DECOMPOSITION OF AQUATIC PLANTS IN LAKES

Dissertation for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY
GORDON LAMAR GODSHALK

1977

This is to certify that the

thesis entitled

DECOMPOSITION OF AQUATIC PLANTS
IN LAKES

presented by

Gordon Lamar Godshalk

has been accepted towards fulfillment
of the requirements for

Ph. D. degree in Botany

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Date April 29, 1977

O-7639

ABSTRACT

DECOMPOSITION OF AQUATIC PLANTS IN LAKES

By

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Decomposition is oxidation of carbon and other elements that have previously been biologically reduced and is the balance of primary production in ecosystems. The difference between the amounts of carbon reduced by photosynthesis and oxidized by decomposition is the true net production of the ecosystem. Past discussion of decomposition in lakes has generally been limited to the mineralization of dead plankton sinking through the epilimnion. The importance of the littoral zone to the productivity of small lakes has become evident, and decomposition of littoral vegetation is a major component of carbon metabolism as well.

This study was carried out to systematically determine the effects of temperature and oxygen concentration, two environmental parameters crucial to lake metabolism in general, on decomposition of five species of aquatic vascular plants of three growth forms. Samples of dried plant material were decomposed in flasks in the laboratory under three different oxygen regimes, aerobic-to-anaerobic, strict anaerobic, and aerated, each at 10°C and 25°C. In addition, in situ decomposition of the same species was monitored using the litter bag technique under four conditions.

Particulate detrital plant material was analyzed after decomposition of up to 180 days for weight loss and content of ash, total carbon and nitrogen, nonstructural carbohydrate, hemicellulose, cellulose, and lignin. The ATP content and dehydrogenase activity of the microflora associated with this material was also determined. The dissolved matter in the flasks of the laboratory experiments was analyzed for pH, redox potential, total carbon and nitrogen content, and fractionated by membrane ultrafiltration into five molecular weight categories. Total dissolved organic carbon (DOC), UV absorbance, and fluorescence activity were determined for each fraction.

Reducing conditions were established within 10 to 25 days during anaerobic decomposition at 10°C and within two days at 25°C. DOC concentrations increased throughout the decomposition period during anaerobic incubation at 10°C. DOC increased and then decreased in media of anaerobic experiments at 25°C. Only low DOC concentrations were found in aerated media at either temperature. Low molecular weight fractions were most rapidly metabolized under all conditions. UV absorbance and fluorescence data indicate that qualitative changes in the DOC were occurring during decomposition.

Weight loss functions, derived from the data, fit best when the functions were exponential with decay coefficients that also decreased exponentially through time, indicating that decay of macrophytic material was rapid initially and then slowed as resistant materials dominated the residual tissue. Decay rates were slightly greater in oxygenated than in anoxic conditions, but increased temperature caused significantly faster weight loss. Presence of

oxygen greatly promoted conversion of DOC to carbon dioxide. Weight loss of the various species was related to total initial fiber and nitrogen concentrations.

The C:N ratios of particulate matter generally decreased under all conditions in all species, and in all species dissolved nitrogen was removed from the media during decomposition. Microbial activity associated with the detrital material generally attained maximal values early in decomposition and then decreased.

The variety of conditions of temperature and oxygen that commonly occur in a temperate dimictic lake causes pulsed decomposition of the annual production of littoral vegetation. Thus, the metabolism of carbon of aquatic macrophytes is displaced in time and space, and a stable continuous input of energy to the detrital dynamic structure of the lake is maintained. Eutrophication, promoting increased production of littoral zone vegetation, causes decomposition processes in the lake to be overloaded, resulting in more extensive reducing conditions in the sediments and greater sedimentation of particulate material.

DECOMPOSITION OF AQUATIC PLANTS IN LAKES

By

Gordon Lamar Godshalk

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

W. K. Kellogg Biological Station
Department of Botany and Plant Pathology

1977

ACKNOWLEDGEMENTS

It is my pleasure to thank Dr. Robert Wetzel, Dr. Michael Klug, Dr. Patricia Werner, and Dr. Earl Werner for their services on my guidance committee. Dr. Wetzel generously provided the technical help of Jayashree Sonnad, Sharon Morrison, Janet Strally, David Duval, and many others whose willing assistance was invaluable. Dr. Klug and John Molongoski helped me with anaerobic techniques and cooperated with several aspects of this project not reported here. Steven Weiss provided patient assistance with all aspects of data analysis, interpretation, and presentation performed on the computer system at the Kellogg Biological Station. I benefited from discussions with my fellow students, particularly Wilson Cunningham, John Molongoski, Robert King, George Spengler, Kelton McKinley, and Amelia Ward, who were always eager to provide ideas and suggestions. I am grateful to members of the staff of the Kellogg Biological Station for their many valuable and usually unrecognized contributions to my efforts: Mary Shaw, Madelon Davidson, Arthur Weist, Mary Hughes, Charlotte Seeley, and Dolores Haire. I thank Dr. George Lauff for his efforts in providing facilities at KBS. Nancy Dyer, who suffered much of the tedium and shared in little of the satisfaction of this research, contributed in countless ways.

I am indebted to Dr. Wetzel not only for his logistical support of this work, but also for his enthusiasm and encouragement. I appreciate the numerous contributions he has made to my education in aspects beyond research and the many opportunities that he has provided for me. Finally, I owe much to Dr. Gerald Moshiri, who first defined "detritus" for me and encouraged me to learn more.

This research was supported by funds granted to Dr. Wetzel from the U.S. Energy Research and Development Agency (EY-76-S-02-1599, COO-1599-121), and the National Science Foundation (BMS-75-20322 and OEC-74-24356-A01). My early efforts were made possible by a National Science Foundation grant to Dr. Lauff et al. for Coherent Areas Studies (GB-40311).

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LIST OF ABBREVIATIONS

AFDW	Ash-free dry weight
ATP	Adenosine triphosphate
C	Degrees Celsius
C:N	Carbon:nitrogen ratio
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
E_h	Redox potential, compared to standard hydrogen half-cell
ETS	Electron transport system
LDOM	Labile dissolved organic matter
MW	Molecular weight
NEP	Net ecosystem production
POM	Particulate organic matter
RDOM	Resistant dissolved organic matter
TNC	Total nonstructural carbohydrates

INTRODUCTION

Production, Decomposition, and Net Ecosystem Production

In its strictest sense, the term "decomposition" as used in this study refers to the conversion of the products of phytosynthesis and subsequent plant syntheses back into the form of the reactants of those syntheses. Carbon and most other nutrient elements, are oxidized to inorganic or mineral form by means of the decomposition or mineralization process. Decomposition includes less complete transformations of organic matter as well. The loss in weight of decaying plant tissue represents decomposition. By the laws of thermodynamics the tissue is not "disappearing" but is being converted into a less obvious form, either gaseous or dissolved. The conversion of particulate organic matter (POM) to dissolved form is a step in the decomposition process, and dissolved detrital carbon is a resource of aquatic systems whose biotic importance is often underestimated (cf. Wetzel et al. 1972). The oxidation of dissolved organic matter (DOM) by microbes is decomposition even if part of the dissolved carbon used as substrate is incorporated into their biomass.

