

## Is in-lake carbon processing phased to correlate with availability?

### Decomposition of *Decodon verticillatus* (L.) ELL. and *Ceratophyllum demersum* L. in Cedar Bog Lake, Minnesota, USA

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With 2 figures and 5 tables in the text

#### Abstract

In an attempt to clarify functional and detrital/trophic relationships in Cedar Bog Lake, Minnesota, we determined species specific detrital processing rates. Decomposition was measured with litter bags using a factorial design. Our plant species were *Decodon verticillatus* (L.) ELL. (an emergent shrub) and *Ceratophyllum demersum* L. (a submerged macrophyte). Decomposition rate was expressed as change in carbon, calculated as percent of ash free dry weight remaining over time. Decay coefficients ( $k$ , where  $e^{-k} = w_t/w_0e^t$ ) for year 1 (259 days) were 0.074 and 0.074, respectively for *Decodon* and *Ceratophyllum*, and for year 2 (205 days) 0.055 and 0.072 in fine mesh bags (1 mm mesh). For year 1 decay coefficients in coarse mesh bags (5 mm mesh) were 0.070 and 0.094 for *Decodon* and *Ceratophyllum*, respectively; and for year 2, 0.059 and 0.041 (based on a log-log model). Rapid initial decay of aquatic material suggests that detritivores may rely on in-lake sources in summer and autumn, and on riparian-allochthonous materials in winter and spring.

#### Introduction

Certain functional and detrital/trophic relationships of lake systems may be clarified through a study of carbon pathways; i.e., pathways including emergent shrub and submerged macrophyte biomass contributions to the lake system, and decomposition rates of those materials. We have measured carbon pathways in Cedar Bog Lake, Minnesota, in order to clarify such relationships. Two plant species represent the principal organic inputs to Cedar Bog Lake: *Decodon verticillatus* (L.) ELL. (an emergent shrub) and *Ceratophyllum demersum* L. (a submerged macrophyte). Our focus was on determining the timing and rates of decomposition for the two species. Based on plant morphology and habitat, we hypothesized that *Decodon* leaves would decompose significantly more slowly than *Ceratophyllum*. If that hypothesis was supported, plant nutrients and carbon would be released from the plant materials at different times; organisms dependent upon such material as a food source could thus

adapt to specific timing of carbon and nutrient inputs, and exploit these resources as they become available.

### Study site

Cedar Bog Lake is situated approximately 50 km north of St. Paul, Minnesota. The 12,600 m<sup>2</sup> lake was formed as an ice-block depression in the Anoka sand plain. LINDEMAN (1941) described successional processes in the surrounding wetland, as well as the geology, vegetation, fauna, and water chemistry of the lake. In 1941, the majority of the lake margin was dominated by a dense mat of *Typha latifolia*. L. BUELL et al. (1968) described the progression of the *Larix laricina* (DU ROI) K. KOCH zone surrounding the lake towards lake edge, and the configuration of concentric vegetation zones around the lake. Currently (1985) 70 percent of the lake perimeter is bordered by *Decodon verticillatus*. The remaining perimeter is bordered by *Carex* spp., *Typha latifolia*, grasses, *Alnus rugosa* (DU ROI) SPRENGEL, *Rhus vernix* (L.) KUNTZE, and *Larix laricina*.

The lake has a median pH of 7.0; maximum recorded is 8.7 (summer 1984). Conductivity ranges from 87 to 175  $\mu\text{S}/\text{cm}$ ; waters of this nature are generally classified as minerotrophic (HEINSELMAN, 1979), and usually reflect groundwater inputs.

### Methods

Decomposition rates were measured as rate of change in ash free dry weight for material enclosed in mesh litter bags; two years' data are presented.

#### Year 1 Design

For Year 1 (fall 1983—June 1984) a five factorial design was used: a) 2 species of plants, *Decodon verticillatus*, and *Ceratophyllum demersum*; b) 2 mesh sizes, 1 mm and 5 mm; c) 3 sites in the lake; d) 6 collection dates, 1, 7, 21, 43, 203, and 259 days; and e) 5 replicates per treatment.

