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DECOMPOSITION IN THE LITTORAL ZONE OF LAKES

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After incubation periods of up to 180 days, particulate material was dried and analyzed for weight loss and contents of ash, hemicellulose, cellulose, lignin, nonstructural carbohydrate, and total C and N. Media of the laboratory experiments were filtered, dissolved material fractionated by membrane ultrafiltration into molecular weight categories, and assayed for total dissolved organic C, UV absorbance, and fluorescence activity; C and N analyses and IR spectrophotometry were performed on unfractionated filtrates.

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Microbial metabolism associated with the decomposing plant tissue was measured by assaying the content of ATP and the activity of dehydrogenase. The data from these 2 assays did not compare favorably with each other, and severe inadequacies were encountered in both methods. Of possible use in estimating microbial colonization of decomposing plant tissue is the total C and N contents and the resultant C:N ratio. As found in many other studies, N generally accumulates through time, with a consequent lowering of the C:N ratio.

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Key words *Aerobic, anaerobic aquatic plants, decomposition, dissolved organic matter, lakes, limnology, marshes, Michigan, oxygen, sediments, temperature.*

INTRODUCTION

Production of biomass by the aquatic macrophytes that grow in freshwater marshes and the littoral zones often constitutes at least half of the total organic C inputs to lake systems. Very little of this photosynthetically synthesized C remains in reduced form over geological time in the permanent sediments of the marsh or lake; a majority continues to be important in the metabolism of the aquatic system. Much of the organic C of the plants is respired and released as extracellular dissolved organic matter. Utilization of the particulate tissue directly in consumption by animals is quantitatively insignificant in most systems as compared to degradation by microbes. A large majority of the particulate and dissolved organic C of the net production of the system is processed during detrital decomposition by the microflora (Wetzel, 1975).

The process of decomposition has received much attention in terrestrial conditions, particularly in relation to agriculturally important species. The processes and environmental factors influencing decomposition of organic materials in streams has been investigated recently in some detail. Very few systematic inquiries, however, have been made on the influence of environmental conditions or the effects of morphology and phylogenetic relationships of aquatic angiosperms in regard to decomposition in freshwater marshes or lacustrine littoral areas (see review in Wetzel, 1975). In the analyses discussed here, a systematic appraisal of temperature and O_2 conditions was made on decomposition of freshwater angiosperms exhibiting a variety of growth forms and phylogenetic ancestry to provide an informational base upon which more detailed mechanistic studies could be made. The results presented here are summary in nature; more detailed results and discussion will be found elsewhere (Godshalk, 1977).

METHODS

Controlled experiments were conducted to evaluate the rates of decomposition of littoral macrophytes and the ultimate fate of these plants and their dissolved and particulate organic fractions in the lake ecosystem. Senescent plants of 5 freshwater species of aquatic angiosperms were collected at the end of the growing season as the plants began to senesce, washed free of sediments, and lyophilized. Replicated samples of dried plant material were put in 1-litre flasks of synthetic lake water (Wetzel Medium 5), inoculated with natural sediment (from the littoral zone of Lawrence Lake, Michigan) containing no coarse (>1 mm) organic matter, and incubated up to 180 days

under anaerobic and aerated conditions at 10°C and 25°C. The various conditions of O_2 concentration were selected to simulate 3 situations under which naturally occurring decomposition proceeds: (1) completely aerobic conditions, as in wave-swept, turbulent littoral regions; (2) completely anaerobic conditions, as in many quiescent littoral regions where plant material compacts at the sediment–water interface under continuously strongly reducing conditions; and (3) aerobic to anaerobic conditions (i.e., synthetic lake water was initially oxidizing but allowed to become anoxic as a result of decomposition).