Primary production is the conversion of kinetic energy and inorganic carbon to potential energy in the form of reduced carbon. Decomposers use this potential energy, and in so doing convert the carbon and nutrient elements into more oxidized states. The conversion

of plant to animal biomass is secondary production and is really a form of decomposition since there is a net dissipation of carbon and energy in the process; the existence of a new form of tissue only delays the utlimate mineralization of the elements present. Thus, autotrophs function to bring reduced carbon into the ecosystem, while the heterotrophs exploit that source of carbon and eventually cause its removal from the ecosystem.

The balance of the two processes, production and decomposition, is the net production of the ecosystem. Net ecosystem production (NEP) has been defined by Woodwell and Whittaker (1968, Woodwell et al. 1973) as

NEP = Gross Production - Respiration

where Respiration includes that of both autotrophs and heterotrophs. NEP represents the mass of organic material produced by the system in a given period of time. Wetzel (1975:618) discusses the NEP concept as it pertains specifically to lakes.

When this equation is used to determine the NEP of a particular system on a short term basis no correction is made for the fact that the Gross Production term includes much living biomass that has not yet had the opportunity to be decomposed, and the resultant value of NEP is a measure of living biomass plus detritus. If totally efficient and instantaneous decomposition were occurring in the system there would be no detritus, i.e. all non-living tissue would be respired, and NEP, as usually determined would be represented by only living biomass. Consideration of this amount as true NEP over long

time periods is erroneous because eventually all currently living biomass will be dead and become available to the heterotrophs. For this reason, calculations of NEP should provide for decomposition (i.e. Respiration) to "catch up" to Gross Production, so that no substrates unavailable for decomposition exist. The result of the calculation then is an estimate of the amount of carbon fixed in the system but not lost by respiration. In ecosystems, detrital NEP theoretically exists as permanent detritus, photosynthate that will never be utilized as heterotrophic substrate.

Practically speaking, in no ecosystem will there not exist a lag time between production and decomposition; indeed, that is the life span of biological tissue. Nor is there permanent detritus, as the residence times of even the most resistant compounds will be less than infinity.

The point being made is that estimates of true ecosystem production should not be biased by amounts of living tissue, but instead should accurately represent the difference between production and decomposition over long periods of time when the rate of each of these processes is stable. Variations in conditions which cause either rate to change will cause the estimate to be in error until a new balance is stabilized. True net ecosystem production is the amount of organic matter that is not later decomposed over periods less than geological time (cf. Ohle, 1956; Batzli, 1974).

For example, even though the productivity of the plant community in a bog is considered low relative to other plant communities, decomposition rates in bogs are even lower, and a bog is in fact a

productive ecosystem (Dickinson and Maggs, 1974). Numerous studies have determined the productivity of several different ecosystems, and this abundance of data has led to ranking and other comparisons of "ecosystem productivity." Usually these estimates are not of true ecosystem productivity and are more equivalent to agriculturalists' yield, that amount of biomass that has not yet decomposed and which can be harvested. The emphasis that comparative short term productivity studies have received has been at the expense of a thorough understanding of the net productivity of ecosystems.

Importance of Decomposition in Lakes

Decomposition of organic matter that is ultimately derived from photosynthetic fixation of carbon dioxide is the process by which a lake functions as an ecosystem. Continuing to consider the metabolism of animals as a form of decomposition, it is apparent that the majority of the transformations of biomass and energy involve heterotrophic relationships among the various components. This is especially true of aquatic ecosystems where the lake or stream is literally the focal point of much of the energetic activities which occur in the drainage area. In a lake with little input of organic matter from outside the water body itself, decomposition will almost equal production, the difference being permanently sedimented and exported. But in a basin where there is much allochthonous organic input to the lake, the flux of carbon through degradative pathways can exceed that in the form of autochthonous production and thus decomposition processes may easily be responsible for well over half

of the total carbon metabolism of the system. Stream ecologists have recognized the dominant heterotrophic nature of small running waters and are presently making progress toward understanding these ecosystems (e.g. Cummins, 1974; Hynes, 1975). Lake limnologists, on the other hand, have been slow to investigate decomposition and relatively little is known of the ecosystem-level effects of heterotrophic metabolism in lakes, especially when compared to the abundance of data that exists on production of phytoplankton. In spite of the paucity of experimental studies on lake decomposition, several ecologists have recognized and described what is coming to be known as the "detrital dynamic structure" of aquatic systems (e.g. Odum and de la Cruz, 1963; Wetzel et al., 1972; Pomeroy, 1974; Wetzel, 1975:606; see also Melchiorri-Santolini and Hopton, 1972).

Saunders (1976) points out that decomposition is the mechanism whereby a system can function when or where no light exists to stimulate photosynthesis. In lakes, in the north temperate zone especially, most primary production occurs during a relatively short growing season when waters are warm and light intensities high. For the remainder of the year, system metabolism depends on displacement of summer production in both space and time. Water movements transport potential energy in the form of plant tissue from the littoral and trophogenic pelagial zone to the tropholytic zone and benthic sediments. Often there is a significant transport of detrital carbon out of the lake to some other system (e.g. Wetzel and Otsuki, 1974). Decomposition, as will be explained in this work, also occurs over extended periods of time, and one role of detrital carbon is as a

store of potential energy which is utilized at some later time, often long after its creation.

Past Studies

Some studies have been done on the in situ decomposition of phytoplankton and detritus from plankton, and in the laboratory on aspects assumed or known to affect decomposition in nature. Kleerekoper (1953) found that detritus derived from plankton undergoes most decay while it is sinking in the epilimnion. The composition of sinking detritus was almost the same by the time it passed through the metalimnion as the organic matter of the bottom sediments. Most nitrogen of the sinking detritus was released in the epilimnion, but phosphorus and silica were not as readily released and accumulated in the sediments. Similar results were described by Kuznetsov (1975: 208). Saunders (1972) followed the decomposition of artificially-prepared radioactively-labelled detritus in situ, and more recently phytoplankton decomposition was investigated in situ by Jones (1976). Several laboratory studies have centered on the mechanisms of decay and resistance to decay of algae (Foree and McCarty, 1970; Otsuki and Hanya, 1972a, 1972b; Mills and Alexander, 1974; Pierre et al., 1974; Gunnison and Alexander, 1975a, 1975b; Verma and Martin, 1976).

Pelagial decomposition predominates heterotrophic metabolism in large lakes and the observations described above are often taken to be the general case of lake decomposition. There are many times more small lakes (e.g.< 5 - 10 hectares in surface area) on the surface of the earth than there are large lakes. In small lakes, where the extent of shoreline and shallow water in relation to total

lake volume is much increased, the plants of the littoral zone assume a greater part in the metabolism of the entire lake ecosystem (Wetzel and Allen, 1972; Wetzel, 1975:355; Mason and Bryant, 1975; Howard-Williams and Lenton, 1975; Gaudet, 1976). Studies on decomposition of macrophytes from the littoral zones of freshwater lakes are few and highly diverse in methodology, plant species and lake types studied, and interpretation. Úlehlová (1970, 1971) studied the zonation of aquatic macrophytes, some aspects of their decomposition, and effects on the sediments of three lakes in the Netherlands. Pieczyńska (1972) examined aspects of both production and decomposition of macrophytes of the eulittoral zone (above mean water level) in several lakes in Poland. The leaching of mineral nutrients from Phragmites was examined in detail by Planter (1970). Isolation and characterization of the microflora associated with decaying freshwater macrophytes have received considerable attention (e.g. Botan et al., 1960; Aliverdieva-Gamidova, 1969; Dickinson et al., 1974; Mason, 1976; Wheatley et al., 1976). The successive colonization of decaying Phragmites particles by various microbes has been documented by Oláh (1972). Virtually all other studies of decomposing macrophytes are referred to during the discussion of various aspects of the present study.

