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A Comparative Study on Litter Decomposition of Emergent Macrophytes in the Littoral Zone of Reservoir

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Litter decomposition is a key process in energy flow and nutrient cycling in the freshwater littoral zone, and is regulated by physicochemical properties of litters. Using a litterbag method, we compared the decomposition rates of 16 different litter types from 10 plant species of the emergent macrophytes for one year in the littoral zone of the Paltangho Reservoir, Korea. The regression analysis fitted to the various decomposition models showed that mass loss of the litters with time best fitted an asymptotic function. The litters of the emergent macrophytes were composed of two compartments, labile and refractory. The macrophytic litters showed a great variety in decomposition dynamics depending on sources of litters. The labile compartment of the initial litter mass was in a wide range between 18% and 99%, and their decomposition rates varied from 0.0037 to 0.0131 day^{-1}. The decomposition processes of the emergent macrophytes were determined by the relative amounts of the labile and refractory compartments and by the decomposition rate of the labile one in the littoral zone.

Emergent macrophytes constitute a significant ecological component among plants that grow in freshwater habitats. These plants include those which are rooted in sediments, with part of their structures above the water surface for most of the year (Hutchinson, 1975). The community of the emergent macrophytes is one of the most productive systems, due to a large reservoir of nutrients and water in sediments (Brinson et al., 1981). Most of the organic matter produced remains ungrazed, however, and the bulk of it typically enters detrital systems (Polunin, 1984). Macrophytes are the main source of autochthonous detritus as they prevail in the total biomass of littoral organisms. The quantity and quality of detritus depend on decomposition rates of macrophytic litters in the littoral zone. Litter decomposition is a key process in energy flow and nutrient cycling in the littoral zone of lakes and reservoirs (Pieczynska, 1993), because it functions as a source of either organic nutrition for detrital food chains or regenerated inorganic nutrients for autotrophs in aquatic ecosystems (Twilley et al., 1986).

Litter decomposition rates are affected by both internal factors, such as chemical and physical characteristics of the litters, and external environmental factors, such as temperature, pH, dissolved oxygen, and nutrients. Litter quality has long been recognized as a major factor controlling litter decomposition. Litter mass loss rates have been correlated with a wide variety of chemical characteristics of litters, such as initial concentrations of nitrogen, phosphorus, lignin, and chemical inhibitors (Webster and Benfield, 1986; Couteaux et al., 1995; Updegraff et al., 1995; Aerts and Caluwe, 1997). The chemical properties of litters can vary with species, and organs. It also varies within organs depending on its age and positions in plants (Polunin, 1984). Therefore, decomposition of various litter types from the emergent macrophytes in the littoral zone may show different dynamics.

Although much information exists on decomposition rates in various emergent macrophytes, comparative studies on decomposition of their litters in the same environments are lacking. Because of various vegetation types, freshwater littoral zones offer an opportunity to investigate how fast different litter types from the emergent macrophytes are decomposed. Only a comparative approach would allow a greater understanding of how variable the dynamics of litter decomposition are. We measured decomposition rates of various litter types from different species or parts of several emergent macrophytes in a littoral zone. To compare the decomposition rates, parameters of best-fitted models were obtained from various mathematical functions on litter decomposition.

Materials and methods

Site description

The study was carried out in the Paltangho Reservoir in Korea located at 37° 30′ N, 127° 20′ E. In the littoral zone of the reservoir, which was mainly

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agricultural land before the dam construction, emergent macrophytes, such as *Typha angustifolia*, *Zizania latifolia*, and *Phragmites australis*, are widely distributed. Details on vegetation and sediments are reported by Cho and Kim (1994) and Cho et al. (1994), respectively. Surface water in the littoral zone was frozen in January and February in 1996, and had the highest temperature of about 30℃ in August.

