Journal of Hydroscience and Hydraulic Engineering
Vol. 20, No.2 November, 2002, 197-206

AN ANALYSIS OF THE GROWTH OF *Typha angustifolia* AND *Typha latifolia*

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SYNOPSIS

A dynamic model of emergent macrophytes associated with each vertical productive structure was developed by improving the bioenergetic model of *Phragmites australis*. The efficiency of this model was verified to simulate the seasonal variation of the aboveground and belowground biomass of *Typha latifolia* at two sites in the U.S.A. The differences in shoot heights, leaf area and aboveground biomass between *T. latifolia* and *Typha angustifolia* are analyzed in relation to various water depths. The model represents well the productivity of the aboveground biomass of each species along a water depth gradient. The seasonal variations in the composition of aboveground and belowground biomasses of *T. angustifolia* during senescent season changes markedly depending on whether the plant forms a panicle or not. The density of fertile shoots is instrumental in understanding the plant strategy accommodating the surrounding environment and belowground production.

INTRODUCTION

Emergent macrophytes, such as *Phragmites australis, Typha angustifolia* or *Typha latifolia*, frequently occur as important components of wetland and littoral ecosystems (1). The biomass changes depend on various environmental conditions, such as water depth (2,3), nutrient conditions (4, 5) and salt concentration (4). Although many studies have analyzed the growth dynamics and have made empirical relations, the biomass has not been fully explained because of a number of factors interacting in natural conditions. The dynamics of competing populations along a water depth gradient have been studied between *P. australis* and *Zizania latifolia* (6), and between broad-leaved *Typha latifolia* and narrow-leaved *T. angustifolia* in a eutrophic lake (7) or experimental ponds over long periods (8). While Grace and Wetzel (3) studied the zonation of these *Typha* species and reported their long-term (23years) stable outcomes that *T. latifolia* has competitive superiority in shallow water in their experimental ponds (8), Weisner (3) concluded that *T. angustifolia* was competitively superior to *T. latifolia* even in shallow water in a eutrophic lake. Therefore, we do not yet understand quantitatively how environmental changes affect the growth or competitive zonation along a water depth gradient of emergent macrophytes.

Bioenergetics has enabled researchers and scientists to use growth dynamics to clarify observations easily, and to apply various different conditions. This can be done by modeling energy transport to and from the plant organs such as producing energy material in aboveground parts of the plant by photosynthesis and translocating photosynthesized material to belowground parts of the plant, respiration and mortality. Therefore, a number of mathematical models have been proposed to reproduce approximately the growth of various plants, including a model of *Potamogeton pectinatus* L.(9, 10). A bioenergetic model of *P. australis* was first attempted by Karunaratne and Asaeda (11) and Hoffmann et al. (12). The biomass of *P. australis* in shallow water can be calculated in the temperate zone and in nutrient-rich and healthy conditions (13). The biomass of *P. australis* varies with location, such as with temperature and radiation (14). Tanaka et al. (15) also examined the effects of water depth by using the maximum oxygen transport distance of Weisner and Stand (2).

The dynamics of monospecific stands of *P. australis* under various influences is unclear. Therefore, in this study we derived a dynamic model of other emergent macrophytes, i.e., *T. angustifolia* and *T. latifolia*, by considering each vertical productive structure to represent their productivity in various environmental conditions.

METHODS

Phenology and governing equations of emergent macrophytes

Asaeda and Karunaratne (13) represented the phenology of *Phragmites australis* using a time scale (*t*) in Julian days. The life cycle is characterized by six Julian days and three seasons to define the growth of *P. australis.* The life stage of *Typha* spp. is similar to that of *P. australis* for the transport of energy material between belowground and aboveground parts of the plant (17). The start of growth of *T. latifolia* and *T. angustifolia* is day 110 (18) and day 120 (18,19), respectively, which is a little after *P. australis* (16). The aboveground biomass reaches its maximum value in August and September, which is about the middle of their flowering season, and is similar to *P. australis.* Therefore, we change only the start of growth, and for other Julian days that represent *Typha* growth, we used the same values as *P. australis.*

The governing equations of the growth of *Typha* spp. are considered the same as the equations of Asaeda and Karunaratne (13). The characteristics of each plant are considered by modeling each term, especially of photosynthesis in the governing equations.