More investigations have dealt with salt water plants and their decomposition (e.g. Odum and de la Cruz, 1967; Fenchel, 1970; Gosselink and Kirby, 1974; Harrison and Mann, 1975a, 1975b; de la Cruz, 1975). Schultz and Quinn (1973) looked in particular at the fatty acid components of Spartina alterniflora detritus; Gallagher

et al. (1976) and Fallon and Pfaender (1976) reported on the microbial metabolism of leachate from this salt water marsh plant.

Much of the most informative investigation of the mechanisms and controlling factors of aquatic and marine decomposition processes was done almost half a century ago by Waksman and co-workers (e.g. Waksman and Stevens, 1928; Waksman et al., 1933; Waksman and Carey, 1935a, 1935b; Waksman and Renn, 1936). These works, in addition to Waksman's classic studies of terrestrial decay, provide much data useful in interpretation of modern experimental approaches and deserve greater attention by contemporary students of decomposition.

Objectives

No systematic studies of decomposition processes in lentic ecosystems have previously been performed in order to examine the biological and environmental controls over the dynamics of such processes. The primary goal of this research was to investigate the effects of plant species (i.e. species-specific structural characteristics), temperature, and oxygen on the transformations of various forms of carbon derived from senescent macrophyte tissue. Special attention was paid to the rates and products of decomposition, and to influences of particular components of the detrital material on overall decay of the whole tissue.

Carbon, in various molecular forms, was selected to be monitored during decomposition because it is the basic atomic constituent of all biotic tissue. Other elements of great biological importance (i.e. hydrogen, oxygen, nitrogen, phosphorus, sulfur) participate in physiological reactions in various chemical combinations with carbon.

Because of the close physiological connection between carbon and the other elements, knowledge of the fluxes of carbon at the same time provide some information on the transformations of the other elements as well.

Much attention has been given to the elemental composition of living and decaying aquatic angiosperms (e.g. Gerloff and Krombholz, 1966; Allenby, 1968; Boyd, 1970b; Adams et al., 1973). Since the chemical composition of vascular aquatic plants is so variable depending on species, environmental, and seasonal factors, care must be taken in interpreting decomposition data based on elemental contents of plants or their derivatives (Boyd and Hess, 1970; Boyd, 1970a).

On the basis of the growth forms of various aquatic macrophytes and their respective needs for rigid supportive tissue it was hypothesized that there would be significant differences in the decomposition of different species. Emergent plants, having at least their upper portions aerial and without water support were expected to be the most lignified and therefore slowest to decompose. Lignin gives plants rigidity and strength and is also important in water and nutrient transport in xylem (Wardrop, 1971). Submersed plants, being almost entirely supported by water and generally flaccid in structure were hypothesized to be relatively rapidly decomposed. Floating-leaved plants were expected to exhibit intermediate rates of decay. Five species were selected for study: the emergent bulrush Scirpus acutus, the floating-leaved yellow water lily Nuphar variegatum, and the submersed water milfoil Myriophyllum heterophyllum and bushy

pondweed Najas flexilis, and the only submersed species of the genus of emergent bulrushes Scirpus subterminalis.

Environmental conditions selected for study in the laboratory experiments were temperature and oxygen concentration. These parameters are well recognized influences of biological processes in general, and are critical in the metabolism of lakes in particular. The lower temperature of 10°C approximates the highest temperature usually attained by pelagial sediments, and the high temperature of 25°C is approximately the highest temperature of surface and littoral waters during the summer in a north-temperate dimictic lake.

Oxygen conditions in the lab experiments represent three natural situations: (1) aerobic-to-anaerobic conditions simulating the situation in a lake when a plant growing in oxygen-containing waters dies and collapses to an anaerobic sediment-water interface, (2) anaerobic, as when a plant is growing in waters that become anaerobic before the plant senesces and begins to decompose, and (3) aerobic, as in a wave-swept littoral area of continually oxygen-rich water.

METHODS

Laboratory Experiments

Sample Preparation and Incubation

Several kilograms of tissue of each of the five species of aquatic macrophytes studied were collected in the autumn, the end of the growing season for most of the species. At the time of collection four of the species were beginning to senesce, but they were not yet dead and had undergone no microbial decomposition. Scirpus subterminalis, however, grows year-round in Lawrence Lake (Barry County, Michigan) where it was collected and so the plant tissue of this species obtained was largely in healthy condition (Rich et al., 1971). Najas flexilis and Myriophyllum heterophyllum were collected by grappling hook from the littoral zone on the west side of Gull Lake (Kalamazoo and Barry Counties, Michigan). Najas was also collected from Pine Lake (Barry County, Michigan). Nuphar variegatum and Scirpus acutus were gathered from Lawrence Lake.

No attempt was made to separate out the small amount of root tissue of the submersed plants, but only the above-sediment portions of the floating-leaved and emergent plants were collected and used. Tissue of all species was washed free of sediments, air dried, and stored in large plastic bags with silica gel desiccant sachets until used.

For each experiment, 14 samples of each species were prepared. Approximately 3.5 g of plant tissue were lyophilized, weighed exactly, and put into a 1000 ml Erlenmeyer flask. One-thousand ml of freshly prepared synthetic lake water (Wetzel Medium 5, See Table 1) were added, followed by a 20 ml inoculum of sediments obtained from the littoral zone of Lawrence Lake.

All media and plant tissues used in the strict anaerobic experiments were deoxygenated for 60 hours in an anaerobic glove box with an atmosphere of 85 N_2:10 H_2:5 CO_2 (by volume). The deoxygenated plant tissue and medium were combined in the flasks, the inoculum added, and the flasks tightly stoppered in this atmosphere as well. This treatment was sufficient to insure initial reducing conditions (E_h < 100 mV). The high content of carbon dioxide in the glove box atmosphere caused a slight drop in the pH of the bicarbonate-buffered medium, but in no experiments was the initial pH different from that of the littoral zone by more than 0.5 pH unit.

Experiments were performed at the appropriate time of year so that the temperature of the littoral zone sediments at the time of collection of the inoculum was as close as possible to the incubation temperature. Sediments to serve as inocula in the anaerobic experiments were obtained using techniques minimizing exposure to oxygen and were kept under a non-oxygenated atmosphere until added to the flasks.

Flasks of aerobic-to-anaerobic and strict anaerobic experiments were sealed tightly with silicon rubber stoppers. Aerobic flasks were stoppered with foam plugs through which Tygon tubing was

Table 1. Components of synthetic lake water (Wetzel Medium 5) used in laboratory decomposition experiments.

Compound*	mg/liter
$NaHCO_3$	500.
K_2HPO_4	200.
KNO_3	100.
NH_4Cl	100.
$MgSO_4 \cdot 7H_2O$	100.
$CaCl_2$	54.
KCl	30.
$Na_2SiO_3 \cdot 9H_2O$	23.
$FeCl_3$	1.38
$ZnCl_2$	0.48
H_3BO_3	0.40
$Na_2MoO_4 \cdot 2H_2O$	0.254
$CuCl_2$	0.0085
$CoCl_2 \cdot 6H_2O$	0.0081
$MnCl_2 \cdot 4H_2O$	0.0055

* All compounds analytical reagent grade, dissolved in distilled-deionized water; pH of medium ~8.2.

installed to provide aeration. The aerobic flasks were bubbled sufficiently to maintain oxygenated conditions (E_h > 100 mV) with synthetic air (Linde Div., Union Carbide Corp.) premoistened by bubbling through distilled water.

