each organ were introduced into the forms of each term in the equations. The governing equations for each plant organ are given in the Appendix.

Modeling the effects of water depth

Two conditions tend to restrict the growth of *P. australis* influenced by a given water depth. One condition, photosynthesis in water, was not considered in this model. The other condition is the morphological change in the rhizome of *P. australis* affected by water depth, due to oxygen transport restriction by a small shoot length over water and by the long oxygen transport distance under water



- A : early growing season, B : photosynthetically growing season, C : senescent season
- start of growth : $t_b = 91(\text{day})$ (19)
- ending of mobilization from rhizome to shoots and roots : $t_e = t_b + 0.14(t_f - t_b)^{1.27} = 145(\text{day})$ (17)
- appearance of panicles : $t_f = 196(\text{day})$
- start of translocation of current photosynthate to belowground plant organs : $t_p = 166(\text{day})$ (21)
- start of shoot senescence : $t_s = t_b + 0.22(t_f - t_b)^{1.36} = 215(\text{day})$ (17)
- formation of new roots : $t_r = 112(\text{day})$

Fig. 1 Schema of the life stage of *Phragmites australis*

through the shoots, investigated by Weisner and Strand (5). They represented the depth of vertical rhizomes and length of horizontal rhizomes as a function of water depth. We include these morphological changes in our model as the initial conditions of shoot height and shoot density.

Initial conditions

The initial conditions of a dynamic model of *P. australis* are initial rhizome biomass, initial shoot height, and initial shoot biomass. Asaeda and Karunaratne (17) used a regression analysis of observed data of Australia (22,23), the Czech Republic (19), and Kasumigaura (20), and conceived of the following equations.

(Initial shoot biomass) = (growth initiation

parameter) \times (initial rhizome biomass)

(Initial shoot height) = (initial shoot biomass) / (initial specific density of shoots)

(Growth initiation parameter) = $0.06 (\text{rhizome biomass})^{-0.19}$ ($r = +0.99$)

(Initial density of shoots (grams per m height/m²)) = $0.22 (\text{rhizome biomass})^{0.74}$ ($r = +0.94$)

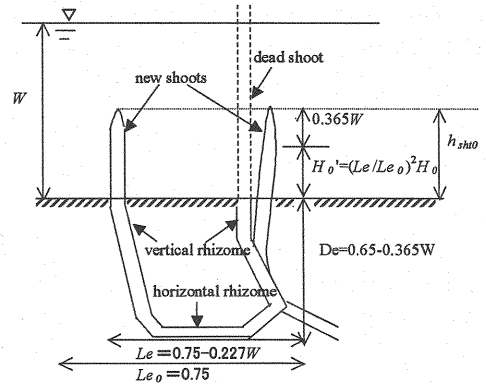
We include these parameters in the water depth function using the morphological relations with water depth of Weisner and Strand (5) (Fig. 2). Weisner and Strand (5) represented the shoot distance, Le (m) and the depth of rhizomes, De (m), by the concept of maximum O₂ transport distance as follows,

$$De = 0.65 - 0.365W \quad (1)$$

$$Le = 0.75 - 0.227W \quad (2)$$

where W (m) is the water depth.

Using this formula, the initial shoot height, H_{sh0} , under the effect of water depth W is given by:



※ H_0 denotes the initial shoot height when $W = 0$.

Fig. 2 Initial shoot height (based on Weisner and Strand (5))

$$H_{shl}=(L_e/L_{e0})^2 H_0 + \Delta De=(L_e/L_{e0})^2 H_0 + 0.365 W \quad (3)$$

where L_{e0} represents the standard rhizome length when the water depth is zero, and ΔDe represents the difference in new bud positions at zero water depth assuming that the sum of the rhizome depth and vertical height from the horizontal rhizome is constant.

The initial shoot density is also represented by L_e and L_{e0} :

$$Den'=(L_{e0}/L_e)^2 \cdot Den \quad (4)$$

where Den is the initial density of shoots when the water depth is zero.

With the initial rhizome biomass, the data observed in Moravia (19) and Lake Kasumigaura (20) were nearly 3000 (g/m^2). In view of this, we examined the three initial rhizome biomass cases as 3000, 2000 and 1000 (g/m^2).