Modeling transport material between aboveground and belowground organs, and the effects of water depth

Asaeda and Karunaratne (13) studied *Phragmites australis* as 1)transport of material from rhizome to shoot and root, 2)transport of photosynthesized material to root growth, 3)respiration and mortality of each organ and 4)photosynthesis. Tanaka et al. (15) included morphological change in the rhizome of *P. australis* affected by water depth, because of oxygen transport restriction by a small shoot length over water surface and by a long oxygen transport distance through the shoots, investigated by Weisner and Strand (2). The depth of vertical rhizomes and length of horizontal rhizomes were represented as a function of water depth (2) and Tanaka et al. (15) included them in a model as the initial condition of shoot height and shoot density.

We assume each plant has an individual model parameter, but as a result of sensitive analysis, the sensitivity of photosynthesis proved to be more important than other terms, 1) transport of material from rhizome to shoot and root, 2) transport of photosynthesized material to root growth, 3) respiration and mortality of each organ, which are much smaller than the photosynthetic term. In view of this, we use a common value to represent 1) to 3) and the effects of water depth. The characteristics of *T. latifolia* and *T. angustifolia* are included in the photosynthetic term.

To understand the growth dynamic model one must consider three important factors: a) a governing equation of biomass, b) a vertical productive structure of the plant that is closely related to photosynthesis, c) a shoot elongation speed. We considered that a) is common and b) and c) are sensitive and genus-specific or species-specific parameter in each plant.

Modeling of the photosynthetic term

The net daily photosynthesis in the *i*-th layer is expressed by a form of the Michaelis- Menten equation.

$$Ph_{sht}(i) = P_m \cdot K_{co} \cdot K_{NP} \cdot \theta^{(T-a)} \cdot \frac{I_{PAR}(i)}{K_{PAR} + I_{PAR}(i)} \times \frac{K_{age}}{K_{age} + Age_{sht}} \cdot b_{sht}(i) \qquad (1)$$

where, P_m is the maximum specific net daily photosynthesis rate of the plant top at 20℃ in the absence of light and nutrient limitations, I_{PAR} is the photosynthetically active radiation in the *i*-th layer, K_{co} is the conversion constant of carbon dioxide to ash-free dry weight (13), K_{NP} is the specific concentration constant of nitrogen and phosphorus, respectively. Age_{sht} is the number of days from the start of shoot growth and K_{PAR} and K_{age} are the half saturation coefficients of photosynthetically active radiation (PAR) and age (13), respectively.

The photosynthetically active radiation, PAR, in the *i*-th layer is given by;

$$I_{PAR}(i) = I_{PAR}.e^{-ak \cdot F_i} \qquad (2)$$

where, I_{PAR} is the PAR intensity in the open and I_{PAR} (*i*) is the PAR in the stand at a level above which is a cumulative leaf area index, F_i.

$$F_i = \sum_{i=1}^{i=i} LAI\,(i) \qquad (3)$$

The extinction coefficient *ak* depends on leaf inclination and on the clustering of leaves, and thus it is typical for a given plant stand at a given stage of development (21). Extinction coefficient values used in the model of *P. australis* were obtained from the observations of Květ (19) and the extinction coefficient of *T. latifolia* and *T. angustifolia* were obtained from Dykyjová (20). A correlation between leaf biomass and leaf area index (*LAI*) of *P. australis* was established (13) in the form of a power function (r=0.962), based on measured data (16) of a *P. australis* stand in Nesyt fishpond in Southern Moravia.

$$LAI(i)(m^2/m^2)=0.0135.[bleaf(i)]^{1.02} \qquad (4)$$

where $bleaf(i)$ is the leaf biomass in the *i*-th layer.