All flasks were incubated in the dark in environmental chambers at 10°C or 25°C; temperature was maintained constant to within 1°C.

Sampling Procedure

Two flasks of each plant species were sacrificed after about 2, 4, 10, 24, 48, 90 and 180 days of decomposition during each experiment. This sampling schedule was selected to provide more information on the initial stages of decomposition when changes, particularly in the dissolved detritus, were occurring more rapidly.

A platinum electrode was put into the flask and the redox potential measured against that of a calomel reference electrode filled with saturated potassium chloride. The reference electrode was joined to the sample by a conductivity bridge of 3.5 M potassium chloride in 1.5 percent (w/v) purified agar in Tygon tubing. The surface of the platinum electrode was burnished with crocus cloth and rinsed with glass distilled water between all determinations; measurement of cell potential was made on a Coleman Model 38A expanded scale pH meter on millivolt mode after an equilibration period of ten minutes. The reference half-cell potential was determined on each sampling day by calibration against ZoBell solution (1/300 M potassium ferrocyanide and 1/300 M potassium ferricyanide in 0.1 M potassium chloride; Whitfield, 1971:102) and the E_h at sample temperature calculated. A small sample of medium was poured from the flask into a

disposable beaker, sealed from atmospheric oxidation, and allowed to attain room temperature. The pH of this sample was measured with a Corning combination pH electrode after a sample-electrode equilibration time of ten minutes on a Beckman Expandomatic pH meter standardized daily to temperature-corrected pH of certified buffer solution (Fisher Scientific Co.).

Medium was poured out of the flask without disruption of the inoculum sediments at the bottom and filtered sequentially through 160 μm nylon mesh (Nytex), precombusted (525°C, three hours) glass fiber filters (Reeve-Angel 984H, pore size 0.4 μm), and finally 0.2 μm pore size membrane filters (Millipore Corp., type GS). Some of the filtrate was lyophilized for later analysis of the residue; the remainder was subjected to membrane ultrafiltration for fractionation by molecular weight of the DOM.

Diaflo type membrane filters (Amicon Corp.) with nominal molecular weight cutoffs at 30,000 (PM-30), 10,000 (PM-10), 1,000 (UM-2), and 500 (UM-05) were selected because these filters provided the most distinct molecular weight fractions in preliminary tests on the dissolved products of decomposing macrophytes (see Figure 1). The filters were prewashed to prevent contamination of the samples by the filter preservative (Wilander, 1972), and the first portion of the filtrate obtained was discarded. The media were put through the PM-30 and PM-10 filters in sequence, some of the filtrate being reserved from each fraction for analysis; most of the PM-10 filtrate was divided into two parts for filtration through the UM-2 and UM-05 membranes.

Figure 1. Results of fractionation of dissolved organic matter produced after 43 days of aerobic-to-anaerobic decomposition of Najas flexilis at 15°C. Fractions are filtrates of several filters of decreasing nominal pore size:

A	0.4 µm	Reeve-Angel 984H glass fiber
B	0.4 µm	Millipore HA membrane
C	0.2 µm	Millipore GS membrane

The following are Diaflo type (Amicon Corp.) membrane ultrafilters:

D	300,000 MW	XM-300
E	100,000 MW	XM-100A
F	50,000 MW	XM-50
G	30,000 MW	PM-30
H	10,000-20,000 MW	UM-20E
J	10,000 MW	PM-10
K	10,000 MW	UM-10
L	1,000 MW	UM-2
M	500 MW	UM-05

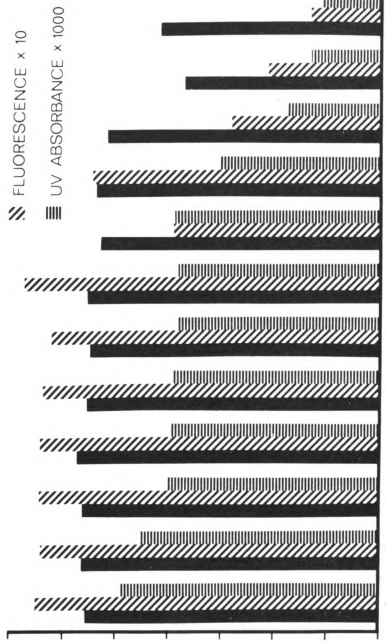
DOC (mg/l)
FLUORESCENCE x 10
UV ABSORBANCE x 1000
300
200
100
0
A
B
C
D
E
F
G
H
J
K
L
M
FRACTIONS

Figure 1

The unfractionated medium (i.e. 0.2 μm filtrate) and each of the four molecular weight fractions were analyzed for total DOC, UV absorbance, and fluorescence.

DOC was determined by a slight modification of the persulfate oxidation method of Menzel and Vaccaro (1964) and measured by infrared carbon dioxide analysis on a Beckman 215A infrared gas analyzer. Samples were variously diluted to provide concentrations of DOC in the analyzed samples of 1 to 10 mg/l in order to insure complete oxidation of the samples. Absorbance of ultraviolet light (250 nm) was measured using a Hitachi Perkin-Elmer Model 139 UV-VIS spectrophotometer, reading the samples at room temperature in quartz cells of 0.5 cm path length against a blank of glass distilled water; corrections were made for dilution when necessary due to high absorbance. Fluorescence was determined on a Turner Model 110 Fluorometer equipped with an ultraviolet lamp and primary filter providing excitation at 365 nm and combined secondary filters to measure emission at 545 nm. Readings were made against a blank of glass distilled water, normalized to scale 3X, and reported as fluorometer units. Fluorescent emission was also measured at 460 nm but is not reported here because of the problem in interpretation resulting from excessive quenching of the samples at this wavelength and the frequent need for dilution of the highly active samples (Guilbault, 1973:147). Fluorescence determinations were made at room temperature, and no correction for or adjustment of sample pH was made.

As much particulate material as possible was recovered from each flask; the amount of inorganic material originating from the

sediment inoculum contaminating the tissue was minimized. Recovered tissue was lyophilized and weighed, and then ground in a micro-Wiley mill (Arthur Thomas Co.) to pass through a 1-mm mesh. Samples of this material were assayed later for content of ash, carbon, nitrogen, total nonstructural carbohydrates, and fiber constituents.

The tissue in the second flask of each species sacrificed each sampling day was used to determine microbial activity associated with the decomposing plant matter by two methods, ATP content and electron transport system (ETS) activity. The latter is essentially an indirect measurement of the activity of dehydrogenase enzymes (Curl and Sandberg, 1961).

Plant tissue was taken from the flask with long forceps and gently blotted to remove excess water. A subsample of about 2.6 g (wet weight) was extracted for ATP, two subsamples of about 0.1 g each (wet weight) were used to determine ETS activity, and the remainder was weighed, lyophilized, and weighed again to correct the analyzed subsamples from wet weight to dry weight. All of the tissue from the second flask not used in the microbial activity assays was lyophilized and combined with the tissue from the other flask of the pair during the grinding procedure.