With radiation, we modeled the radiation accumulated on daily basis, $S_{df} \downarrow$ ($\text{MJm}^{-2}\text{d}^{-1}$) as a function of latitude on a fine day as proposed by Kondo and Kuwagata (24). We used the daily mean air temperature T from the averaged yearly air temperature T_{ave} using the following equations of Tsuboi et al. (25),

$$T_{ave}=271-449 \cdot \sin^2(\phi-6.5) \quad (5)$$

$$T=T_{amp} \cdot \sin(2\pi \cdot (Jday-80-Jday_*)/365)+T_{ave}+T_{const} \quad (6)$$

where ϕ is the latitude of the site, T_{amp} is amplitude of temperature, $Jday_*$ is the time difference of peaks between temperature and radiation. In this case we chose 30 days, T_{const} is the difference in average temperature compared with eq.(5). For the purpose of this study, we chose $\phi=35^\circ$, $T_{amp}=10^\circ\text{C}$, $T_{const}=0^\circ\text{C}$, to form moderate temperature and radiation curves.

RESULTS

Fig. 3 shows the relationship between shoot height and water depth. The plot 'day 145' means the end of the transport of the rhizome material in the early growing stage and the plot 'day 215' represents the start of senescence. Fig. 3 shows that *P. australis* must grow over the water surface by the end of the early growing stage. Moreover, the shoot length grown from day 145 to day 215 was almost the same from 0 to 1.1 m water depth, but the growing length after day 145 changed much from 1.1 m to 1.4 m water depth. The reason for this was that even if the shoots grew above the water level at day 145, a clearance height was needed to recover the biomass decreased by respiration and mortality of shoots and rhizomes under the water level using material from photosynthesis above the water level. This clearance height, H_I , was about 30cm in this case.

Fig.4 shows the simulated seasonal variation of aboveground and belowground biomass at 1.1 m and 1.4 m water depth. The

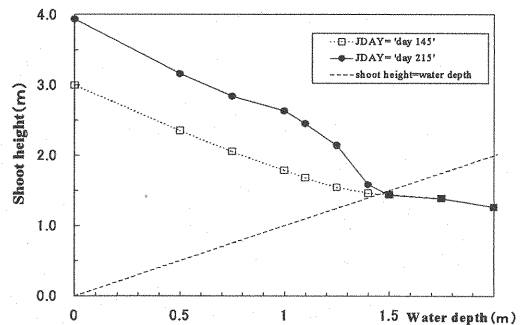


Fig. 3 Comparison between the shoot height at day 145 and that at day 215 in relation to water depth (the shoot height is equal to the water depth at the dashed line)

biomass of total rhizomes decreased during the initial growing period, but it recovered because of the transport of the photosynthate by the shoots. When the water depth reached 1.1 m, a flow existed that recovered the biomass of rhizomes because of the morphological change by the maximum oxygen transport distance. However, when the water depth reached 1.4 m, the recovery was small because the shoot length above the water level was very short, and the effects of photosynthesis were very slight. The aboveground biomass also decreased markedly at water depth 1.4 m.

Fig. 5 shows the variation of aboveground, total rhizome and new rhizome biomasses related to water depth. Up to 1.1m water depth, the aboveground and belowground biomass difference was not significant, but over depth 1.1m the shoot length above the water was greater than H_1 , hereafter called 'strongly influenced water-depth zone'; the aboveground and belowground biomasses strongly decreased. Therefore, in the strongly influenced water-depth zone, *P. australis* is thought to be affected considerably by the change in environmental conditions, such as, water depth, temperature and radiation. The belowground biomass did not change much up to 1.1 m water depth compared with the aboveground biomass. The reason for this was that transport of photosynthesized material to rhizomes began before the shoot reached its maximum height, and that the material transport in the period had priority over the growing shoot height or panicle inflorescence. The morphological changes in rhizome by the maximum oxygen transport distance (5) contribute to minimizing the decrease of not only photosynthesis of shoots but also to belowground biomass production.

The aboveground biomass did not decrease much compared with the decrease in shoot height (Fig. 3). Since morphological change of horizontal rhizome to transport oxygen causes an increase in shoot density, the productivity of aboveground biomass was maintained from 0 m to 1.1 m water depth where *P. australis* grew.