Fresh leaves of *Decodon* or whole plant sections of *Ceratophyllum* were collected prior to autumnal senescence. Approximately 5 grams of air-dried *Decodon* or spun-dry *Ceratophyllum* were placed in tared, labelled mesh bags. Fresh-to-ash free dry weight ratios were calculated from 15 bags per mesh, per species at the same time experimental bags were placed in the lake. These 15 bags were handled in the same manner as experimental bags (Fig. 1). Carbon as a percent of ash free dry weight was determined at the University of Minnesota Analytical Soils Laboratory. Conversion summaries are presented in Table 1.

Handling losses associated with the litter bag technique have been discussed by several authors (e.g., BROCK et al., 1982; ROGERS & BREEN, 1982; SUTTLING & SMITH, 1974). We measured handling effects in this study; ten bags per mesh, per species were placed in the lake water for one hour at the time experimental bags were introduced to the lake. Plant material from the bags was processed as in Fig. 1. "Handling effects"

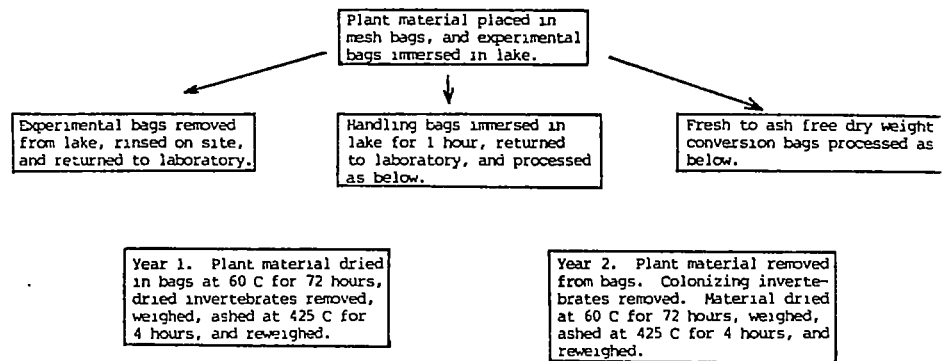


Fig. 1. Procedure to determine dry weight and ash free dry weight of plant material.

ratios (Table 1) were used to adjust final ash free dry weights of the experimental bags for further calculations.

Experimental bags were randomly located along anchor lines at each of three randomly chosen sites around the lake, 1 metre from and parallel to the vegetative mat edge. Lines were anchored on one end, the rest being allowed to float several days as normally occurs for plant material (GASITH & HASLER, 1976; ROGERS & BREEN, 1982). Bags were sunk several days later and remained at the sediment-water interface for the duration of exposure.

On each collection date, bags were rinsed in the lake, returned to the laboratory, and processed as above (Fig. 1). Later collections (days 203 and 259) were additionally rinsed in the laboratory to remove material adhering to the surface of the bags. Loss of fine particulate matter from additional rinsing was assumed to represent a minimal percentage of total loss over 203 to 259 days since percent remaining after these periods was small. Decay coefficients were calculated for each species-mesh-site combination by calculating the natural log of percent remaining carbon with respect to time (semi-log plot) (OLSON, 1963; PETERSEN & CUMMINS, 1974), and with respect to the natural log of time (log-log plot).

### Year 2 Design

Modifications implemented during Year 2 in order to reduce experimental error were as follows:

1) The factorial design was refined to a) three plant types — *Decodon* leaves, *Decodon* stems, and *Ceratophyllum*; b) 5 collection dates (1, 7, 21, 44, and 205 days); c) 2 sites within the lake instead of 3 sites; d) 2 mesh sizes (5 mm and 230  $\mu$ m instead of 1 mm); e) 5 replicates per treatment.

2) Invertebrates were separated from detrital material before litter bags and their contents were dried.

3) Invertebrate influences were not delineated by 1 mm mesh size bags during year 1. Although the 1 mm mesh was used to prohibit entrance by invertebrates, organisms were found inside the bags after collection. In order to prohibit entrance by invertebrates 230  $\mu$ m mesh bags replaced 1 mm mesh bags.