With *Typha* spp., we use a similar relation as,

$$LAI(i) \;=\; ALAI \cdot [b_{leaf}\,(i\,)]^{BLAI} \qquad (5)$$

$$b_{leaf}(i) = a_{fr} \cdot b_{sht}(i) \qquad (6)$$

where *ALAI*, *BLAI*, a_{fr} are the constants which characterize each plant structure of leaf and stem. We set these values by regressional analysis using the data of Květ et al. (16) and Weisner (3) (Table 1). The leaf area index in each horizontal layer of the plant stand was calculated by using the above equation. Shoot elongation in each day in meters is expressed by;

Table 1 Species-dependent parameters used in the model

Notation	Parameter	Value			Dimension
		P. australis	*T. angustifolia*	*T.latifolia*	
y	Fraction of shoot assimilates translocated for old rhizomes	0.6^{c}	0.2^{c}	0.2^{c}	$gg^{-1}d^{-1}$
a_{fr}	rate of leaf biomass within shoot biomass	0.22^{ca}	0.57^{ca}	0.8^{ca}	-
ε_p	Fraction of shoot assimilates translocated for panicle formation	0.00027^{ca}	0.0027^{ca}	0.0027^{ca}	-
$ALAI$	Fraction of biomass-leaf area relation	0.01352^{d}	0.0087^{f}	0.0226^{f}	-
$BLAI$	Fraction of biomass-leaf area relation	1.0179^{d}	0.9286^{f}	0.8214^{f}	-
P_m	Maximum specific net daily photosynthesis rate at 20℃	0.225^{a}	0.165^{b}	0.165^{b}	$gC0_2g^{-1}m^{-2}d^{-1}$
q	Fraction of shoot biomass for elongation	0.48^{c}	0.42^{c}	0.3^{c}	-
ak	extinction coefficient(91～120day)	0.3^{g}	0.12^{e}	0.12^{e}	-
ak	extinction coefficient(121～151day)	0.4^{g}			-
ak	extinction coefficient(152～180day)	1.05^{g}			-
ak	extinction coefficient(181～212day)	0.965^{g}			-
ak	extinction coefficient(213～242day)	0.88^{g}			-
ak	extinction coefficient(243～273day)	0.78^{g}			-
ak	extinction coefficient(274～365day)	0.6^{g}			-

c:Calibrated
ca:Calibrated based on Dykyjová(20)
a:Gloser(23), b:Knapp&Yavitt(25), d:Květ et al. (16), e:Dykyjová(20)
f:calibrated based on Weisner(7), Květ et al.(16), g:Květ(19)

$$\frac{(\text{biomass increase in the } i\text{ - th layer}).q.(\text{thickness of the stratified layer})}{(\text{biomass in the } i\text{ - th layer}) - (\text{biomass increase in the } i\text{ - th layer}).q} \qquad (7)$$

where, q is a parameter that depends on the average rate of elongation of a plant stand.

The daily accumulated radiation and the daily mean air temperature was modeled as a function of latitude on a fine day as proposed by Kondo and Miura (22) and Tanaka et al. (15), respectively.

Model parameter

Table 1 shows the genus or species-specific parameters. The values of Table 1 was set because, 1) almost every shoot of *P. australis* has panicles, but *T. latifolia* and *T. angustifolia* have panicles when the rhizome is 2 years old and is fertile. When *T. latifolia* and *T. angustifolia* develop panicles, they have a flowering stalk. The aboveground biomass of *Typha* spp. has three nonphotosynthetic organs: panicles, flowering stalk and shoot base. The panicle and flowering stalk are formed only in fertile shoots of *Typha* spp. at proportions of about 30-40 % of aboveground biomass (20). But the proportion of panicles of aboveground biomass of *P. australis* is only 2.5% (16). Therefore, when the shoot is fertile and panicles and flowering stalks are formed, the composition of the biomass of *Typha* spp. changes greatly. Therefore, when we analyze the biomass of the fertile shoot of *Typha* spp., we must use a larger ε_p than *P. australis*. With sterile shoots, no panicle is formed, so we use ε_p as zero.
2) The leaf of *T. latifolia* is broader and thinner than of *T. angustifolia.* The shoot height of *T. angustifolia* is higher than of *T. latifolia* in the same habitat (7). The proportion of leaf biomass in aboveground biomass of *T. latifolia* and *T. angustifolia* is greater than of *P. australis* (20).
3) The leaf inclination of *T. angustifolia* and *T. latifolia* is steeper, resulting in an extinction coefficient

smaller than *P. australis* (20).
4) The rhizome survives four to five years after formation in *P. australis* (1), but only 2 years in *T. latifolia* and *T. angustifolia* (1).