Samples were taken after 2, 4, 10, 24, 50, 90, and 180 days of decomposition and the contents of the flasks filtered (0.22 μm Millipore® GS membrane filters). Dissolved organic compounds (<0.2 μm) were fractionated by Amicon® membrane ultrafiltration into several molecular weight categories (<30,000 *M*; <10,000 *M*; <1,000 *M*; and <500 *M*). Each fraction was examined for total dissolved organic C, ultraviolet absorbance, and fluorescence (Wetzel and Otsuki, 1974); unfractionated filtrate was analyzed for dissolved C and N content, and by infrared spectrophotometry. The particulate material recovered was lyophilized, weighed to determine organic weight loss during decomposition, and analyzed for content of ash, total nonstructural carbohydrates (Smith, 1969), hemicellulose, cellulose, lignin (Goering and Van Soest, 1970), and particulate C and N. In addition, microbial activity of identical fresh detritus at each time interval was assessed by determining dehydrogenase activity (Zimmerman, 1975) and ATP content (Suberkropp and Klug, 1976).

In conjunction with the laboratory experiments we conducted a series of experiments involving the decomposition of the same plant species contained in mesh bags placed in the littoral zones of 2 lakes. These experiments were designed to provide data on decomposition in the natural environment under the conditions that were simulated in the laboratory experiments. Replicate litterbags, sacrificed periodically during the course of incubation, were placed in the moderately developed littoral zone (2 m) of Lawrence Lake (a hard water mesotrophic lake) during spring and summer seasons. Additional sets of litterbags were incubated during fall and winter at the same location, the pelagial zone (7 m) in Lawrence Lake, and in the littoral zone (1.5 m) of Wintergreen Lake (a hypereutrophic hard water lake with a well-developed littoral zone). Assay procedures were identical to those used in the laboratory experiments with the exception that no data could be obtained concerning DOM associated with the decomposing macrophyte material.

RESULTS AND DISCUSSION

Laboratory Experiments

Consistent with the knowledge of basic principles of decomposition in general, temperature would likely affect primarily the rates of decay whereas

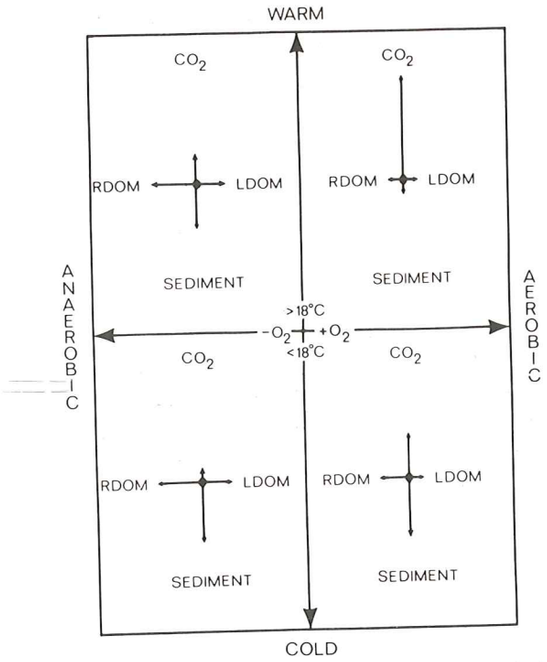

Fig. 1. Relative importance, with respect to rates and total accumulation, of the 4 possible fates of macrophytic tissue observed during laboratory decomposition under various conditions of temperature and O_2 concentration. LDOM = labile dissolved organic matter, RDOM = resistant dissolved organic matter. (From Godshalk and Wetzel, 1977.)

O_2 would influence the efficiency and completeness of decomposition. The relationships between decomposition of aquatic angiosperms and temperature and O_2 concentrations were not found to be that direct but to interact significantly.