Litter samples

Sixteen different litter types from 10 species of the emergent macrophytes were studied to compare their decomposition rates in the littoral zone of the Paltangho Reservoir. These were as follows: leaf blade (Zlb) and leaf sheath (Zls) of *Zizania latifolia*, leaf (Pal) and stem (Pas) of *Phragmites australis*, leaf (Msl) and stem (Mss) of *Miscanthus sacchariflorus*, leaf (Srl) and stem (Srs) of *Scirpus radicans*, leaf (Tal) and stem (Tas) of *Typha angustifolia*, leaf lamina (Nnl) and petiole (Nnp) of *Nelumbo nucifera*, leaf (Acl) of *Acorus calamus* var. *angustatus*, stem (Sts) of *Scirpus tabernaemontani*, stem (Sqs) of *Scirpus triqueter*, and stem (Bfs) of *Bidens frondosa*. Senescent standing shoots of the emergent macrophytes above the water surface were collected in the field on December 1995, and air-dried for two weeks at room temperature. For each species and litter type, subsamples of the air-dried materials were dried for 48 h at 80℃ in an oven to determine oven-dry weight from air-dry weight.

Litterbag experiment

Decomposition rates of the macrophytic litters were determined in the field using the standard litterbag method. The air-dried litter samples, except for the leaf lamina of *Nelumbo nucifera*, were cut into 10-cm segments. For each litter type, 10.0 g of the cut litter was put in a nylon bag (20×20 cm) with a mesh size of 1 mm. For *Nelumbo nucifera*, one leaf lamina was put in a litterbag with an aluminum tag with its air-dry weight. On Marh 12, 1996, 30 litterbags of each litter type, totaling 420 litterbags, were placed on the sediment surface at a place of the littoral zone of the Paltangho Reservoir where *Typha angustifolia* dominated. The litterbags of each litter type were sampled in triplicate after 0.5, 1, 2, 3, 4, 5, 6, 7, 9, and 12 months. After gently removing sediments and roots, dry mass of each litter was determined after drying for 48 h at 80℃ in an oven. The oven-dried samples were ground in a laboratory mill equipped with a screen of 1-mm mesh. Ash contents of all the litter samples were measured after combustion for 4 h at 550℃ in a furnace, from which the ash-free dry mass was determined for each litter sample.

Data analysis

To compare litter decomposition rates of 16 different litter types from 10 species of emergent macrophytes that might have different litter quality, we needed a mathematical model that best explain dynamics of litter decomposition among four decomposition functions examined; single-exponential model, asymptotic model, double-exponential model, and double-exponential model with asymptote. The ash-free dry mass remaining for each litter type was fitted to the following mathematical models, assuming that the litters were composed of one, two, or three compartments with different rates of decomposition (Gillon et al., 1994).

1) Single-exponential decomposition model (Olson, 1963)
$M_t = Ae^{-bt}$ (eq. 1)
2) Asymptotic decomposition model (Stanford and Smith, 1972)
$M_t = Ae^{-bt} + E$ $(A+E=100)$ (eq. 2)
3) Double-exponential decomposition model (Andren and Paustian, 1987)
$M_t = Ae^{-bt} + Ce^{-dt}$ $(A+C=100)$ (eq. 3)
4) Double-exponential decomposition model with asymptote (Gillon et al., 1994)
$M_t = Ae^{-bt} + Ce^{-dt} + E$ $(A+C+E=100)$ (eq. 4)

where M_t is expressed as a percentage of the initial mass at time t in days, A, C, and E are labile, resistant, and refractory compartments (%), respectively, and b and d are decomposition rate constants (day^{-1}) of A and C over time, respectively.

The single-exponential decomposition model can be developed from one assumption, that the decomposition rate is a constant fraction of the amount of litters remaining. Because of the complex nature of litter material, the major problem encountered in using this model is that decomposition rates are seldom constant (Webster and Benfield, 1986). In three more complex models, each class of chemicals breaks down at a constant rate, and the overall rate of decomposition is the sum of the individual decomposition rates. Litter materials can be divided into labile, resistant and refractory compartments. The refractory compartment is assumed to be completely resistant to decay and remains unchanged while labile and resistant fractions disappear at different decomposition rates.