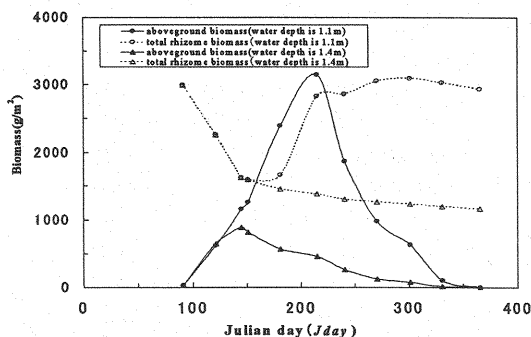


Fig. 4 Comparison of growth curve between 1.1m water depth and 1.4m water depth.

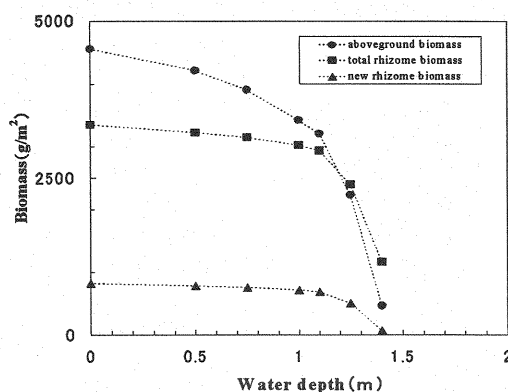


Fig. 5 Calculated aboveground biomass, total rhizome biomass, and new rhizome biomass in relation to water depth.

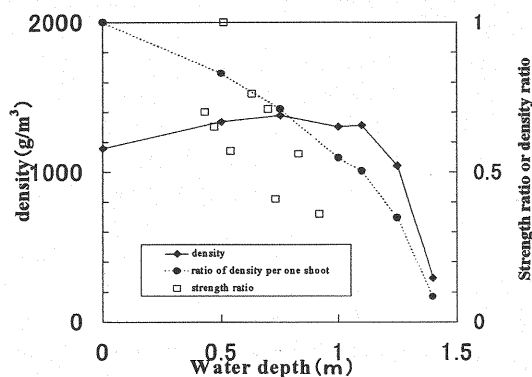


Fig. 6 Comparison of calculated shoot density ((g/m²)/m), calculated ratio of shoot density of each shoot and the shoot density when the water depth is zero, and the observed shoot strength ratio obtained by Suzuki et al. (26), normalized by the strength when the water depth is zero

With each increase in water depth, shoot height decreased in proportion to the decrease in photosynthesis under the water. However, productivity in a unit area, not for one shoot, increases nominally (Fig. 6). This is due to the shoot density increment by the horizontal shoot length decrement (Fig. 2). Fig. 6 shows the relation between shoot density (g/m^3) and water depth, where shoot density means the shoot biomass (g/m^2) divided by shoot height (m). The aboveground productivity decreased somewhat at the whole shoot height and the density at each unit height increased up to 1.25 m water depth. However, the density ratio of each shoot compared with when the water depth is zero decreased by 50 % at 1.1 m water depth and by 90 % at 1.5 m water depth. Suzuki et al. (26) surveyed *P. australis* in Lake Biwa and showed that the strength of shoots decreased with increasing water depth and the strength ratio at 90 cm depth was about 30-50% of the strength ratio at 50cm (Fig. 6), and the shoot diameter in the water was apparently small. In their study it was found that the strength was proportional to the cross-sectional area of the shoot. The strength ratio data for water depth was found to be similar to the density ratio of each shoot of our simulation. Therefore, the simulated density represents qualitatively the characteristics of shoot strength. When waves or fluid forces induced by water flow, wind or motorboats occur, the shoot should be broken off if the water depth is over 1.1 m deep. Mortality rate should become greater and the maximum penetration depth presumed to be shallower under such conditions.