The response of decomposing macrophytes to temperature and O_2 concentration at various levels is diagrammed in Fig. 1. Because anaerobic conditions (E_h <100 mV) were established rapidly in the aerobic-to-anaerobic cultures for all species (i.e., ≤10 days at 10°C, ≤2 days at 25°C), the results of these experiments are not differentiated in this report from those of the strict anaerobic experiments. The interaction of temperature and O_2 appears to be as important as either parameter by itself, causing a gradient of decompositional rates from slow in cold anaerobic conditions, to fast in warm aerobic situations. Most notable with respect to environmental control of decomposition are the apparent dependence on temperature of the process of converting particulate organic matter to dissolved organic matter and the constraints put on the conversion of dissolved organic matter to CO_2 by

Table 1. Parameters Describing Equations of Best Fit to Data for Weight Loss during Decomposition of 5 Macrophyte Species under 4 Laboratory Conditions[a]

Species	Anaerobic (25°C)		Aerobic (25°C)	
	a	*b*	*a*	*b*
Nuphar variegatum	0.1114	0.0692	0.1439	0.0930
Myriophyllum heterophyllum	0.0831	0.0625	0.0619	0.0335
Najas flexilis	0.0626	0.0487	0.0444	0.0244
Scirpus subterminalis	0.0167	0.0145	0.0280	0.0182
Scirpus acutus	0.0138	0.0248	0.0170	0.0103
	Anaerobic, 10°C		Aerobic, 10°C	
Nuphar variegatum	0.0436	0.0350	0.0465	0.0451
Myriophyllum heterophyllum	0.0284	0.0328	0.0264	0.0417
Najas flexilis	0.0101	0.0080	0.0148	0.0168
Scirpus subterminalis	0.0003	−0.0193	0.0057	0.0040
Scirpus acutus	0.0791	0.5080	0.0104	0.0219

[a] Equations are exponentials of the form $dW/dt = -kW$, where the decay coefficient, k, decreases exponentially with time ($k = ae^{-bt}$). W = percent of initial ash-free dry weight remaining, t = days of decomposition, *a* = initial rate of weight loss which declines exponentially at a rate of *b*.

the presence or absence of O_2. The seasonal and morphometric occurrence of the various conditions of temperature and O_2 in a temperate lake, and the ecological ramifications of environmental constraints on decomposition are presented elsewhere (Godshalk and Wetzel, 1977).

It was further hypothesized that the simple rates of decay of plant material, i.e., the loss in weight over time, would vary in any one environmental condition according to the structure of the plants involved. Emergent plants requiring more structural tissue (hemicellulose, cellulose, lignin) because of their erect growth form and lack of water support for most of the upper portions of the plant, would be more resistant to decomposition and therefore persist in the system for relatively long periods of time. By this same argument, submersed plants, because of their lack of rigid supportive tissue, would contain less of the resistant structural tissue and would decompose fairly rapidly. These general relationships between growth form and structural tissue content are supported by the survey of 21 species of aquatic macrophytes by Polisini and Boyd (1972) who found 53.4 ± 4.2, 66.6 ± 3.1, and 33.7 ± 2.6 g non-cell wall material ±2 SE/100 g plant for submersed, floating-leaved, and emergent macrophytes, respectively.

In our experiments, least-squares regression analysis of organic weight loss through time was used to determine the equation of best fit to the data. These equations for all species decomposing under the various conditions tested are presented in Table 1. It will be noted that under all conditions the floating-leaved water lily *Nuphar variegatum* Engelm. (the plant with the

Table 2. Content (as Percent of Total Ash-Free Dry Weight) of Fiber Components of Senescent Tissue of 5 Macrophyte Species before Decomposition