Seasonal variations in aboveground biomass and belowground biomass of *T. latifolia* were validated using the field data obtained by Garver et al. (17) and Smith et al. (26). Peak aboveground biomass of *T. latifolia* and *T. angustifolia* in relation to water depth is discussed using the model.

In order to set the initial rhizome biomass conditions, we set the initial rhizome biomass and the start of growth by using observed data to validate the model. When we analyze the aboveground biomass variation in relation to the water depth, we set the initial rhizome biomass as 2000 and 1000 g/m^2 for *T. angustifolia* and *T. latifolia*, respectively.

With seasonal variations of belowground biomass of *T. angustifolia*, data observed in the field, including the senescent season, was sparse. Therefore, we observed the plant by examining the relation between belowground and aboveground biomass during the senescent season. Special focus was also placed on examining the difference between sterile and fertile shoots.

RESULTS AND DISCUSSION

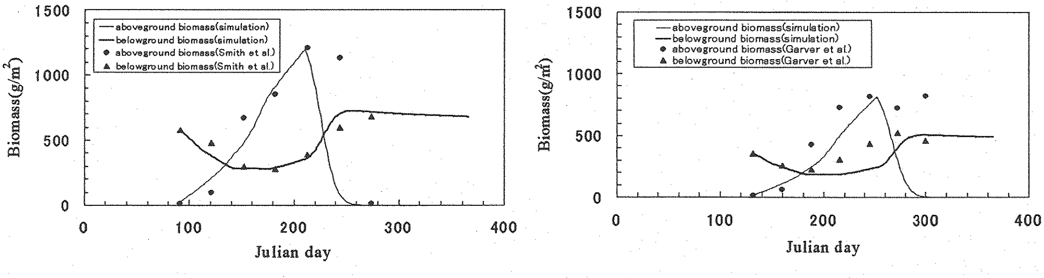
Seasonal variation of aboveground and belowground biomass of Typha latifolia

Smith et al. (26) sampled *Typha latifolia* in a stand (0.1ha) on the shore of Lake Mendota, Wisconsin, U.S.A. They sampled the plant's belowground and aboveground biomass every 2 weeks during the growing season from April to October.

Garver et al. (17) studied *Typha* spp. in a minerotrophic fen in northeastern Minnesota, U.S.A.(47° N, 93° W). The area was drained for approximately 25 years, and was cultivated intermittently. In a paddy at the study site, *T. latifolia* was planted with 90-day-old seedlings at a density of 5m^{-2}, and *T. angustifolia* was also planted with rhizomes at the same density. The study was carried out between June 1982 and May 1984. The water depth was maintained at 20cm during both growing seasons, and was drained to the paddy bed surface level during the fall and winter. The observed initial belowground biomasses of *T. angustifolia* and *T. latifolia* in the 1983 growing season were 214 g/m^2 and 358 g/m^2, respectively.

The *Typha* species are characterized by an approximately two-year growing cycle (1). In the second growing season, most shoots are fertile and rhizomes of the same age connecting these shoots die at the end of the growing season (20). However, the initial belowground biomass of *T. angustifolia* observed by Garver et al. (17) was very small and was 3.5 times higher in September at 726 g/m^2, so we surmised that it had not matured even in the second season. Therefore, we used only *T. latifolia* for seasonal variation of the biomass.