ATP was extracted by the method used by Suberkropp and Klug (1976). Fifteen ml of 0.6 N sulfuric acid were added to the tissue sample in a 50 ml polycarbonate centrifuge tube and the mixture homogenized for two minutes in an ice bath by a Virtis 23 homogenizer; total extraction time was 30 minutes. The supernatant was vacuum filtered (Reeve-Angel 984H glass fiber filter), diluted with an equal

volume of 0.05 M HEPES (N-2-hydroxyethyl-piperazine-N^1-2-ethane sulfonic acid) - magnesium sulfate buffer (pH 7.5), and the final pH adjusted with sodium hydroxide to 7.2. The extracts were frozen at -60°C until assayed. The efficiency of extraction was not determined but was assumed to be constant, as in the reference study, allowing relative comparisons of samples within this study.

The frozen samples were thawed, centrifuged, and kept on ice when assayed. The amount of ATP extracted was determined by measuring the light emitted when the sample reacted with a luciferin-luciferase enzyme complex (Sigma Chemical Co.) in an Aminco Chem Glow photometer with output to a CSI-208 integrator and compared to an ATP (Sigma Chemical Co.) standard curve. Corrections were made for interfering substances which caused a quenching of the light emitted by repeating the reaction with sample material to which was added an internal standard of ATP.

The analysis of ETS activity was similar to the method described by Zimmerman (1975). All the moist tissue samples for assay of ETS activity, except those which were from aerated flasks, were handled and incubated in the reduced atmosphere of the glove box so that the transport system would not be poisoned by oxygen. The two 0.1 g samples of plant tissue from the second flask were put into 50 ml polypropylene centrifuge tubes and 2 ml of phosphate buffer (pH 7.7) added. To one tube (the treatment sample) was added 1.00 ml of solution containing 1 g INT (2-P-iodophenyl)-(3-P-nitrophenyl)-5-phenyl tetrazolium chloride (Schwarz-Mann) in glass distilled water to make 500 ml, and to the other tube was added 1 ml of glass distilled

water; the second tube served as a correction for colorimetric interferences caused by extraction of pigments from the plant material. All tubes were tightly capped and incubated 20 minutes at the same temperature from which the samples were taken. The reaction was stopped by addition of a 2:3 solvent mixture of tetrachloroethylene: acetone. Reduction of INT by microbial electron transport systems during incubation produced formazan which is insoluble in water but soluble in this solvent. Formazan was extracted overnight in a freezer (-20°C), after which the biphasic mixture was vacuum filtered (Reeve Angel 984H glass fiber filters), and the residue quantitatively washed with solvent until no more color was removed. Intensity of formazan color was measured spectrophotometrically at 490 nm, corrected for solvent volume and absorbance of the blank to which no INT was added, and reported in relative absorbance units per g tissue ash-free dry weight.

Particulate Matter Analyses

A 50 - 100 mg portion of the ground plant tissue was combusted in a muffle oven at 550°C for three hours to determine the mineral ash in each sample. The data of subsequent assays (except carbon-nitrogen analyses) were then corrected for ash content, and these data are reported on an ash-free dry weight basis.

The total carbon and nitrogen as percent of total weight of the recovered plant material, and in the residue of the lyophilized unfractionated media, were determined on an automated analyzer (Carlo Erba Elemental Analyzer Model 1104).

Total nonstructural carbohydrates (sugars, starches, etc.) were determined enzymatically by the method of Smith (1969). Approximately 100 mg of ground plant tissue was boiled in glass distilled water for two minutes to gelatinize the starches, then cooled to room temperature. Acetate buffer (pH 4.45) and 0.5 percent (w/v) takadiastase enzyme solution (Clarase 900, Miles Laboratories, Inc.) were added, and the mixture incubated at 38°C for 48 hours. This enzyme preparation hydrolyzes disaccharides and starches to monomers and has little effect on structural carbohydrates. The dissolved carbohydrates were filtered off quantitatively (Whatman #1 filter paper), quantitatively rinsed with glass distilled water, and the filtrate diluted to exactly 100 ml. Protein was precipitated by the addition of 2 ml of 10 percent (w/w) lead acetate trihydrate; after pouring off the supernatant from centrifugation, excess lead was removed by incubation of the samples with potassium oxalate (ca 100 mg, crystals) overnight in a refrigerator (4°C).

Aliquots free of lead oxalate precipitate (by filtration through Whatman #2 filter paper) were then analyzed colorimetrically for reducing sugars (Dubois et al., 1956). Phenol (0.5 ml of 10 percent in water, 89 percent stock solution diluted to 10 percent by volume) and concentrated sulfuric acid (5.0 ml) were added to 200 µl of solution containing the nonstructural carbohydrate. Sample color intensity was read on a spectrophotometer at 490 nm against a phenol-sulfuric acid reagent blank, corrected for apparent sugar content of a TNC-extraction reagent blank, and compared to a standard curve of D-glucose solutions. Testing of some samples for color formed by

reaction of sulfuric acid and contaminants from the extracts were consistently negative so this correction was not routinely made (Gerchakov and Hatcher, 1972).

Structural components of the plant tissue remaining were determined following the general procedure for analysis of forage fiber described by Goering and Van Soest (1970). Tissue samples weighing 250 - 300 mg were refluxed one hour in 50 ml of neutral detergent solution (sodium dodecyl sulfate, pH 7) to remove non-cell wall constituents, followed by similar extraction in acid detergent solution (cetyl trimethylammonium bromide in 1.0 N sulfuric acid). Weight loss between the two extractions is an estimate of hemicellulose content. Lignin was removed from the residue of the detergent extractions by oxidation at room temperature for 90 minutes in a saturated potassium permanganate solution; the cellulose remaining was combusted in a muffle oven at 525^{0}C for three hours. Content of lignin and cellulose was measured by weight loss between the steps of this procedure. This assay determined the percent of recovered tissue in each of the hemicellulose, cellulose, and lignin fractions. Multiplying these data by the weight of the recovered sample gave the absolute mass of each of these fractions remaining after decomposition, which could then be compared to the mass of each present before decomposition to determine the real loss (or gain) of each fraction through time (i.e., [percent component in sample after decomposition X sample final weight] / [percent component in sample before decomposition X sample initial weight] = percent of initial mass of component remaining after decomposition).

In Situ Studies

Samples weighing 6.0 g of the same dried senescent plant tissue were incubated in various lake habitats in bags made of fiberglass screen with a mesh opening of approximately 1.5 mm. The bags were about 15 cm square, and in no case were they so full that the plant tissue was unrealistically compacted in the bag. Two bags of each species were tethered to a wood stick about 15 cm apart and placed on the sediment-water interface in the lake with a construction brick serving as an anchor. Periodically the bags attached to one stick were collected and taken, sealed in plastic bags on ice, to the laboratory for immediate analysis of ATP content and ETS activity; weight loss and content of ash, total nonstructural carbohydrates, and fiber components were determined later on the lyophilized samples. All analytical methods were the same as those previously described for the laboratory samples; incubation temperature for the ETS assays was the same as that of the field incubation site.

A set of these bags was incubated in Lawrence Lake in the littoral zone on the east shore at a water depth of 2 m during the late spring and summer (beginning 6 June 1975). Lawrence Lake is a mesotrophic hardwater lake with a surface area of five hectares and a moderately developed littoral zone; detailed description of Lawrence Lake can be found in Wetzel et al. (1972).