Species	Hemicellulose	Cellulose	Lignin	Total
Nuphar variegatum	12.33	17.58	4.79	34.70
Myriophyllum heterophyllum	10.31	17.34	4.69	32.34
Najas flexilis	19.99	31.55	8.44	59.98
Scirpus subterminalis	34.55	26.43	2.59	63.57
Scirpus acutus	32.27	33.67	3.76	69.70

least amount of structural tissue) lost weight faster than all other species. The next most rapid to be decomposed were the submersed species *Najas flexilis* (Willd.) Rostk. & Schmidt, and *Myriophyllum heterophyllum* Michx., followed by *Scirpus subterminalis* Torr. which lost weight at a rate similar to that of the emergent *Scirpus acutus* Muhl. It is important to note the significance of phylogenetic ancestry here. *Scirpus subterminalis* grows vegetatively totally submersed through its entire life cycle and in Lawrence Lake, Michigan, constitutes >50% of the total annual primary production of the lake (Rich, et al., 1971). This locally important plant does not, however, decompose as would be predicted from its growth habit; *S. subterminalis* is the only submersed species in this bulrush genus, but it retains the structural and decompositional characteristics of the genus.

Under anaerobic conditions and 10°C, the proportions of hemicellulose, cellulose, and lignin in the recovered plant material of all species, except *N. flexilis*, remained approximately constant; in *Najas* both hemicellulose and cellulose declined while lignin increased proportionally. Under aerobic conditions, the percentage of lignin increased in all species while hemicellulose and cellulose either remained constant or decreased slightly. At 25°C, changes in proportions of fiber constituents become greater. During anaerobic decomposition, the proportion of lignin increased in all other species but was constant in *S. acutus*, that of cellulose decreased among all species except *Najas* where it increased, and that of hemicellulose increased in *Myriophyllum* and *Nuphar* but declined in *S. subterminalis* and *N. flexilis*. The greatest increases in the proportion of lignin in the recovered plant tissue of all species occurred during aerobic decomposition at 25°C. Hemicellulose content remained approximately constant while cellulose content declined in all species. The rate of lignin "accumulation" was most rapid in *Myriophyllum*, indicating that the other components (hemicellulose, cellulose) were being decomposed more rapidly in this species.

The structural characteristics of the plant which control its decomposition are not necessarily the proportions of hemicellulose, cellulose, and lignin in each species but rather the total content of these structural materials. The initial composition of the fiber fractions of each species used in our experiments is shown in Table 2. It can be seen that the most rapidly decomposing

plants, *Myriophyllum heterophyllum* and *Nuphar variegatum*, have the lowest total concentrations of fiber. *Najas*, which decomposed about as fast as these other 2 species, had a very high fiber content but this is probably the result of a high density in the plant material of nearly ripe seeds whose protective coats are resistant to breakdown during fiber analysis procedures and would cause an overestimate of the cellulose fraction. The 2 species of bulrush were the slowest decomposers and had the highest total fiber content of all plants studied. As seen in Table 2, no single fiber constituent seems to be correlated with potential decomposition rate. The constant or only slightly shifting proportions of all structural components throughout the experimental period during even precipitous declines in organic weight demonstrate that macrophyte tissue decayed uniformly with respect to its various individual components. For example, substantial amounts of all fiber fractions were present in *Najas* and *Myriophyllum* samples after 90 days of decomposition, aerobically at 25°C, and yet after another 90 days not enough tissue could be recovered to allow fiber assays to be performed.

Total nonstructural carbohydrate (TNC), present only in low concentrations even initially in these senescent plants, was lost rapidly from particulate material, as would be predicted. The TNC values remained approximately constant in all species during anaerobic decomposition at 10°C, and TNC concentrations decreased in all species at 25°C, the decrease in *Najas, Myriophyllum*, and *Nuphar* being faster than those in *S. subterminalis* and *S. acutus*. Under aerobic conditions, loss of initial content of TNC was much more rapid than under anaerobic conditions; TNC levels fell to ≈0 in all species and remained constant for the duration of sampling (180 days) at 10°C. At the higher temperatures, decomposition of TNC of all species, except *Najas*, showed rapid initial decline in the first 10 to 25 days, no measurable change until after 50 to 90 days, and then a slight increase during the last 90 days of decomposition. *Najas flexilis* initially exhibited a high content of TNC, probably resulting from many nearly mature seeds in the axils of leaf material, which declined steadily throughout the decomposition period. These results imply that losses of simple carbohydrates from decomposing plant matter may not be simply from leaching. However, such results must be interpreted with caution because of probable interferences of humic compounds present during the enzyme extraction of the TNC.