Fig. 1 shows the seasonal variation of aboveground and belowground biomasses of *T. latifolia*



(a) (b)

Fig. 1 Seasonal variation in aboveground biomass and belowground biomass of *Typha latifolia*. Model simulations are represented by lines. Observed data are represented by symbols. (a)Comparison with Smith et al.(26), (b) Comparison with Garver et al.(17) (1983 growing season).

compared with those of Smith et al. (26) and Garver et al. (17), respectively. The aboveground biomass of *T.latifolia* from the start of growth to the maximum growing stage is represented clearly by our model. The simulated belowground biomass decreased from the start and increased by modeling the transport of photosynthesized material from aboveground. The variation of aboveground and belowground biomasses corresponded to the results of the observation. The seasonal variation of *P. australis* was previously verified by Asaeda and Karunaratne (13) for the Czech Republic (16), Australia (24) and Japan (27), and by Katunaratne and Asaeda (28) for Scotland (29). Fig. 1 shows that the bioenergetic model is also useful for *T. latifolia*, if we consider the difference in each vertical productive structure.

Effects of water depth on the growth of T.latifolia and T. angustifolia

The difference between *T. latifolia* and *T. angustifolia* was examined by focusing on the characteristics of the productivity of aboveground biomass and the water depth gradient. Fig. 2 shows the total leaf area index, *TLAI*, at maximum aboveground biomass of *T. latifolia* and *T. angustifolia* in relation to water depth. Fig.2 represents the genetic characteristics: the shoot height of *T. angustifolia* was about 1.5 to 2 times higher than *T. latifolia*, *T. latifolia* had a broad leaf and a larger *TLAI* than *T. angustifolia*. The maximum penetrated depths of *T. latifolia* and *T. angustifolia* were 0.75m and 1.2m, respectively, representing accurately the observations of Grace and Wetzel (3). Furthermore, the *TLAI* of *T. angustifolia* increased more than *T. latifolia* when the water depth was greater than 0.75m, indicating that *T. angustifolia* grew more than *T. latifolia* above 0.75m water depth.

Fig. 3 shows the peak aboveground biomass and percentage productivity. The findings of this study show clearly that the productivity of *T. latifolia* decreases above 0.7m water depth, but the falling curve was slight compared with the observed data. In our model, we did not change the mortality rate below water, but we presumed it increased the mortality below water. The percentage productivity of *T. angustifolia* that can penetrate a deeper water depth than *T. latifolia* by growing higher is shown clearly.

Fig. 4 shows the total leaf area from plant

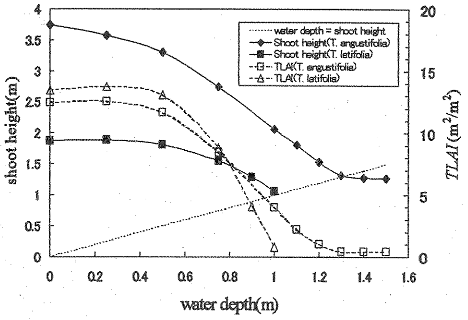


Fig.2 Calculated shoot height(right axis) and total leaf area index(*TLAI*)(left axis) of *Typha latifolia* and *Typha angustifolia* in relation to water depth.

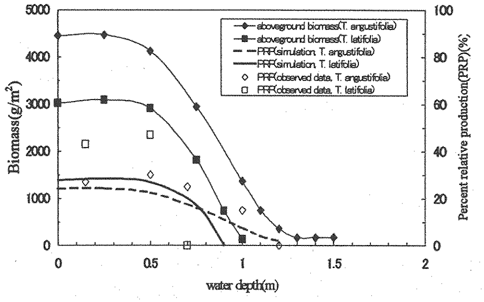


Fig.3 Calculated aboveground biomass(left axis) and percentage relative production standardized by total production along a water depth gradient (right axis) of *Typha latifolia* and *Typha angustifolia* in relation to water depth. Model simulations are represented by lines. Observed data (represented by symbols) are from Grace and Wetzel (3).