The simplest mathematical model that best fitted the data was selected to compare the mass losses and the parameters of decomposition in different litter types. The various models for each litter type were obtained by regression analysis (SAS, 1985). They were compared to fit model 4, which always had the highest coefficient of determination (R^2), using the F-test (Sokal and Rohlf, 1981). We also calculated the half-life ($t_{1/2}$) required for 50% of each compartment to be decomposed in an exponential model as follows:

$$t_{1/2} = \ln 2 \,/\, (b \text{ or } d) \qquad \text{(eq. 5)}$$

Table 1. Coefficients of determination (R^2) of the regressions fitted to different decomposition models

Litter type		Abbreviation	Model			
			1[a]	2[b]	3[c]	4[d]
Zizania latifolia	Leaf blade	Zlb	0.964**	0.975	0.975	0.975
	Leaf sheath	Zls	0.973	0.973	0.973	0.973
Phragmites australis	Leaf	Pal	0.905***	0.951	0.951	0.951
	Stem	Pas	0.860***	0.935	0.935	0.935
Miscanthus sacchariflorus	Leaf	Msl	0.933***	0.965	0.965	0.965
	Stem	Mss	0.869***	0.921	0.921	0.921
Scirpus radicans	Leaf	Srl	0.882*	0.909	0.909	0.909
	Stem	Srs	0.921	0.924	0.924	0.924
Typha angustifolia	Leaf	Tal	0.924***	0.969	0.969	0.969
	Stem	Tas	0.862***	0.928	0.928	0.928
Nelumbo nucifera	Leaf lamina	Nnl	0.956	0.964	0.964	0.964
	Leaf petiole	Nnp	0.868***	0.969	0.969	0.969
Acorus calamus var. *angustatus*	Leaf	Acl	0.879***	0.963	0.963	0.963
Scirpus tabernaemontani	Stem	Sts	0.944	0.946	0.946	0.946
S. triqueter	Stem	Sqs	0.951*	0.963	0.963	0.963
Bidens frondosa	Stem	Bfs	0.941***	0.975	0.975	0.975

[1]Single-exponential function ($M_t=Ae^{-bt}$), [2]asymptotic function ($M_t=Ae^{-bt}+E$), [3]double-exponential function ($M_t=Ae^{-bt}+Ce^{-dt}$), [4]double-exponential function with asymptote ($M_t=Ae^{-bt}+Ce^{-dt}+E$). Significant difference with the model 4: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

Results

Comparison of the various decomposition models

To compare the decomposition rates of the different litter types of the emergent macrophytes, the powerful function that best fitted the data obtained from the litterbag experiment had to be selected among the various mathematical models. The model most commonly used to describe litter mass loss with time is the single-exponential decomposition model (Olson, 1963). In the emergent macrophytes, this simple model (eq. 1) generally had coefficients of determination that were much lower than the other complex models (eq. 2, 3, and 4) (Table 1). The single-exponential models for 12 litter types out of the 16 types were significantly different from those fitted to the most complex function (eq. 4).

Regressions fitted to the more complex models (eq. 2, 3, and 4) had no different coefficients of determination, and did not differ from each other on the results of the *F*-test (Table 1). The regression fitted to the asymptotic decomposition model (eq. 2) were therefore adopted to compare decomposition rates of litter types (Fig. 1), because it provided a better estimate of the regression parameters and did not differ significantly from those obtained with the more complex models (eq. 3 and 4). The asymptotic model has a labile compartment (*A*) which decreases at a decomposition rate (*b*) and a refractory compartment (*E*) that remains constant for a long time.