Concentrations of dissolved organic carbon (DOC) exhibited marked contrasts in rates of change through time among molecular weight fractions and under differing conditions of temperature and O_2. Concentrations of DOC > 30,000 *M* and > 10,000 *M* were consistently 2–3× those of *M* < 1,000. Decomposition of DOC in all fractions was much more rapid under aerobic conditions than anoxic and much more complete at 25°C than at 10°C (an example is given in Fig. 2). Higher molecular weight compounds of the DOC were degraded less, proportionately, than low molecular weight fractions at the colder temperatures. Under anaerobic conditions the levels of high

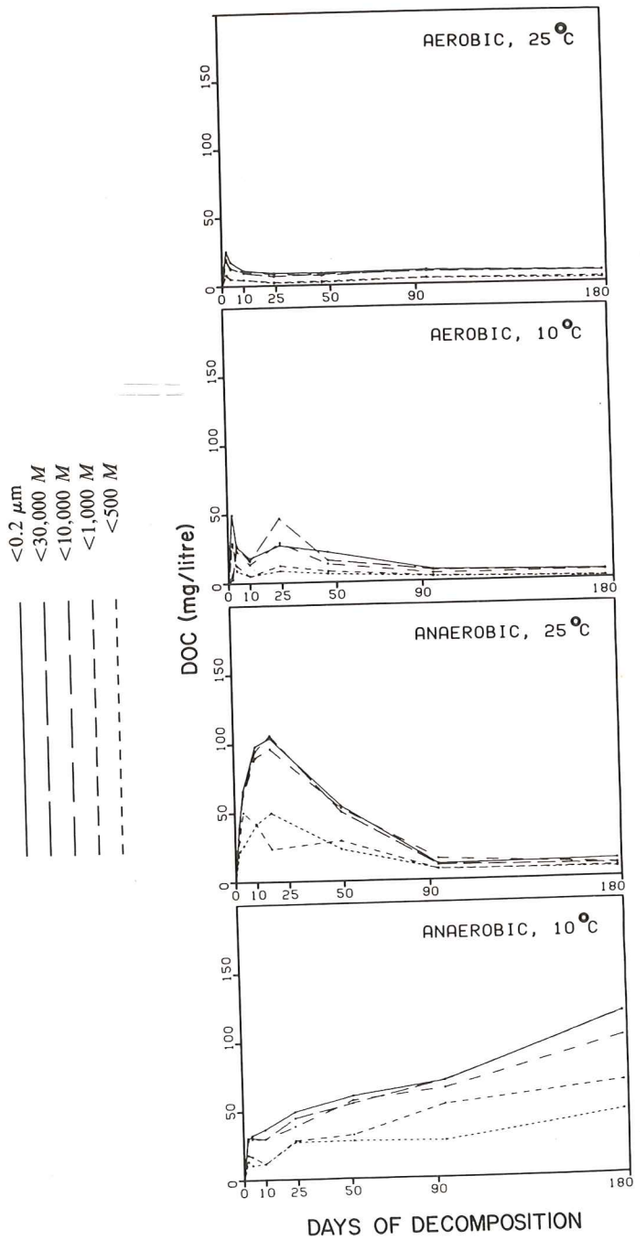

Fig. 2. Concentration (mg/litre) of dissolved organic carbon in various molecular weight fractions of media during laboratory decomposition of *Myriophyllum heterophyllum* under 4 conditions. (From Godshalk and Wetzel, 1977.)

molecular weight DOC were much higher and were degraded very much more slowly than under aerobic conditions at 25°C. At 10°C and when anoxic, all molecular weight fractions increased progressively throughout the half-year of experimentation. Analyses of ultraviolet light absorption and fluorescence indicated a progressive accumulation of yellow organic acids of polyphenolic type under these latter conditions (Wetzel and Otsuki, 1974).