Table 1. Laboratory determination of A. Organic carbon as percent of ash free dry weight, B. Fresh to ash free dry weight ratios, and C. handling ratios.

## A. Organic Carbon as Percent of AFDW

<i>Ceratophyllum</i>	46.3	<i>Naja flexilis</i>	48.1
<i>Decodon</i> leaves	51.3	<i>Decodon</i> stems	49.2

## B. Fresh Weight to AFDW Ratio

Year	Mesh	Species	Mean Ratio*	s.d.	CV (%)
1983-84	Coarse	<i>Ceratophyllum</i>	0.047	0.006	12.9
		<i>Decodon</i>	0.210	0.011	5.43
	Fine	<i>Ceratophyllum</i>	0.048	0.004	9.26
		<i>Decodon</i>	0.210	0.030	15.8
1984-85	Coarse	<i>Ceratophyllum</i>	0.078	0.006	7.89
		<i>Decodon</i> leaves	0.220	0.010	4.70
		<i>Decodon</i> stems	0.240	0.029	12.1
	Fine	<i>Ceratophyllum</i>	0.084	0.008	9.57
		<i>Decodon</i> leaves	0.210	0.011	5.36
		<i>Decodon</i> stems	0.220	0.200	9.23

## C. Handling Ratio

(Handling Ratio  $\times$  100 = mean % remaining after placing and removing bags).

Year	Mesh	Species	Mean Ratio**	s.d.	CV (%)
1983-84	Coarse	<i>Ceratophyllum</i>	0.89	0.167	13.1
		<i>Decodon</i>	1.05	0.110	10.0
	Fine	<i>Ceratophyllum</i>	0.96	0.190	20.1
		<i>Decodon</i>	1.02	0.068	6.67
1984-85	Coarse	<i>Ceratophyllum</i>	0.91	0.071	7.77
		<i>Decodon</i> leaves	1.03	0.026	2.50
		<i>Decodon</i> stems	0.87	0.064	7.36
	Fine	<i>Ceratophyllum</i>	0.85	0.095	11.2
		<i>Decodon</i> leaves	0.97	0.140	14.6
		<i>Decodon</i> stems	0.92	0.110	11.9

\* Fresh: ash free dry weight ratio, n = 15 each.

\*\* Handling ratio, n = 10 each for 1983-84, n = 5 each for 1984-85.

s.d. = standard deviation.

CV (%) = % coefficient of variation.

4) Additionally, *Ceratophyllum* samples were immersed in 90 percent ethanol for several seconds and rinsed (prior to placement in bags) in order to remove colonizing invertebrates (POLLARD & MELCANON, 1984). A parallel series of bags without ethanol was used to test the influence of ethanol on rate of decay (by eliminating initial fungi and bacteria, leaching of soluble organic matter, or reducing desirability of the plant material as a food source). Collections of untreated bags were made on days 1, 9, 44; no signif-

icant difference ( $p > 0.05$ ) in percent remaining carbon was found between bags treated with ethanol and untreated bags.

In both years some bags of the last collection (259th and 205th days, respectively) contained living *Ceratophyllum* due to regrowth. That living material was sorted separately and omitted from weight loss analysis. It is important to recognize the plants' perennial habit and regenerative capabilities. This problem was only evident during the last collection; weight loss was measurable throughout the study period with the exception of approximately half of the samples in the last collection. This problem has not been reported before, and is not common with studies of other aquatic macrophytes (Th. Brock, personal communication).

### Results

In Cedar Bog Lake macrophytic material and *Decodon* stems gained or lost little weight during the first 24 hours, and thereafter lost weight exponentially (see Figs. 2 a—d). Analysis of variance (Table 2) for year 1 and year 2 data reveals significant ( $p < 0.05$ ) interactions between mesh and collection, mesh and species, collection and site, and collection and species with the exception that the year 2 study reveals no significant interaction ( $p > 0.05$ ) between mesh and collection.

Typically, an equation of the form  $\ln W_t/W_0 = -kt$  is used to estimate the decay coefficient  $k$ .  $W_0$  equals the initial amount of material,  $W_t$  equals the final amount. Evaluation of  $k$  is based on a least squares fit of data to a semi-log

Table 2. Factorial analysis of variance of decomposition results.