Fig. 7 shows the aboveground biomass (left axis) and R_{brhi} (right axis) when the initial biomass was 1000, 2000 and 3000 (g/m^2). In this figure, R_{brhi} means the ratio of belowground biomass after one growth season and the initial rhizome biomass. The aboveground biomass itself was small when the initial biomass was small, but the ratio R_{brhi} was much larger. As a result, the biomass increase in the strongly influenced water depth zone was affected considerably by the smaller initial biomass, because the leaf area index (LAI) in the *Phragmites* canopy increased as the increase in initial rhizome biomass and photosynthesis is less in the strongly influenced water depth zone. The values of R_{brhi} in Fig. 7 show that the rhizome biomass increase ratio after one season was larger for smaller initial rhizomes biomasses, that is, the increase for 3000 g/m^2 was smaller compared with 1000 g/m^2 . As a result, the water depths at which the rhizomes were smaller than initial biomass were 1.1 m, 1.2 m and 1.3 m for the initial biomasses of 3000, 2000 and 1000 g/m^2 , respectively. Therefore, the height above the water level in the initial growing stage also changed. The height above the water level, H_1 , increased 0.2, 0.3, 0.4 m for the initial rhizome biomass of 1000, 2000 and 3000 g/m^2 , respectively. This

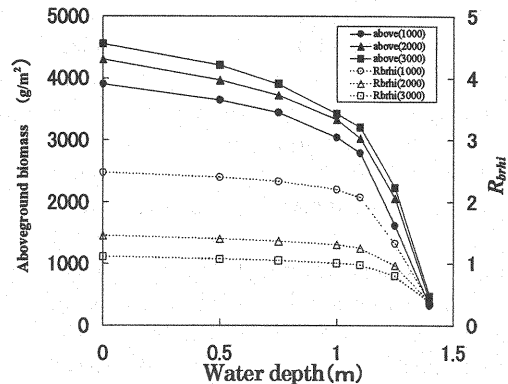


Fig. 7 Aboveground biomass and the ratio of rhizome biomass after one growth season and initial rhizome biomass, R_{brhi} , on three initial rhizome biomasses of 1000, 2000 and 3000 g/m^2 in relation to water depth.

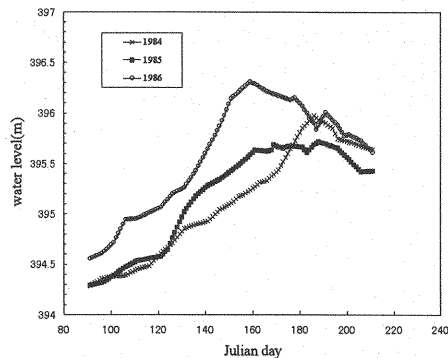
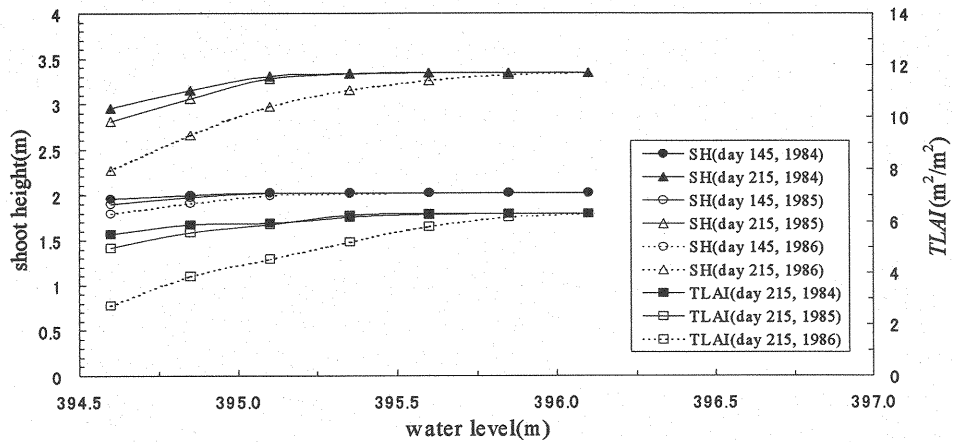
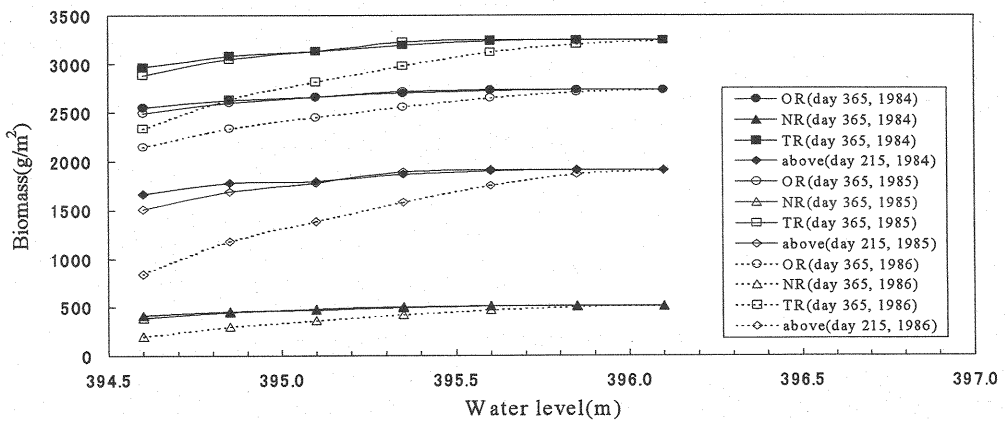