Table 2. Parameters of the asymptotic regressions $M_t=Ae^{-bt}+E$, where $E=100-A$, M_t expressed as the percentage of initial mass, and t in days (estimated standard error in parentheses)

Litter type		Labile Compartment(A) (%)	Rate constant (*b*) (day^{-1})
Zizania latifolia	Leaf blade	94.9 (3.5)	0.0070 (0.0006)
	Leaf sheath	99.2 (4.0)	0.0074 (0.0007)
Phragmites australis	Leaf	60.9 (4.1)	0.0062 (0.0008)
	Stem	29.7 (2.7)	0.0052 (0.0009)
Miscanthus sacchariflorus	Leaf	65.5 (4.1)	0.0057 (0.0007)
	Stem	17.9 (2.6)	0.0038 (0.0009)
Scirpus radicans	Leaf	52.8 (7.2)	0.0043 (0.0010)
	Stem	84.6 (13.6)	0.0037 (0.0009)
Typha angustifolia	Leaf	59.5 (3.2)	0.0059 (0.0006)
	Stem	28.6 (3.1)	0.0049 (0.0009)
Nelumbo nucifera	Leaf lamina	86.0 (4.3)	0.0069 (0.0007)
	Leaf petiole	51.9 (2.1)	0.0080 (0.0007)
Acorus calamus var. *angustatus*	Leaf	76.4 (2.1)	0.0131 (0.0011)
Scirpus tabernaemontani	Stem	89.8 (8.5)	0.0049 (0.0008)
S. triqueter	Stem	83.0 (4.5)	0.0066 (0.0007)
Bidens frondosa	Stem	48.8 (3.3)	0.0044 (0.0005)

Comparison of decomposition process

Compartment *A*, that represents the labile component of the litters, ranged from 18% to 99% of the initial litter mass for the various litter types of the emergent macrophytes from the littoral zone of the Paltangho Reservoir (Table 2). The refractory compartment *E*, which is a complement of compartment *A* (*A*+*E*=100%), represents a more resistant component to decomposition. It varied between 1% and 82% of the initial litter mass. The labile compartment *A* was less than 30% in stem litters of *Miscanthus sacchariflorus*, *Typha angustifolia*, and *Phragmites australis*, and more than 80% in leaf blade and sheath litters of *Zizania latifolia*, stem litters of *Scirpus radicans*, *S. tabernaemontani*, and *S. triqueter*, and leaf lamina litter of *Nelumbo nucifera*. Other litter types had values between those of these two groups.

The decomposition rate constant (*b*) of the labile compartment in the asymptotic model ranged from 0.0037 to 0.0131 day^{-1} (Table 2). The labile compartment had a half-life (time required for 50% dry mass loss) between 187 and 53 days in the littoral zone of the Paltangho Reservoir. The rate constant *b* was highest in leaf litter of *Acorus calamus* var. *angustatus*, and higher in leaf lamina and petiole litters of *Nelumbo nucifera* and leaf litter of *Zizania latifolia* than stem litters of *Miscanthus sacchariflorus* and *Scirpus radicans*.

Because the single-exponential model has been commonly used in other litter-decomposition studies,