Factor	P-values	
	1983-84	1984-85
Mesh	0.084	0*
Collection	0*	0*
Site	0.044*	0.584
Species	0.817	0*
Interactions:		
Mesh days	0.003*	0.096
Mesh site	0.473	0.763
Mesh species	0*	0*
Days site	0.020*	0.047*
Days species	0*	0*
Site species	0.841	0.412
Mesh days site	0.178	0.718
Mesh days species	0.588	0.584
Mesh site species	0.910	0.152
Days site species	0.269	0.124
Mesh days site species	0.442	0.357

\* Differences significant at the 5% level.

Table 3. Decay coefficients (k) for plant species, 1983-84 (year 1) (coarse = 5 mm, fine = 1 mm).

k values for 1983-84 (year 1)					
(log-log) regression model					
Species	Mesh	Site	k	s.e.	r <sup>2</sup>
<i>Ceratophyllum</i>	Coarse	1	0.093	0.014	.67
		2	0.101	0.013	.72
		3	0.089	0.011	.73
	Fine	1	0.077	0.001	.66
		2	0.073	0.009	.76
		3	0.072	0.007	.84
<i>Decodon</i>	Coarse	1	0.065	0.008	.72
		2	0.074	0.008	.76
		3	0.072	0.007	.84
	Fine	1	0.056	0.074	.81
		2	0.074	0.004	.92
		3	0.063	0.006	.85

(semi-log) regression model					
Species	Mesh	Site	k	s.e.	r <sup>2</sup>
<i>Ceratophyllum</i>	Coarse	1	0.003	0.001	.45
		2	0.002		.49
		3	0.002		.36
	Fine	1	0.002		.44
		2	0.002		.67
		3	0.003		.68
<i>Decodon</i>	Coarse	1	0.002		.63
		2	0.002		.67
		3	0.002		.58
	Fine	1	0.001		.66
		2	0.001		.71
		3	0.001		.56

\* all standard errors 0.001.

function (PETERSEN & CUMMINS, 1974; OLSON, 1963). However, for our Cedar Bog Lake data a log-log equation ( $e^{-k} = W_1/W_0 e^t$ ) best explained variation of different treatments with respect to time. We present both estimates of k in Tables 3 and 4.

Over the two years of study, *Decodon* leaves and *Ceratophyllum* decay coefficient values of 0.001-0.003 for the semi-log equation had r<sup>2</sup> values of 0.23 to 0.78. Decay coefficients based on the log-log model ranged from 0.056 to 0.101 for year 1, and 0.039-0.077 for year 2; r<sup>2</sup> values ranged from 0.33 to 0.92 for coarse and fine mesh bags. *Decodon* stem material decays more slowly than leaf tissue; k coefficients measured during year 2 ranged from 0.025-0.033 based on type of mesh and site (see Table 4).

Table 4. Decay coefficients (k) for plant types, 1984-85 (year 2) (coarse = 5 mm, fine 230  $\mu$ m).

k values for 1984-85 (year 2)

(log-log) regression model

Species	Mesh	Site	k	s.e.	r <sup>2</sup>
<i>Ceratophyllum</i>	Coarse	1	0.039	0.015	.62
		2	0.043	0.013	.33
	Fine	1	0.077	0.015	.55
		2	0.066	0.010	.70
<i>Decodon</i> leaves	Coarse	1	0.059	0.010	.62
		2	0.059	0.008	.70
	Fine	1	0.054	0.006	.76
		2	0.056	0.009	.63
<i>Decodon</i> stems	Coarse	1	0.030	0.008	.38
		2	0.025	0.010	.19
	Fine	1	0.033	0.011	.29
		2	0.028	0.007	.45

(semi-log) regression model

Species	Mesh	Site	k	s.e.	r <sup>2</sup>
<i>Ceratophyllum</i>	Coarse	1	0.002	0.001*	.43
		2	0.001		.26
	Fine	1	0.002		.62
		2	0.001		.60
<i>Decodon</i> leaves	Coarse	1	0.001		.50
		2	0.002		.77
	Fine	1	0.001		.76
		2	0.002		.78
<i>Decodon</i> stems	Coarse	1	0.001		.23
		2	0.001		.16
	Fine	1	0.001		.23
		2	0.001		.41

\* all standard errors 0.001.