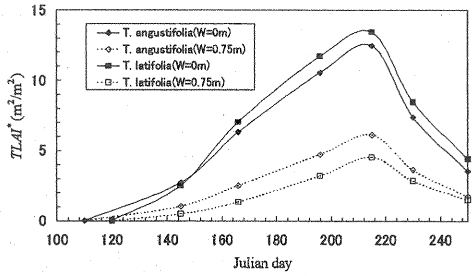


Fig.4 Simulated seasonal variation in total leaf area index above water of *Typha latifolia* and *Typha angustifolia* at water depths(*W*) 0.75m and 0m.

top to water surface, *TLAI**. When the water depth was 0m, broad-leaved *T. latifolia* had a larger *TLAI** than *T. angustifolia* except in the initial growing season. However, when the water depth was 0.75m, *T. angustifolia* revealed an obvious competitive superiority because it can form a shade for other plants by growing higher and having a larger *TLAI**. When the water depth was 0m, the *TLAI** of *T. latifolia* was superior. However, *T. angustifolia* grew higher than *T. latifolia* and forms shade for *T. latifolia*. Therefore, the superiority or inferiority of the competition between *T. latifolia* and *T. angustifolia* can be easily changed by the nutrients at 0m water depth, which produces a different competitive result (7,8): 1) Grace and Wetzel (8) reported that *T. latifolia* was superior to *T. angustifolia* in shallow water and the competitive zonation was maintained for long time; 2) Weisner (7) observed that *T. angustifolia* displaced *T. latifolia* even in shallow water in a eutrophic lake.

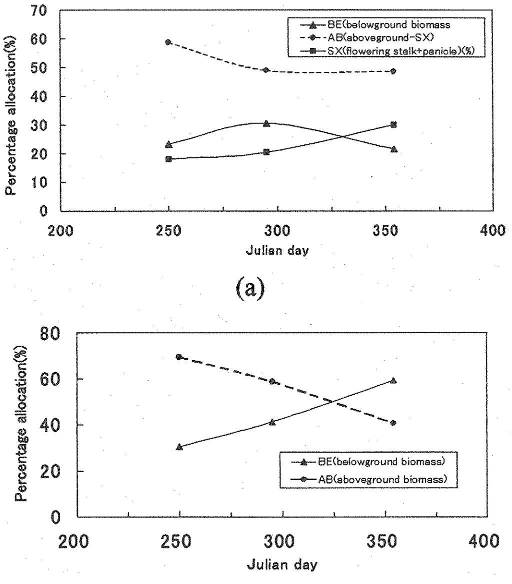
These findings indicate that by considering the differences in the vertical productive structure and composition of each organ in each plant, we can analyze the seasonal variation of leaf area index, shoot height and the characteristics of aboveground productivity in relation to the water depth.

Field observations of T. angustifolia

Sample of *T. angustifolia* were collected at the following three sites:

1) The Toemon river, a branch of the Siba river : The area of the plants was 1-2 m wide and 500 m long in the downstream direction. The upstream river basin of the site was 7.6 km^2.
2) The Denu river, a branch of the Ayase river : The area of the plants was 10 m wide and 20 m long in the downstream direction. The upstream river basin of this site was 10.24 km^2.
3) Biotope pond in Ukima Golf club, hereafter is called Ukima biotope

Growth dynamics was observed during the senescent season from September to December.



(a)

(b)

Fig.5 Seasonal variation in biomass allocation of *Typha angustifolia* in the senescent season that is the averaged data of the three sites. (a)fertile shoots, (b) sterile shoots.