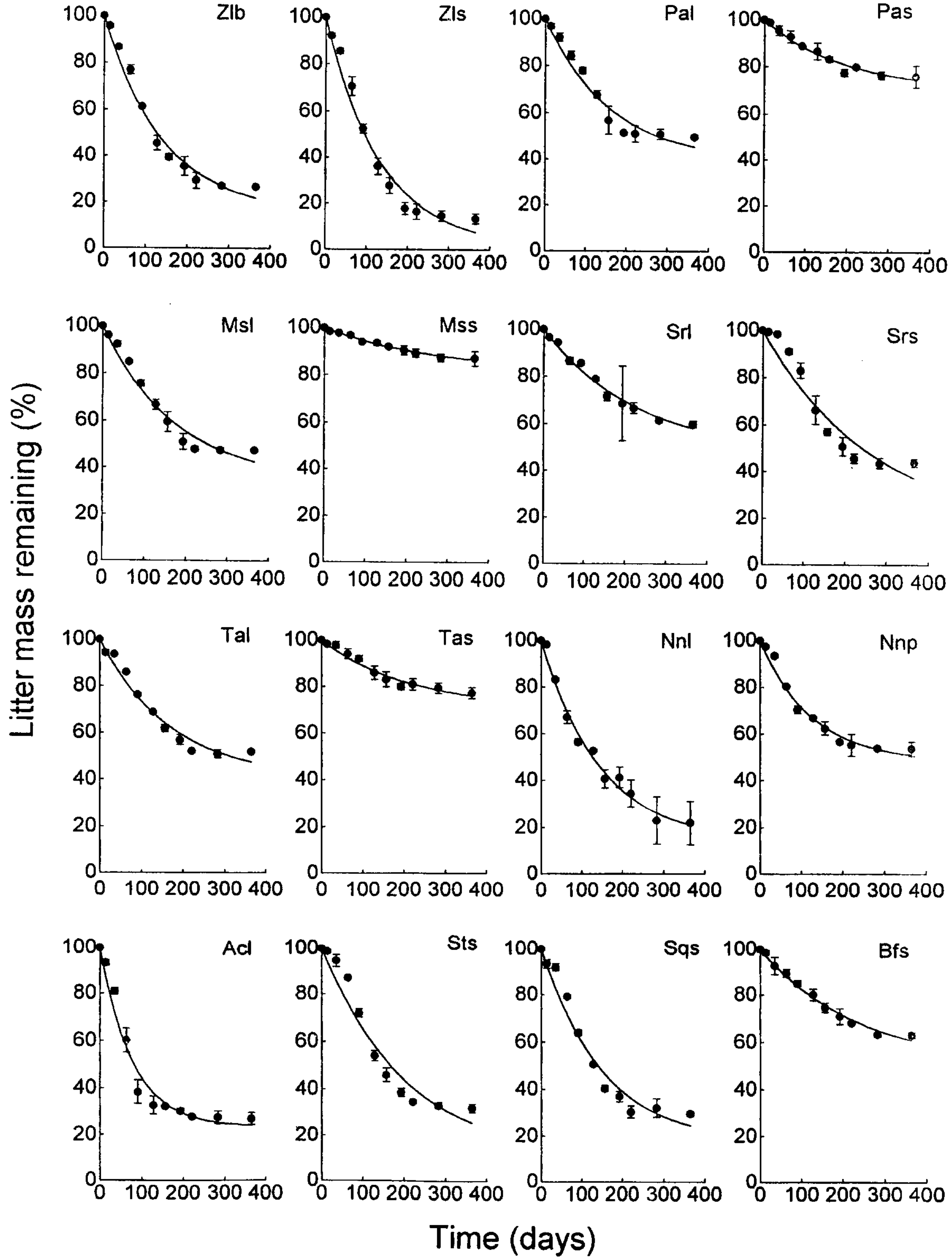

Fig. 1. Measured values of litter mass remaining expressed as the percentage of initial ash-free dry mass with incubation time, and predicted asymptotic decomposition regression ($M_r=Ae^{-bt}+E$, where $A+E=100$) of the 16 litter types studied. Vertical bars indicate standard deviation (n=3). The names and abbreviations of the litter types are shown in Table 1.

Table 3. Parameter of the exponential regression $M_t = Ae^{-bt}$, M_t expressed as the percentage of initial mass and t in days (estimated standard error in parentheses), and half-life ($t_{1/2}$) of litters

Litter type		Rate constant (b) (day^{-1})	Half-life ($t_{1/2}$) (day)
Zizania latifolia	Leaf blade	0.0051 (0.0002)	136
	Leaf sheath	0.0073 (0.0003)	95
Phragmites australis	Leaf	0.0026 (0.0002)	227
	Stem	0.0009 (0.0001)	770
Miscanthus sacchariflorus	Leaf	0.0028 (0.0001)	248
	Stem	0.0004 (0.0000)	1733
Scirpus radicans	Leaf	0.0016 (0.0001)	433
	Stem	0.0029 (0.0001)	239
Typha angustifolia	Leaf	0.0024 (0.0001)	289
	Stem	0.0008 (0.0001)	866
Nelumbo nucifera	Leaf lamina	0.0051 (0.0002)	136
	Leaf petiole	0.0023 (0.0002)	301
Acorus calamus var. *angustatus*	Leaf	0.0064 (0.0005)	108
Scirpus tabernaemontani	Stem	0.0041 (0.0002)	169
S. triqueter	Stem	0.0047 (0.0002)	148
Bidens frondosa	Stem	0.0015 (0.0001)	462