Incubation of a late fall-winter series of bags was begun on 18 November 1975 at three locations: (1) the same Lawrence Lake littoral site where the spring-summer series was placed, (2) in the pelagial zone on the east side of Lawrence Lake at a depth of 7 m,

and (3) at a depth of 1.5 meters in the littoral zone on the west shore of hardwater, hypereutrophic Wintergreen Lake (described in Manny, 1971).

RESULTS AND DISCUSSION

Redox Potential and pH

The measurements of pH and redox potential made during the laboratory experiments are diagrammed in Appendix Figures 1 through 24. The response of E_h in flasks of the aerobic-to-anaerobic experiments quickly showed a drop from initial values of greater than +350 mV to 0 mV in 10 to 25 days at 10°C and within 2 days at 25°C. This drop in redox potential can be attributed to the rapid depletion of dissolved oxygen by microbial respiration as the leachate immediately produced by the rehydrated plant tissue was metabolized. The rate of decline of E_h for any given plant species was not necessarily proportional to the amount of DOC produced (Appendix Figures 25-48). In the strict anaerobic experiements where the media and dry plant tissue were equilibrated in an oxygen-free atmosphere to insure anoxic conditions from the beginning of incubation, rarely was a negative redox obtained shortly after combination of the deoxygenated media and plant tissue (i.e. $\leq$ two hours), although such negative E_h values were obtained in media samples before addition of the plants. Initial positive E_h values in these deoxygenated flasks may have been the result of the immediate solubilization of oxidative compounds from the plant tissue which raised the redox potential of the media. Negative redox conditions were reestablished very quickly in these

flasks (< two days at both temperatures). The magnitude of the potentials in the aerobic-to-anaerobic flasks was not very different from those in the strict anaerobic flasks, for all species and at both temperatures; most non-aerated decomposition cultures maintained E_h values of -100 to -200 mV. The intensity of reducing conditions in the anaerobic samples was probably limited by the abundant supply of the alternate electron acceptor nitrate in the media. Because reducing conditions were established so soon after the beginning of decomposition in the aerobic-to-anaerobic experiments, this treatment is considered to be a replicate of strict anaerobic conditions; for that reason, all following discussion relating to "anaerobic" conditions will include results from both aerobic-to-anaerobic and strict anaerobic experiments unless the two conditions were specifically different. Oxic conditions (E_h +300 - +500 mV) were maintained by aeration of the flasks in the aerobic decomposition experiments. All species showed a decrease in redox potential in the first 10 to 25 days of decomposition because of high oxygen demand by metabolism of leached organic materials. Flasks incubated at 25°C required about two to four times the volume of air bubbled through the media as the 10°C flasks to maintain highly positive E_h values.

The usefulness of redox potentials empirically determined in natural systems has been questioned by Stumm (1966). The major problems stem from interpretation of the measurement. Natural systems are rarely dominated by a single redox system as the elements carbon, nitrogen, oxygen, sulfur, iron, and manganese all have more than one oxidation state in which they can exist. The potential measured by a

platinum electrode is a mixture of the potentials of the redox couples present. Further, some couples have no potentials that can be measured electrometrically (e.g. NO_3^- - NO_2^- - NH_4^+, SO_4^{-2} - HS^-). E_h, like pH, is a measure of intensity and indicates nothing as to how well poised the system is, that is, its capacity to buffer or resist change in redox potential.

Thus, the magnitudes of E_h values maintained in experiments reported in this study are more a function of the proportions of chemical constituents present than indicators as to what particular redox couples were in flux between oxidized and reduced states. The E_h values are useful, though, to give a general impression of the types of chemical and bacterial transformations that may have been occurring under particular conditions. Under well-aerated conditions, dissolved oxygen acts as the terminal electron acceptor in the oxidation processes, both chemical and those facilitated enzymatically by microorganisms; E_h will be high, relatively. If oxygen is in limited supply, it will be depleted, and experimental studies have shown that redox potential quickly drops (Engler et al., 1976; Reddy and Patrick, 1975). At this point, alternate electron acceptors such as nitrate and sulfate ions become important. The actual oxidation-reduction state of lake sediments is critical to the budgets of many mineral nutrients in the lake (Gorham and Swaine, 1965; Mortimer, 1941-1942). Under reduced conditions decomposition processes will be incomplete and many nutrients will remain bound in biotic tissue. Oxidizing conditions, on the other hand, cause chemical precipitation of many mineralized nutrients. Alternation of

oxidized and reduced conditions of the hypolimnion often promotes both decomposition and release of essential nutrients, e.g. phosphorus from the sediments.

The role of oxygen in decomposition is complex. Often aerobic and anaerobic pathways of metabolism are compared on the basis of "efficiency," and anaerobism is judged a relatively poor process in relation to aerobic metabolism. This is true if the criterion is the conversion of organic carbon to carbon dioxide with the simultaneous synthesis of ATP, as is frequently the case when dealing with the physiology of individual organisms. However, at an ecosystem level greater diversity and stability of potential pathways of carbon flux result from the existence of anaerobic bacteria.

During aerobic metabolism, oxygen serves as the ultimate hydrogen acceptor and is required for stoichiometric conversion of organic matter to carbon dioxide and water. Oxidations occur in the anoxic sediments and hypolimnion of a lake by utilization of other oxidants which can be either inorganic or organic electron acceptors. A gradient of such electron acceptors exists in both space (depth) and time (season) in a lake, and no matter how reduced a particular stratum of the system is, the probability exists for oxidation by some hydrogen acceptor in close proximity (Richards, 1965; Stumm and Morgan, 1970; Whitfield, 1971:101; Rich and Wetzel, 1977).

The theoretical products of total decomposition are carbon dioxide and water plus various mineral nutrients. During anaerobic decomposition, although some quantity of these compounds are produced, not all organic material is totally oxidized. While the more volatile

products of anaerobic respiration and fermentation such as methane, hydrogen, and numerous short and long chain fatty acids may exist in measurable concentrations in the lower depths of stratified lakes, they are reactive and will be either biologically or chemically oxidized if conditions change so that a more energetically favorable electron acceptor, specifically oxygen, becomes available. Decomposition will then be completed.

Hydrogen ion concentrations generally paralleled redox potentials in the same flask (Appendix Figures 1 through 24). Usually the more quickly E_h values dropped in the initial stages of decay, the faster the media became slightly acidic. This correlation could not be made for all species-condition combinations, however; pH and E_h parameters behaved independently in several cases, implying the relationship between the two was not entirely dependent (e.g. Appendix Figures 17, 19). Initial decreases in pH may have been the result of release of acidic organic compounds during leaching, and as oxygen was used as the terminal electron acceptor in the catabolism of these compounds, E_h declined as well. Later in decomposition other organic compounds may have been produced which caused continued reducing conditions but return of the bicarbonate-buffered media to more alkaline pH values. The pH measured in these experiments was the net result of the interactions of chemcial buffering systems in the medium and gaseous atmosphere in the flask as well as chemical species put into the system from biological origins: leachate, fatty acid end-products of anaerobic decomposition, carbon dioxide, ammonia, etc.

In all cases, pH remained lower in anaerobic flasks (usually 6 - 7) than in aerated flasks (7.5 - 8.5). At 10°C, anaerobic samples showed a continual decline in pH through time while at 25°C, after a decrease at the beginning, pH values increased through the remainder of the experimental period.