Fig. 8 The increase in the water level of Lake Constance in 1984, 1985 and 1986 (based on Stark and Dienst (8)).



(a)



(b)

Fig. 9 Simulated results of the relation between water level and the growth of *P.australis* in 1984,1985 and 1986; (a)shoot height(SH) and total leaf area index(TLAI), (b)Aboveground biomass and rhizome biomass. (OR:old rhizome, NR : new rhizome, TR : total rhizome, above: aboveground biomass)

finding indicated that the rhizome biomass at the early stage of growth was presumed to be a value decreasing with increasing water depth. This finding agreed with the ratio between the shoot biomass and rhizome biomass decreasing with increasing water depth (27).

To evaluate the effect of seasonal variation of water depth, the selection of field data must include matured stands of *P. australis* up to 1.0 m water depth and data of rhizome biomass, aboveground biomass, shoot height, and nutrient concentration in the soil at every water depth. However, such data is very difficult to obtain and few observations are available from previous studies. Also, field observation data affected by water depth are affected by other factors, such as nutrient in soil, rhizome biomass, or shoot density. In view of this, we compared the model qualitatively by using the reduction rate of biomass or LAI from the field observation data of Stark and Dienst (8).

Stark and Dienst (8) investigated lakeside borders of *P.australis* at Lake Constance (Untersee) in

Switzerland from 1984 to 1986 and found that there was a decline of the *P. australis* belt in 1986 because of a steeper rising curve for 1986 than the curves for 1984 or 1985 (Fig. 8). Hereafter, using the water depths of 1984 to 1986, we verify the change in shoot height, *LAI*, aboveground biomass and rhizome biomass under the three rising curves of water depth. To verify the water depth effect itself, we chose daily standard radiation curves and daily averaged temperature curves by using latitude (47.7° N) and T_{amp} equal to 10°C . Fig. 9(a) shows the shoot height and the total leaf area index (*TLAI*) affected by the three rising curves of water from 1984 to 1986 at various above-sea levels (a.s.l.). When the water depth increased in the spring, the height of water affecting *P. australis* was deeper, and so the strongly influenced water-depth zone was deeper and its growth was gradually affected. The increases in shoot height from day 145 to day 215 at 394.6 m a.s.l. in 1984 and 1985 were 77 % and 70 %, respectively, of that in the same season at 395.6 m a.s.l., but in 1986, the proportion was about 35 %. Furthermore, at each water depth, the shoot height and *TLAI* in 1986 was the smallest of the three years. Therefore, it was concluded that the rhizome biomass also decreased sharply due to the influence of the decreasing aboveground biomass (Fig. 9(b)). In 1984 and 1985, the total rhizome biomass was larger than the initial rhizome biomass at 394.85 m, 0.75 m lower than the average water level. However, in 1986 the biomass decreased about 10% at 394.85 m. The total rhizome biomass in 1986 did not maintain the initial value until over 395.35 m, 0.25 m lower than the average water level. Our model can therefore represent the increase or decrease in *P. australis* in Lake Constance by considering the change in daily averaged water depth.

DISCUSSION

The focus of this study has been to develop a descriptive model which can simulate the growth potential of *P. australis* under various climatic conditions and water depths. The results (Fig. 3-5) agree with the observations made by Weisner and Strand (5) which indicate that the depth limit of the growth of *P. australis* is about 1.4m. The variation of the density of each shoot (Fig. 7) also agrees closely with the change in strength of *P. australis* (26). Therefore, our model provides a good representation of the effects of water depth.