Microbial Metabolism

Measurement of ATP content provides an approximate estimate of living biomass because ATP is not stored appreciably by organisms and degrades extremely rapidly upon death of an organism. The ATP content of microorganisms associated with decomposing macrophytic tissue of *Najas, Nuphar*, and *Myriophyllum* decaying anaerobically at 10°C reached maximum values after ≈25 days and then slowly declined during the rest of the experimental period. The ATP content of both species of *Scirpus* remained very low throughout the entire 180-day incubation period. The ATP levels were somewhat greater at 25°C than at 10°C among all species.

The ATP content was higher during aerobic decomposition than during anaerobic at both temperatures. Content associated with *Najas, Nuphar* and *Myriophyllum* also reached maximum levels early in the incubation period and then declined, whereas ATP associated with both species of *Scirpus* increased continually through time. Highest content of ATP among communities associated with all macrophytic species was found during aerobic decomposition at 25°C. Content of ATP associated with *Najas, Myriophyllum*, and *S. subterminalis* reached maximum values within ≈10 days, *S. acutus* after 50 days, and *Nuphar*, although highly erratic, attained maximum values after 180 days. Only under the latter conditions (aerobic, 25°C) were the differences in ATP content associated with the various species appreciable. The maximum values for microflora associated with decomposing *Najas* and *Myriophyllum* were ≈4× those of *S. subterminalis* and *Nuphar*, but averaged over the entire incubation period, the overall ATP contents of the 4 species were probably not different. The emergent *S. acutus*, on the other hand, had a maximum ATP content about 5× that of *S. subterminalis* and *Nuphar* and at least 2× the content for nearly all of the decomposition period, thus implying a significantly greater microbial biomass associated with this species.

Observed concentrations of ATP were difficult to interpret because of the subtlety of the differences among the conditions and the large numbers of samples precluded replication. Further complications arose from chemical interferences by humic compounds and $CaCO_3$, both of which were abundant in these samples (Cunningham and Wetzel, 1977). We believe that the values found are useful within this study but should not be used in comparisons of ATP values obtained by other investigators because of the disparities caused by organic interferences, variations in sample material, and differ-

Table 3. Initial Nitrogen and Carbon Content (as Percent of Total Dry Weight) and the C:N Ratio of Senescent Macrophytes

Species	N	C	C:N
Nuphar variegatum	2.4	39.3	16.4
Myriophyllum heterophyllum	2.0	24.7	12.3
Najas flexilis	1.8	31.2	17.3
Scirpus subterminalis	1.2	30.4	25.3
Scirpus acutus	1.5	43.6	29.1

ences in assay efficiencies (G. L. Godshalk and R. G. Wetzel, *personal observation*).

The other method of assaying microbial activity directly during our investigations involved the reduction of a tetrazolium salt by the microbial electron transport system (ETS), specifically a measure of dehydrogenase activity. Anaerobic decomposition at 10°C caused moderate and about equal increases in dehydrogenase activity in all species during the entire experimental period, except in *S. acutus* which peaked after only 50 days then declined. This increase through time was not seen during cold aerobic decomposition as ETS values for *S. subterminalis, Najas*, and *Myriophyllum* consistently remained low. However, values for *Nuphar* and *S. acutus* approached the highest values of all species studied under all conditions by day 50, and then declined to values about the same as for the other species by the end of the experiments. At the higher temperature, anaerobic decomposition produced very high ETS values, especially in *Nuphar*, but exhibited no discernible trends over time. Aerobically, at 25°C all species had ETS values approximately equal to those obtained during 10°C aerobic decomposition, and all species shared the trend of higher initial values in the first 25 days preceding a gradual but steady decline through the remainder of the sampling period.