Decomposition rates were compared between fine and coarse mesh bags, within a species and within a given year using a least significant difference test with planned multiple comparisons (STEEL & TORRIE, 1980). No significant influence of mesh size was detectable for either year, nor for either species. Further, percent remaining carbon over the duration of the study period did not differ between the two plant species for year 1, or among three plant types (*Ceratophyllum*, *Decodon* leaves, *Decodon* stems) for year 2 (Table 5). Although decay rates for the stem material did not differ significantly from that of leaves nor macrophytes, actual quantities of plant material remaining differed substantially. Essentially no macrophyte material or leaf tissue remained after 250 days in the lake (year 1), and little remained (30 %) after 205 days (year 2). The

Table 5. LSD planned multiple comparisons of k values for 1983-84 and 1984-85 decomposition study.

Differences between decomposition rates for species and mesh size  
1983-84

Species	Slope	MSE
<i>Ceratophyllum</i> , coarse mesh	0.094	0.963*
<i>Ceratophyllum</i> , fine mesh	0.074	
<i>Decodon</i> leaves, coarse mesh	0.070	
<i>Decodon</i> leaves, fine mesh	0.065	

No significant differences between species or mesh. The slopes were estimated from a natural log-log model.

\* The test is:  $t(0.05, df) * mse * (2/r)^{-2}$

1984-85

Species	Slope	MSE
<i>Ceratophyllum</i> , coarse mesh	0.067	1.03**
<i>Ceratophyllum</i> , fine mesh	0.071	
<i>Decodon</i> leaves, coarse mesh	0.059	
<i>Decodon</i> leaves, fine mesh	0.055	
<i>Decodon</i> stems, coarse mesh	0.028	
<i>Decodon</i> stems, fine mesh	0.031	

No significant differences between species or mesh. The slopes were estimated from a natural log-log model.

\*\* The test is the same as above.

stem material lost weight more slowly than the other plant types: 80 percent remained after 205 days.

### Discussion

Typically, senescent plant material placed in an aquatic environment decays exponentially. Up to 50 percent of the original dry weight is lost due to leaching within the first 24 hours of incubation (KAUSHIK & HYNES, 1971; PETERSEN & CUMMINS, 1974; GODSHALK & WETZEL, 1978). Many investigators have used pre-dried or lyophilized plant material in their design (CARPENTER & ADAMS, 1979; HANLON, 1982). BROCK et al. (1982) determined that fresh *Nymphaeodes peltata* (GMEL.) O. KUNTZE leaves incubated 7 days in water lost significantly less organic material than pre-dried material; leaf petioles gained weight after seven days. In Cedar Bog Lake, slight gains in weight (see Figs. 2 a-d) during the first day may be attributed to 1) conversions calculated to compensate for handling losses and initial ash free dry weight, i.e., errors in estimating handling losses and initial ash free dry weight may be greater than actual weight gained or lost during the first 24 hours. 2) Some fine particulate