our data on mass loss of litter were fitted to the less explainable single-exponential decomposition model than the asymptotic decomposition model for comparison with other results (Table 3). The decomposition rate constant in the single-exponential decomposition model was between 0.0004 and 0.0073 day^{-1}, and the time required for a 50% reduction in the initial mass of litter from the emergent plants ranged from a few months to more than four years in the littoral zone of the Paltangho Reservoir.

Discussion

After the one-year litterbag incubation in the littoral zone of the Paltangho Reservoir, litter masses of various emergent macrophytes were lost within the wide range of 10-90% of their initial ash-free dry masses (Fig. 1). From the single-exponential decomposition model, the range of variations in the decomposition rate constants in this study (Table 3) was on the same order of magnitude when compared with those of other decomposition studies of emergent macrophytes (Table 4). The rate of litter decomposition in the emergent macrophytes is lower than for submerged plants, macroalgae or phytoplankton (Twilley et al., 1986). The relative resistance of standing litter to further breakdown is caused by the high content of structural carbohydrate and the low nutrient content (Graneli and Solander, 1988). When litters of emergent perennials fall into the water, the nutrient content is already low because of translocation and early leaching (Graneli and Solander, 1988).

The litters originate from many different macrophytes in the littoral zone, and they have different chemical and morphological characteristics from their initial litters that can affect their decomposition rates. For all the litters in this study, the asymptotic decomposition model used by Stanford and Smith (1972) accounted well for the mass loss during litterbag incubation in the littoral zone of the Paltangho Reservoir (Table 1). The asymptotic model can be considered to be just a special case of the double-exponential decomposition model, in which the rate constant d can be considered to be zero (eq. 3). Therefore, the litters of the emergent macrophytes behaved as if they were composed of two compartments, one labile that decreased relatively rapidly, and the other refractory that showed no significant decrease within one year. Litter chemical components can be classified in terms of their availability to the microorganism's enzyme systems (Couteaux et al., 1995). The labile compartment is composed of hydrosolubles, non-lignified cellulose, and hemicellulose, and the refractory compartment is mainly lignified carbohydrates in which carbohydrates are chemically bound to native lignin (Berg 1986).

The decomposition process of emergent macrophytic litters in this study can be classified into two phases. The first phase takes place in litters which are dominated by the labile compartment that is decreased

Table 4. Comparison of decomposition rate constants of various litters in emergent macrophytes

Species	Locality	Rate constant (day^{-1})	Reference
Alisma plantago-aquatica	Russia (60° N)	0.042	Belova, 1993
Carex spp.	Michigan (44° N)	0.0012	Chamie & Richardson, 1978
Equisetum fliviatile	Russia (60° N)	0.053	Belova, 1993
Juncus americana	N. Carolina (36° N)	0.0116	Twilley et al., 1985
J. squarrosus	England (54° N)	0.0009	Latter & Cragg, 1967
Nelumbo lutea (leaf lamina)	Texas (32° N)	0.0108	Hill, 1985
(leaf petiole)		0.0033	
Phragmites australis	England (52° N)	0.0035-0.0030	Mason & Bryant, 1975
	Russia (60° N)	0.0013-0.0017	Belova, 1993
Scirpus fluviatilis	Iowa (42° N)	0.0009	Davis & van der Valk, 1978
S. lacustris	Russia (60° N)	0.007	Belova, 1993
S. validus	Iowa (42° N)	0.0056	Davis & van der Valk, 1978
Typha angustifolia	England (52° N)	0.0020-0.0018	Mason & Bryant, 1975
	Texas (32° N)	0.0047	Hill, 1985
	Korea (37° N)	0.0038	Cho, 1992
T. glauca	Iowa (42° N)	0.0022	Davis & van der Valk, 1978
T. latifolia	S. Carolina (33° N)	0.0035	Boyd, 1970
T. natans	New York (41° N)	0.0008	Findlay et al., 1990
Zizania aquatica	Virginia (38° N)	0.0077	Odum & Heywood, 1978
Z. latifolia	Korea (35° N)	0.0049	Oh, 1988
	Korea (37° N)	0.0050	Cho, 1992