The effects of the rising curve of water depth in the growth season are verified by the simulated results at each above sea level in 1984-6, especially in deeper zones (Fig. 9 (a), (b)). Although comparing the detailed results is difficult, the model shows that *P. australis* declined in 1986, not in 1984 or 1985. This provides evidence that our model can predict the effects of water level control on the growth of *P. australis* in reservoirs. However, the morphological changes in vertical rhizome length or horizontal rhizome distance of each terminal shoot (see Fig. 2) under the seasonal variation of water depth are not included in our model. The differences of water depth between formation season and the next growing season are thought to be important. However, the belowground situations, such as the distribution of rhizome depths and density, were the productive results under four to five years' environmental conditions, because rhizomes can survive about four to five years. Therefore, investigation of the characteristics of rhizome formation as the water depth changes is important, and must be included in further studies.

If *P. australis* is greatly affected by forces, such as wind shear, waves, or fluid force, the plants may not grow in water up to 1.4 m deep and the biomass and shoot heights are thought to decrease greatly. If these forces cause a loss of the plant biomass, we can establish *D*, representing not only natural mortality, but also the function of the forces. Thus an understanding of the relationship between the forces and mortality *D* is also important.

Seasonal variation of daily water depth changes the nutrient conditions or redox potential in the soil around *P. australis* and affects its productivity. The productivity which is affected also influences the ability to transport oxygen and the soil condition. Therefore, seasonal variation of water depth is not only the function of stem growing speed or rhizome morphological characteristics, but also other soil conditions. When one makes generalizations about the effects of daily water depth on the growth of *P. australis*, many environmental factors should be examined. However, the model can show the

difference in production by the shape of the rising water curve. What is noticeable is that the curve shows a difference in the aboveground productivity of about 50 % in the 3-year simulation. Usage of natural lake water or water stabilization by river mouth weirs can sometimes greatly affect aquatic vegetation (11). The findings of this study show that our model is a useful tool for evaluating better artificial usages of lake water or the operation of weir from the viewpoint of conservation of *P. australis* in the long term.

CONCLUSION

A dynamic model associated with radiation, temperature and water depth has been developed to simulate the growth dynamics of *P. australis*. Using the model quantitatively, the following conclusions can be made: 1) morphological changes are important to maintain the productivity in deeper water; 2) *P. australis* must grow above a critical height in its early growing stage when stored material of rhizomes is used; 3) biomass of each area and the height of each plant greatly decreases in deeper water; 4) *P. australis* has the ability to grow in deeper water when belowground biomass is sparse; 5) seasonal variation of water depth has considerable effects on the production of *P. australis*. We propose that our model can be used to evaluate the influences on the production of *P. australis* affected by artificial use of the lake.

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APPENDIX

Governing equations of rhizome, roots, new rhizome, shoot and panicle are as follows (17).

$$\frac{dB_{rhi}}{dt} = -R_{rhi} - D_{rhi} - Rhif \cdot f_{rhi} + y \cdot \sum_{i=1}^{i=\max} \varepsilon_{sht} \cdot b_{sht}(i) \cdot f_{sht} + y \cdot \sum_{i=1}^{i=\max} \varepsilon_{ph} \cdot Ph_{sht}(i) \cdot f_{ph} \quad (A1)$$

$$\frac{d B_r}{dt} = G_r \cdot f_r - R_r - D_r + x \cdot Rhif \cdot f_{rhi} \quad (A2)$$

$$\frac{dB_n}{dt} = -R_n - D_n + (1-y) \cdot \sum_{i=1}^{i=\max} \varepsilon_{sht} \cdot b_{sht}(i) \cdot f_{sht} + (1-y) \cdot \sum_{i=1}^{i=\max} \varepsilon_{ph} \cdot Ph_{sht}(i) \cdot f_{ph} \quad (A3)$$