Table 2 shows the composition of the biomass of each organ in the aboveground biomass; previously observed results are also included. The water depth of Toemon river was deeper than Denu river. A gate is located at the upstream site of the Denu river and it is closed while flooding, so the velocity and duration of floods of the Denu river are milder than floods of the Toemon river. The shoots of *T. angustifolia* in the Denu river were vertical, but many shoots in the Toemon river were inclined after floods. The water depth of the Ukima biotope was the deepest. The density of shoots with sexual structures (flowers, fruits and flowering stalk) differed at each site: the densities of the Ukima biotope, the Denu river and the Toemon river around the center of the communities were 1 shoot/m^2, 3-5 shoots/m^2, 5-7 shoots/m^2, respectively. The field observations indicate that the plants have many panicles with increasing water velocity conditions. Table 2 shows that the proportion of panicle and shoot base increased, and that the proportion of leaf decreased as the velocity increased. Sexual structures decrease with increasing water depth (3). The water depth at the three sites was different, so the proportion of sexual structures was affected not only by the velocity condition but also by the water depth conditions. The low rate of panicles in the Ukima biotope was thought to have been caused by the highest water depth among the three sites. However, upon comparing the Denu river with the Toemon river, we found that that the plant

Table 2 Percentage allocation of each aboveground organ in sterile and fertile shoots

Site	Water depth	Fertile(F) or sterile(S)	Allocation among aboveground parts(%)		
			shoot base	leaves	flowering stalk & panicle
Toemon river	0.3m～1.0m	F	32～40	0～24	42～62
		S	22～63	37～78	0
Denu river	0m～0.4m	F	23～64	0～24	40～56
		S	25～52	48～75	0
Ukima biotope	0.4m～0.7m	F	22～44	0～23	44～56
		S	28～37	63～72	0
South Bohemian fishpond(20)	0m a)	F	36.9	21.9	41.2
		S	53.8	46.2	0
	0.8m	S	31.2	68.8	0
Experimental pond of Michigan State Univ.(3)	0.5m～1.0m	F	50～62.5		37.5～50
Simulated results	0m	F	21.8	28.1	50.2
		S	43.5	56.5	0.0
	0.5m	F	21.6	27.9	50.5
		S	43.5	56.5	0.0

a)This data is for *Typha latifolia* and all other data is for *Typha angustifolia*

transports to aboveground sexual structures for targeting dispersal to new habitats when the environmental conditions are severe. In view of this, the effects of water depth and velocity conditions on the biomass allocation of *T. angustifolia* should be clarified more quantitatively in the future.

Fig. 5 shows the seasonal variation of biomass allocation of aboveground sexual structures, aboveground non-sexual structures(leaves and shoot base) and belowground organs in fertile shoots(Fig. 5(a)) and in sterile shoots (Fig. 5(b)) that is the averaged data of the three sites. Fig. 5(a) shows a comparison of data taken in September to those taken in November in fertile shoots which reveals that the proportion of sexual structures increased about 10 %, aboveground non-sexual structures decreased about 10 % and belowground organs did not increase. However, in sterile shoots, the aboveground non-sexual structures (AB) decreased about 30% and belowground organs increased about 30% from September to November (Fig. 5(b)). In addition to clonal expansion, seeds play an important role in *T. angustifolia*. Fertile shoots transport material to the panicle for the next generation, but sterile shoots must transport material to their belowground structures for the next growing season. Therefore, translocation of each organ in their senescent season is distinctly different from fertile shoots and sterile shoots.

The difference in biomass allocation between fertile shoots and sterile shoots are represented clearly by our model (Table 2). Leaf biomass allocation greatly changed the shoots depending on whether the aboveground had sexual structures or not. The leaf area allocation also changed the belowground biomass in the senescent season and the next growing season. Therefore, what determines the density of fertile shoots is very important, but this must be clarified in further studies under conditions of water depth and velocity to evaluate their belowground biomass.

CONCLUSIONS

This study reveal the following findings:

1) The dynamic growth model of *Phragmites australis* can be applied to other emergent macrophytes, that is, *Typha latifolia* and *Typha angustifolia*, that have a similar life cycle of energy transport

between aboveground and belowground organs.

2) The productive characteristics of *Typha* spp., such as shoot heights, leaf area index or peak biomass, in relation to water depth, can be analyzed by representing each vertical productive structure.

3) The composition of biomass of each organ of *T. angustifolia* is changed markedly depending on whether the plant forms a panicle or not. The density of fertile shoots is a key factor in understanding the plant strategy accommodating the surrounding environment and belowground production.

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(Received July 23, 2001 ; revised February 22, 2002)