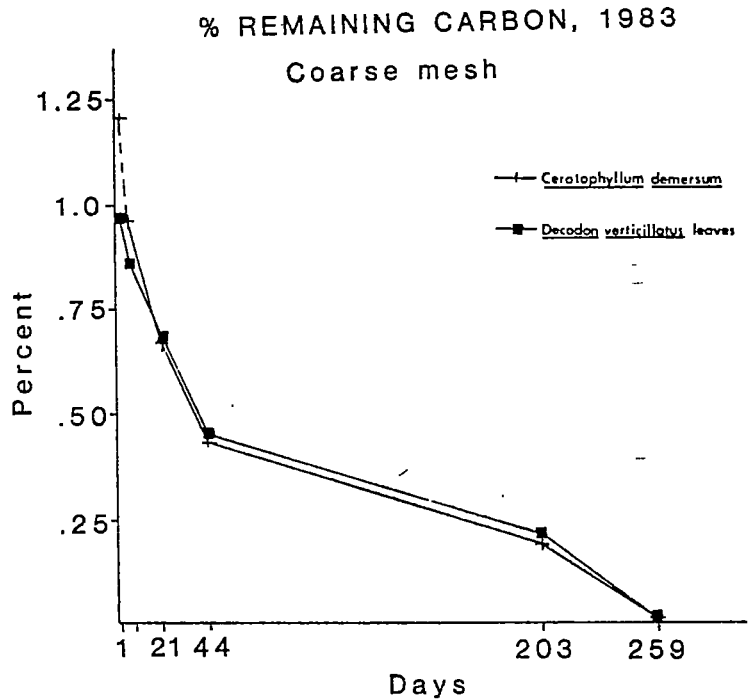


Fig. 2 a. Percent remaining carbon in coarse mesh bags, 1983-84 (year 1).

organic material may accumulate in the bags upon placement in the lake. This plant material and associated fine particulate organic matter may have caused an increase in ash free dry weight in the experimental bags.

We have seen no literature that reports decomposition rates for *Ceratophyllum*; however, investigators have studied decomposition of other submerged macrophytes. ROGERS & BREEN (1982) reported that less than 10 percent of the dry weight of *Potamogeton crispus* L. remained after 25 days exposure in litter bags in a lake. PIESZYNSKA (1972, cited by WETZEL, 1975) estimated that 6-92 percent of *P. lucens* L. and *P. perfoliatus* L. remained after 7-14 days in situ. In Cedar Bog Lake 40-50 percent of the original *Ceratophyllum* carbon (depending on mesh size) remained after 15 days in place. In a Wisconsin lake semi-log decomposition curves for *Myriophyllum spicatum* L. had  $k$  values ranging from 0.076 to 0.141 per day (CARPENTER & ADAMS, 1979). GODSHALK & WETZEL (1978) described weight loss of several submerged aquatics including *Myriophyllum heterophyllum* MICHAUX and *Najas flexilis* (WILLD.) ROSTK. & SCHMIDT. Their results were expressed with an exponential model  $dW/dt = -kW$ ,

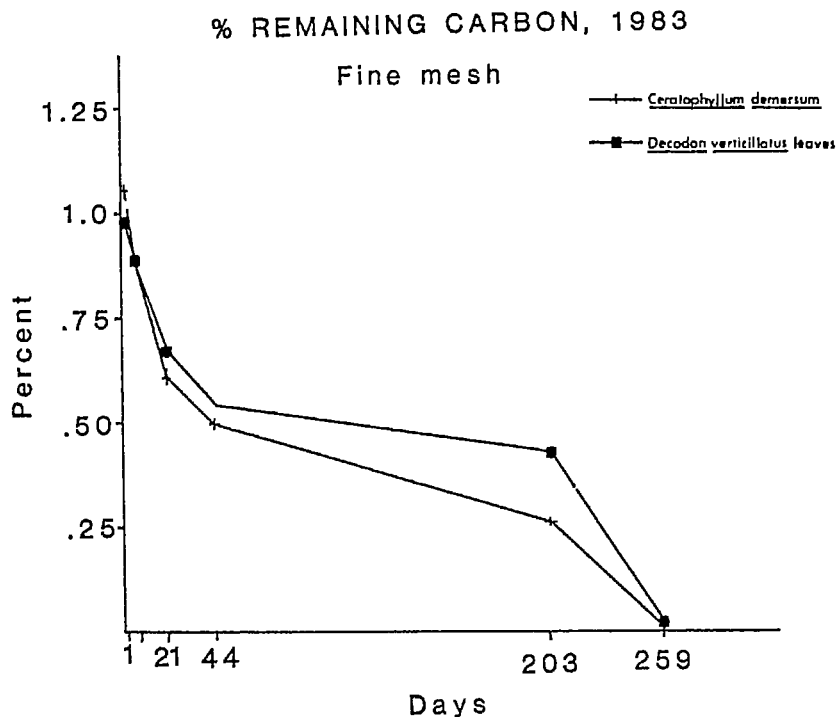


Fig. 2 b. Percent remaining carbon in fine mesh bags, 1983–84 (year 1).

where  $k = ae^{-bt}$ . Decay coefficients are used to standardize results of decomposition studies. However, when different decomposition equations are used to derive  $k$  values from studies that vary in length, careful comparisons of  $k$  values are required.