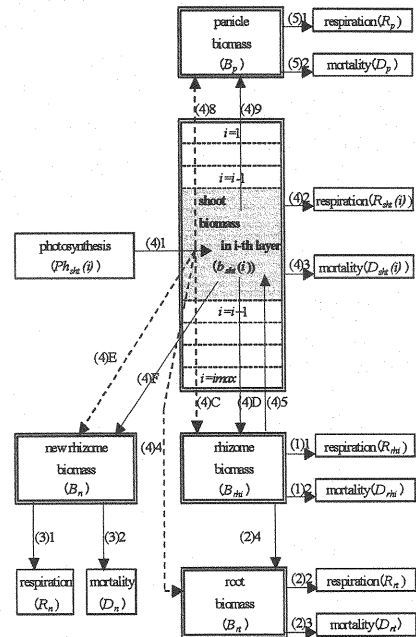
$$\begin{aligned} \frac{db_{sh}(i)}{dt} = & Ph_{sh}(i) - R_{sh}(i) - D_{sh}(i) - G_{rt} \cdot f_{rt} \cdot (b_{sh}(i)/B_{sh}) \\ & + (1-x) \cdot Rhif \cdot f_{rhi} \cdot (b_{sh}(i)/B_{sh}) - \varepsilon_{sh} \cdot b_{sh}(i) \cdot f_{sh} - \varepsilon_{ph} \cdot Ph_{sh}(i) \cdot f_{ph} \\ & - b_{sh}(i) \cdot \varepsilon_p \cdot ff - Ph_{sh}(i) \cdot k \cdot ff \end{aligned} \quad (A4)$$

$$\frac{dB_p}{dt} = -R_p - D_p + \sum_{i=1}^{i=\max} Ph_{sh}(i) \cdot k \cdot ff + \sum_{i=1}^{i=\max} \varepsilon_p \cdot b_{sh}(i) \cdot ff \quad (A5)$$

The notations are listed in Table A. The aboveground plant stand was stratified into 1-cm-thick horizontal layers in which the dry matter budget and elongation were calculated separately. For mobilization of stored material from rhizome to shoots, respiration, mortality and shoot elongation, see Asaeda and Karunaratne (17). Fig. A shows the relation of each term in the five governing equations.

Table A Notations used in the governing equations

Notation	Parameter	Dimension
1) term of Governing equation		
B	biomass	(g/m ²)
b	biomass in 1cm height	(g/m ² /cm)
R	respiration	(g/m ² /day)
D	mortality	(g/m ² /day)
Ph	photosynthesis	(g/m ² /day)
$Rhif$	material transport to roots and shoots from rhizome	(g/m ² /day)
G_{rt}	transport of photosynthetic material for root growth	(g/m ² /day)
2) Subscripts		
rhi	old rhizome	-
rt	root	-
n	new rhizome	-
sh	shoot	-
p	panicle	-
3) coefficients related to the life stage of plants		
f_{rhi}	$f_{rhi}=1$ when $t_b < t < t_e$, otherwise $f_{rhi}=0$	-
f_{sh}	$f_{sh}=1$ when $t_s < t$, otherwise $f_{sh}=0$	-
f_{ph}	$f_{ph}=1$ when $t_p < t < t_e$, otherwise $f_{ph}=0$	-
f_{rt}	$f_{rt}=1$ when $t_r < t < t_e$, otherwise $f_{rt}=0$	-
ff	$ff=1$ when $t_f < t$, otherwise $ff=0$	-
4) fraction for the transportation between each organ		
ε_{sh}	Fraction of shoot assimilates translocated to belowground structures	-
γ	Fraction of shoot assimilates translocated for old rhizomes	-
ε_{ph}	Fraction of current photosynthesis translocated to belowground structures	-
x	Fraction mobilized from rhizomes for root formation	-
k	Fraction of current photosynthesis translocated for inflorescence	-
ε_p	Fraction of shoot assimilates translocated for panicle formation	-



(A)B denotes right hand term B in equation(A).

dotted lines represent fluxes of photosynthesized material.

Other terms of equations(1) to(5) not expressed in the figure are as follows,

where $\sum (4)B$ denotes summation of (4)B

(1)3 = $\sum (4)5 + (2)4$, (1)4 = $\sum (4)D$, (1)5 = $\sum (4)C$,

(2)1 = $\sum (4)4$, (3)3 = $\sum (4)F$, (3)4 = $\sum (4)E$,

(4)6 = $(4)D + (4)F$, (4)7 = $(4)C + (4)E$

(5)3 = $\sum (4)8$, (5)4 = $\sum (4)9$

(4)C: (4)E = (4)D: (4)F = $\gamma : (1-\gamma)$

Fig. A Schema of the relation between the differential equations