Otsuki and Hanya (1972a, 1972b) observed pH changes similar to those just described in their experiments on the decomposition of an alga. In their aerobic decomposition cultures pH increased, which they attributed to presence of undetermined organic compounds. The pH of their anaerobic cultures decreased as a result of production of acetic, formic, and propionic acids. Results of these laboratory experiments fit well the observations made in mesotrophic or eutrophic temperate lakes which typically have lower pH and E_h values in the hypolimnion, especially close to the sediments where decaying organic matter accumulates (cf. Wetzel, 1975:174). However, Reddy and Patrick (1975) found the opposite relationship between pH and redox potential in flooded soil in experimental chambers which were made aerobic and anaerobic alternately by modifying the gaseous atmosphere. Aerated soils had lowered pH values, which they explained as being the result of accumulations of nitrate and sulfate. Anaerobic conditions were brought about from bubbling argon through the soil suspension, and the increased pH values observed were thought by these investigators to be due to sparging of carbon dioxide out of the soil-buffering system by the bubbling argon. Such a reaction may have occurred during the current experiments on macrophyte decomposition,

explaining the pH being consistently above initial values in flasks aerated with synthetic air (which contained no carbon dioxide).

Dissolved Organic Matter

Dissolved Organic Carbon

Readily soluble constituents of the dried plant material were leached immediately upon rehydration. As microbial populations grew, DOM was not only utilized but also produced, especially as products of anaerobic metabolism. The total amounts of organic matter present in solution over the decomposition periods in this study are diagrammed in Appendix Figures 25 through 48. These amounts represent the net DOC produced by the detritus and its associated microflora but which had not yet been converted to microbial biomass or inorganic products of decomposition. Therefore, accounting for different leaching rates of different species under the various conditions, the relative decomposition rates of detrital DOM can be estimated as well.

In all experiments, the effect of leaching is readily apparent at the first sampling date (day 2). The greatest amount of leachate was usually produced by Nuphar, followed by Myriophyllum, the two Scirpus species, and least by Najas. The respective maximum and minimum leaching rates of Nuphar and Najas were consistent over all experiments, but the ranks of the remaining three species were variable. Under all conditions except anaerobic at 25°C the concentration of DOC declined in the second two-day period of decomposition from the initial leachate peak. During anaerobic decay at 25°C the DOC content continued to increase at the same rapid rate until day

10 or 25. This relationship most likely resulted from the interaction of the effects of temperature on accelerating both leaching and also the rate of microbial production of DOM. At 10°C the initial maximum from rapid leaching was distinct from later accumulations of DOM which resulted from anaerobic microbial metabolism. Aerobically at 25°C leaching was probably just as rapid as in the anaerobic experiments (if not more so because of the agitation of aeration), but oxic conditions allowed for very fast, efficient utilization of the DOM and thus no accumulations were seen.

Losses resulting from leaching of plant tissue have been widely observed in experimental studies of freshwater and marine macrophyte decomposition (e.g. Planter, 1970; Otsuki and Wetzel, 1974; Hough and Wetzel, 1975; Harrison and Mann, 1975b; Gallagher et al., 1976) and particularly of allochthonous plant tissue in running waters (Kaushik and Hynes, 1971; Nykvist, 1963). The effects of predrying the plant samples might be expected to result in an increase in the quantity of materials leached because of damage to the cell walls during the drying process and therefore greater solubilization during rehydration. This effect was tested in preliminary experiments comparing the quantity and quality of lyophilized versus fresh, senescent tissue of Najas flexilis at 15°C under aerobic-to-anaerobic oxygen conditions. Results showed that the DOC content of media containing fresh plants was approximately 50 mg/l and that of dried plants 63 mg/l after two days of incubation. On day 15 there was significantly more DOC in the media of the fresh plants than the dried (200 and 116 mg/l, respectively). By day 32 DOC content was

equivalent in the two treatments. UV absorbance and fluorescence remained higher in the dried tissue samples until day 32; pH and redox of the two types were never significantly different.

After leaching, which is more a passive solubilization process than a microbially mediated decomposition, levels of DOM were controlled mainly by the presence or absence of oxygen. DOC continued to accumulate over the entire decomposition period during decay at 10°C without oxygen, but with oxygen only small temporary increases in DOC were observed between days 25 and 50 in Najas, Myriophyllum and Nuphar. At 25°C DOC reached very high levels in the first 25 days in anaerobic experiments, followed by steady decline for the remainder of the experiments. This decline was contrasted to the extremely low concentrations measured over the entire 180 days of aerobic decomposition. The presence of oxygen, regardless of temperature, caused only very small amounts of organic matter to be present in solution; higher temperature did promote the eventual decline of DOM which accumulated during early phases of anaerobic decomposition.

The effects of aeration were particularly significant with respect to the lower molecular weight fractions. Under anaerobic conditions about half of the DOM which was initially leached passed through a 1,000 MW cutoff filter: this proportion remained constant or decreased slightly throughout the decomposition period at both temperatures. Aerobically, however, the proportion of total DOC that passed through the 1,000 MW filter was much less than one-half, even during the initial leaching period, indicating that these lower molecular weight compounds were very rapidly metabolized when oxygen

was present, even at the lower temperature. This proportion stayed low through both aerobic experiments, and the concentrations of lower molecular weight fractions were less variable through time than were the total DOC concentrations. There were no apparent differences between plant species in the proportions of DOM in various molecular weight fractions.

Fractionation studies of the organic matter dissolved in natural waters have increased with the development of ultrafiltration technology. Ogura (1974) found maximum DOM in the 10,000 - 100,000 MW range in Tokyo Bay, and Wheeler (1976) narrowed the range of this maximum to 1,000 - 30,000 for Georgia coastal water just off shore from a Spartina marsh. The next most abundant fraction was that of low molecular weight compounds (< 500 - 1,000) followed by higher molecular weights (> 30,000) and then by the largest molecules (> 100,000). This relationship is in contrast to results obtained in a soft-water lake by Allen (1976) where the lowest and highest molecular weight fractions of DOC were greatest, and the least concentrated fraction was in the midrange of 1,000 - 10,000 MW. Ogura (1975) found that the proportion of low molecular weight DOM decreased during laboratory incubation of water samples from Tokyo Bay.

Ultraviolet Absorbance, Fluorescence

Determination of the absorbance of ultraviolet light and the fluorescent activity of the DOM was made in these studies in order to detect changes in the qualitative nature of the dissolved detritus produced during decomposition. These assays are relatively non-specific

but are particularly useful when interpreted in conjunction with other data. The absorbance of light of wavelengths of 200 - 400 nm is caused mainly by multiple bonds (C=C, C=O) and unshared electron pairs ($C-OH_2$, $C-NH_2$) in the organic molecules. These chemical bonds empart to or enhance the color of natural waters. Several organic structures, particularly ring formations, actively fluoresce when irradiated by ultraviolet light (Schnitzer, 1971). These characteristics of dissolved organic matter are being taken advantage of by some investigators in attempts to develop methods which rapidly estimate the DOC content of natural waters based on constant relationships between spectroscopic properties and actual DOC measurements (Smart et al., 1976; Lewis and Tyburczy, 1974).

Graphs of UV absorbance of DOM of the laboratory experiments appear in Appendix Figures 49 through 72, and fluorescence activity is shown in Appendix Figures 73 through 96. All data were normalized to a per gram initial ash-free dry weight basis (AFDW).

Nearly all species under all conditions showed trends in UV absorbance which roughly paralleled the corresponding DOC concentrations. Generally less UV absorbance was found in DOM of aerobic than in anaerobic flasks, while there was as much or more absorbance in DOM of flasks incubated at 25°C as in those of 10°C.