Decay coefficients of willow in an oligotrophic lake were reported as 0.005 and 0.001 for fine and coarse mesh bags (HANLON, 1982). *Decodon* leaf material, like willow, is considered to be a moderately fast decomposer. Decay coefficients for *Decodon* leaves, using the same equation that HANLON used, ranged from 0.001 to 0.002. Decay coefficients for *Ceratophyllum* in the Cedar Bog Lake study coincided with HANLON's (1982) *Potamogeton* values of 0.001 to 0.007 for fine and coarse mesh bags, respectively.

The similarity between HANLON's results and ours is surprising in that he studied an oligotrophic system and Cedar Bog is eutrophic. It is possible that organisms central to decomposition processes in the eutrophic system are numerous, whereas the oligotrophic system harbors few, but efficient popula-

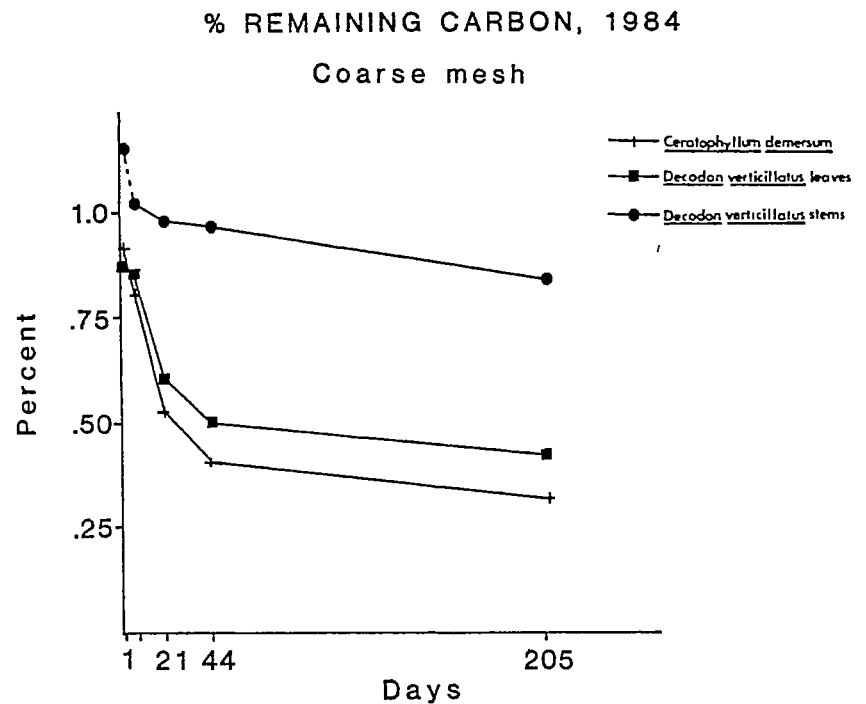


Fig. 2 c. Percent remaining carbon in coarse mesh bags, 1984—85 (year 2).

tions; hence, decomposition proceeds at the same rate. Both systems may be functionally similar, but structurally quite different.

The fact that decay coefficients were not significantly different is a reflection of the high variance found in these types of studies. Non-significant differences that were noted are probably due to differences in chemical composition of the plant material; submerged macrophytes contain much less structural materials, such as hemicellulose, lignin, and cellulose, than alchthonous leaf tissue (GODSHALK & WETZEL, 1978).