relatively rapidly (half-life time between 53-187 days). Thereafter, the second phase occurred in litters composed of a small labile compartment and a dominant refractory compartment that is expected to decrease slowly. The refractory compartment in this study did not significantly decrease during litterbag incubation of one year, because incubation time was too short to detect its decomposition. These results showed that litter decomposition could depend on the relative amount of the labile compartment (A) and its decomposition rate constant (b) in the emergent macrophytes. The litter mass which remained after one year of incubation was correlated with the labile compartment and decomposition rate constant at significant levels of $p < 0.001$ and $p=0.015$, respectively. However, there was no significant correlation between the amount of labile compartment and its decomposition rate constant ($r=0.364$, $p=0.083$).

The litters of the emergent macrophytes showed a great variety in their decomposition processes for different litters from various species and plant structures in the littoral zone (Table 2). The labile compartments of the initial litter mass and their decomposition rates were in a wide range between 18% and 99% and between 0.0037 and 0.0131 day^{-1}, respectively. The litters can be classified according to the relative size of their labile and refractory compartments. Litters from leaves of *Zizania latifolia*, and *Acorus calamus* var. *angustatus*, and leaf lamina of *Nelumbo nucifera*, and stems of *Scirpus* spp. were mostly composed of the labile compartment (more than 80% of the initial litter mass). These litters lost most of their masses in one year. In contrast, the refractory compartment (more than 70% of the initial litter mass) typified litters from stems of *Phragmites australis*, *Miscanthus sacchariflorus* and *Typha angustifolia*. These litters lost the least amount of the initial mass during the litterbag incubation. Other litters, such as leaves of *Phragmites australis*, *Miscanthus sacchariflorus*, and *Typha angustifolia*, and leaf petiole *Nelumbo nucifera*, and stem of *Bidens frondosa* were of an intermediate type in their decomposition processes.

Litters of the same part of plants or related species and similar anatomy act somewhat similarly in their dynamics of litter decomposition. Stems of *Typha*, *Phragmites*, and *Miscanthus*, which function as the support structures for the leaves and have a larger proportion of sclerified and lignified tissues, had the large refractory compartment and the slowest decomposition rate. Conversely, leaves of *Zizania* and *Acorus*, and leaf lanimae of *Nelumbo* and stems of *Scirpus*, which are a photosynthetic organ with relatively less support tissues, had the large labile compartment and decomposed rapidly (Hill, 1985). The chemical property of litters, such as contents of nitrogen, phosphorus and lignin, could also affect the decomposition rate. More studies are required to reveal the details of the relationship between the decomposition rate and initial characteristics of macrophytic litter.

Litter decomposition is a key process in energy flow and nutrient cycling in the freshwater littoral zone (Polunin, 1984). In the Paltangho Reservoir, the littoral vegetation is composed of various emergent macrophytes with various litter decomposition processes depending on relative amounts of labile and refractory compartments of their litters and decomposition rate of the labile one. Decomposition of the labile compartment of macrophytic litters supplies either organic nutrition for detrital food chains or regenerates inorganic nutrients for autotrophs in aquatic ecosystems. On the other hand, the creation of organic matters, such as peat versus a mineral soil must depend on the relative inputs of refractory litter compartment from the emergent macrophytes in the littoral zone.

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