In all species, and in particular for parallel experiments on a marine species decomposing in synthetic sea water, all anaerobic conditions produced ETS values substantially higher than those of aerobic conditions, thus implying a chemical reduction of the tetrazolium salt that was not dependent on enzymatic activity (cf. Schindler et al., 1976). Further, data for ATP and ETS did not correlate, and values of each through time varied independently.

Analysis of the C and N content of decaying macrophyte tissue and the calculated C:N ratio may prove to be a useful parameter to describe microbial colonization. During anaerobic decomposition at 10°C, particulate N remained constant over the entire 180 days of sampling in both *Scirpus* species, the slowly decomposing plants. The more rapidly decomposing plants, *Najas, Myriophyllum* and *Nuphar*, showed an increase in N, which was especially rapid in *Nuphar*, and a resultant drop in the C:N ratio. Aerobically, N content increased continuously in *S. subterminalis* and *Nuphar*; a similar increase occurred in *Najas* and *Myriophyllum*, but only to day 50 and then a decline occurred. The N content of *S. acutus* remained about constant. The C:N ratios for all species under these anaerobic conditions gradually and continually decreased.

At 25°C under anaerobic conditions, N content increased initially in all species then declined gradually for the remainder of the experiments in *Najas, Myriophyllum*, and *Nuphar*. These changes were in contrast to a rapid initial increase and decrease during the first 10 days in *S. subterminalis* and 25 days in *S. acutus*, followed by continual gradual increase in N. Consequently, C:N remained constant for 180 days in *Myriophyllum* and *Nuphar*, declined gradually in *S. subterminalis* and *Najas*, and increased for the first 50 days then declined in *S. acutus*. All species showed an increase in N content during aerobic decay during the first 4 to 10 days and then a decline, except in *S. acutus* which increased through the entire decomposition period. As a result C:N of *S. acutus* slowly decreased for the entire 180 days. In all other species C:N declined during the first 4 to 10 days and then remained constant. Increases in the N content of decomposing macrophyte tissue have previously been observed (e.g., de la Cruz and Gabriel, 1974; Mason and Bryant, 1975). This increase typically has been attributed to accumulation of microbial protein.

Rates of weight loss of the plant tissue were related to the initial N content of the senescent plant material (Table 3). The faster decomposing plants had greater initial N concentrations and low C:N ratios while the slower decomposing plants had low initial N and high C:N ratios.

In situ Studies

Overall, the rates of decay observed in the lake samples did not differ very much qualitatively from those observed under laboratory experiments. In situ decomposition during the spring—summer experiments was somewhat faster than 25°C aerobic decomposition in the laboratory, but the fall—winter series of samples decayed at rates slightly less than those seen in the controlled experiments conducted at 10°C. In all cases, the various species decomposed at the same rates with respect to each other as in the laboratory experiments, i.e., *Nuphar* > *Myriophyllum* > *Najas* > *S. subterminalis* > *S. acutus*. No discernible differences were found between decomposition occurring at the ecologically different incubation sites.

CONCLUSIONS

Based on the data obtained in these experiments, the needs for future work on the decomposition of macrophytes are clear to us. Attention must be paid to the variety of plant species colonizing the habitat of interest because different species do decompose at different rates. This differential decomposition, taken along with the production of each species, affects the

total annual metabolism of C in the system and even within zones of ecosystems. The nutritive value of detrital vegetation to consumers is influenced by the qualitative species-specific characteristics of the decaying macrophytes. In addition, there will surely be long-term effects on sedimentation and system geomorphology as a result of accumulation and deposition of undecomposed material.

The single most important fate of reduced C in aquatic ecosystems (viz, the ultimate conversion to CO_2 in the detrital food chain) has received attention far short of its ecological significance. Further progress depends on the perfection and application of methods to assay microbial products and to study processes which are associated in marshes and littoral waters with interfering complex organic compounds and inorganic salts. Only with careful attempts to answer questions of ecological importance concerning microbial metabolism of reduced C compounds of macrophytic origin will insight into the metabolism of aquatic ecosystems be achieved.

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