Mesh size differences are also important; carbon was initially lost at a more rapid rate from the coarse mesh bags, although the differences were not statistically significant ( $p > 0.05$ ). Coarse mesh bags were intended to allow greater invertebrate access, and thus highlight differences attributable to invertebrate utilization. However, coarse mesh bags may cause greater handling losses. Macroinvertebrate influences on rates of decay may have been overshadowed by high variance attributable to the litter bag technique. Enumeration of invertebrates proved difficult, and results lacked clear implica-

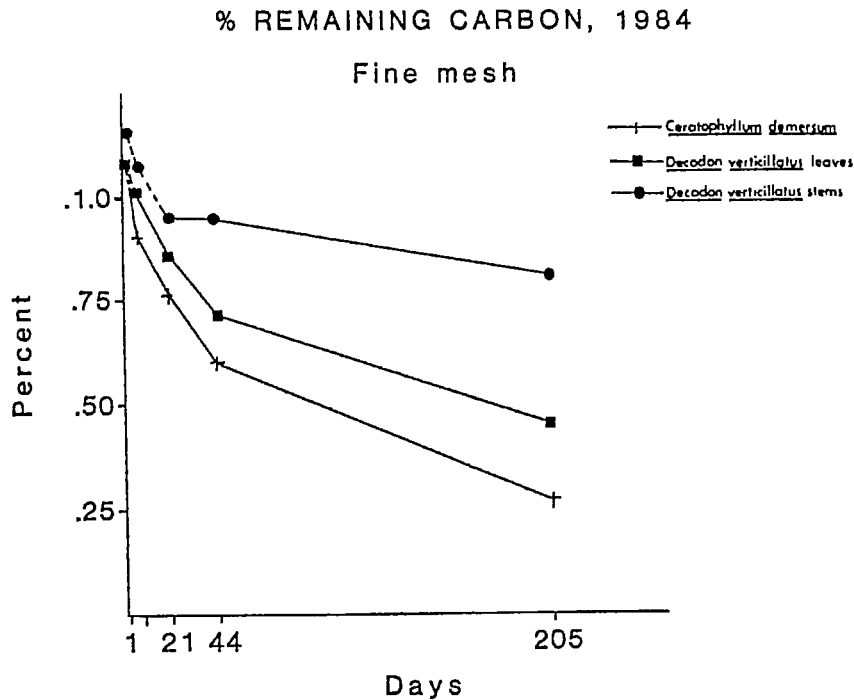


Fig. 2 d. Percent remaining carbon in fine mesh bags, 1984—85 (year 2).

tions. Differences in percent remaining or differences in  $k$  coefficients between coarse and fine mesh bags were more likely related to increased exposure of plant material to water and sediments (via larger mesh size) and to increased handling losses, than to macroinvertebrate influences.

#### Summary

Results from this study show that both *Decodon* leaves and *Ceratophyllum* plants decomposed within a one year period. The rapid decay of *Decodon* leaves and *Ceratophyllum* plants suggest that these materials would not add considerably to a lake fill-in process, but instead would contribute to rapid recycling of nutrients and carbon. To the contrary, slower decay of *Decodon* stem material seems to be important for mat edge stabilization and organic matter accumulation.

Carbon contributions from these sources are seasonally variable. Carbon contributions from *Decodon* leaves occur during autumn; *Najas flexilis* also contributes carbon to the lake in early fall. *Ceratophyllum*, however, may decompose or slough material throughout the growing season. Varied timing of carbon and nutrient inputs is important to consumers; different food resources may be exploited efficiently at appropriate times in the organisms' life cycle.

## Sommaire

Les résultats de l'étude montrent que les feuilles de *Decodon verticillatus* et les plantes de *Ceratophyllum demersum* décomposent dans une année. La pourriture rapide des feuilles de *Decodon* et *Ceratophyllum* suggère que ces matériels n'ajouteraient pas considérablement au processus de remblayer le lac mais plutôt contribuerait au recyclage rapide des nutriments et du carbone. Au contraire, la pourriture plus lentement de la tige de *Decodon* semble être importante pour la stabilisation du bord de la natte et de l'accumulation de la matière organique.

Les contributions carbonées des feuilles de *Decodon* arrivent pendant l'automne; *Najas flexilis* contribue le carbone au lac au premier l'automne. *Ceratophyllum*, pourtant, peut décomposer ou se dépouiller peut être pendant toute la saison de développement. Le chronométrage varie des ressources de carbone et de nutriment peut être exploité efficacement au temps approprié pendant le cycle de vie de l'organisme.

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