The UV absorbance of the whole fraction (i.e. GS filtrate) increased through time in all species during anaerobic decomposition at 10°C. DOM of experiments of Nuphar, Myriophyllum, and Najas exhibited absorbance maxima initially due to leaching and either showed constant or increasing absorbance in anaerobic flasks and

constant or decreasing absorbance in the aerated flasks. This trend was not observed, however, in experiments with the two species of Scirpus, where UV absorbance of DOM increased dramatically in most cases, particularly under the conditions expected to be most conducive to decomposition of detrital DOM, namely aerobic at 25°C (compare Appendix Figures 50 and 69).

The DOM of lower molecular weight fractions (i.e.< 500, < 1,000) showed much less absorbance than would be predicted from the ratio of DOC concentrations in high and low molecular weight fractions. This corresponds exactly to the visual appearance of the filtered samples: fractions of greater than 1,000 MW were definitely colored, depending on the species, ranging from pale yellow-green (Nuphar) through light yellow (both Scirpus species) to deep gold Najas, Myriophyllum). Colors were more intense in media from the anaerobic experiments. Low molecular weight fractions (< 1,000) had no visual color in any experiments. Experiments of all species incubated at 10°C anaerobically exhibited constant or slightly increasing levels of absorbance in low molecular weight fractions over time (other than the initial leaching peak and immediate decline). This response is in contrast to that observed under the other conditions where absorbance of smaller compounds consistently decreased through time, especially in the aerated flasks, even when absorbance of higher molecular weight fractions was increasing (e.g. see Appendix Figure 66).

Fewer trends were discernible in the comparisons of fluorescence activity of the DOM of the five species under the different decomposition conditions. Generally, high molecular weight fractions

maintained fairly constant levels of fluorescence activity over time during decomposition at 10°C; low molecular weight fractions showed little fluorescence activity at 10°C, especially in the aerated flasks where fluorescence by small molecules decreased with time. At 25°C generally all species under all conditions showed slightly increasing fluorescence during decomposition. Again, fluorescence by low molecular weight compounds was proportionately greater in anaerobic than in aerated experiments. DOM from Nuphar had the greatest fluorescence activity, that from S. acutus the least.

The non-specific nature of these spectrophotometric assays allows detection of differences in the chemical nature of DOM by comparison of spectrophotometric response with DOC determination under various conditions. Extreme examples of negative correlation between absorbance and fluorescence and the concentration of DOC are shown in Figures 2 and 3. In each case, even though the total amount of organic carbon was present in low or decreasing concentrations, the dominant forms of the organic compounds are such that fluorescence and/or UV absorbance were heightened drastically. In addition, UV absorbance and fluorescence are not necessarily quantitatively related (see Figure 4).

Such results are not unique to this study. Wheeler (1976) found that the [DOC]/absorbance ratio was not constant over all molecular weight fractions of water from a salt marsh. The complexity of individual humic molecules and the number and kinds of substituted functional groups that they have will affect not only the wave lengths

Figure 2. DOC and UV absorbance of various molecular weight fractions of DOM from flasks containing Scirpus subterminalis during aerobic decomposition at 25°C.

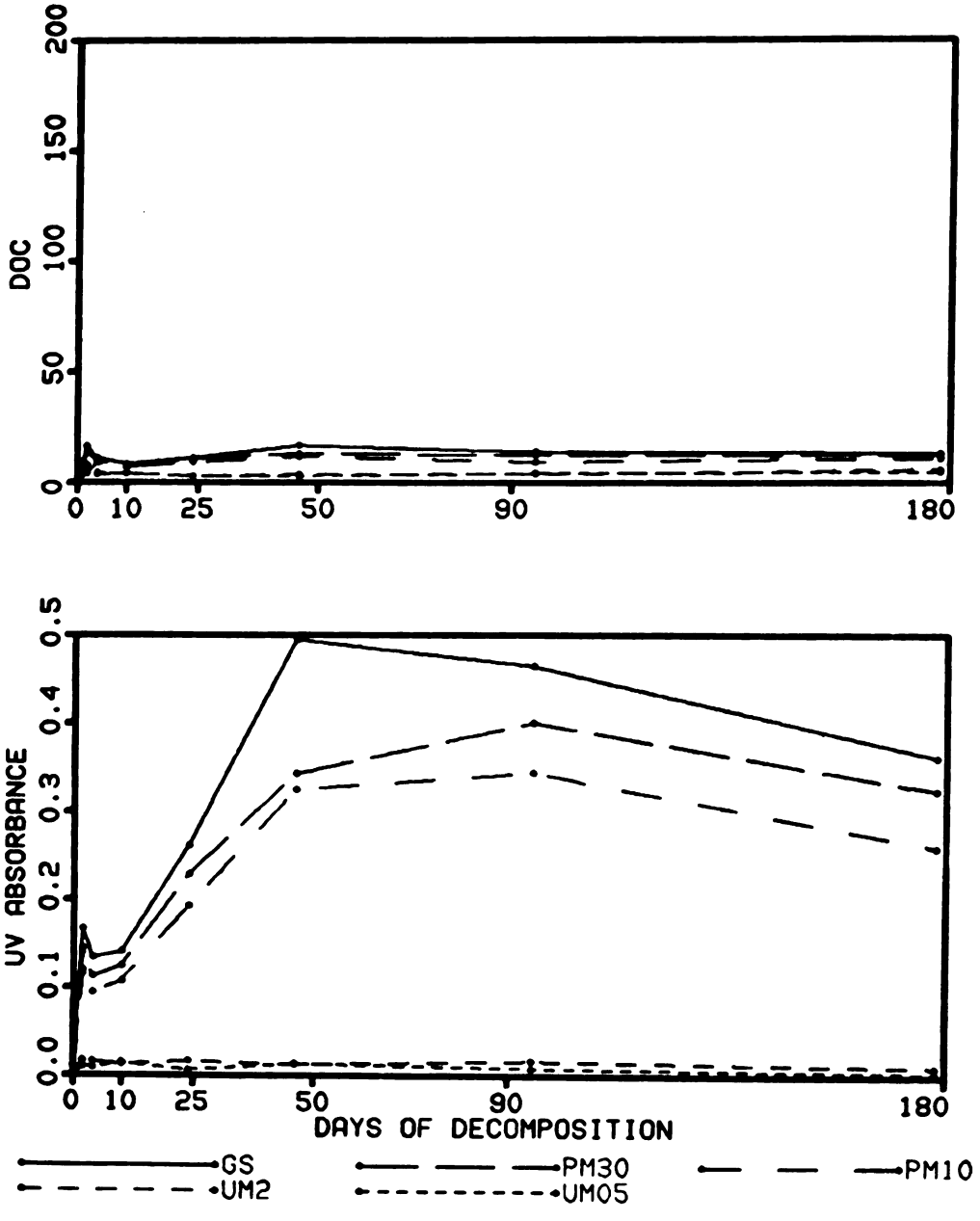
DOC
0
50
100
150
200
0 10 25 50 90 180
UV ABSORBANCE
0.0
0.1
0.2
0.3
0.4
0.5
0 10 25 50 90 180
DAYS OF DECOMPOSITION
GS
PM30
PM10
UM2
UM05

Figure 2

Figure 3. DOC and fluorescence activity of various molecular weight fractions of DOM from flasks containing Nuphar variegatum during aerobic-to-anaerobic decomposition at 25°C.

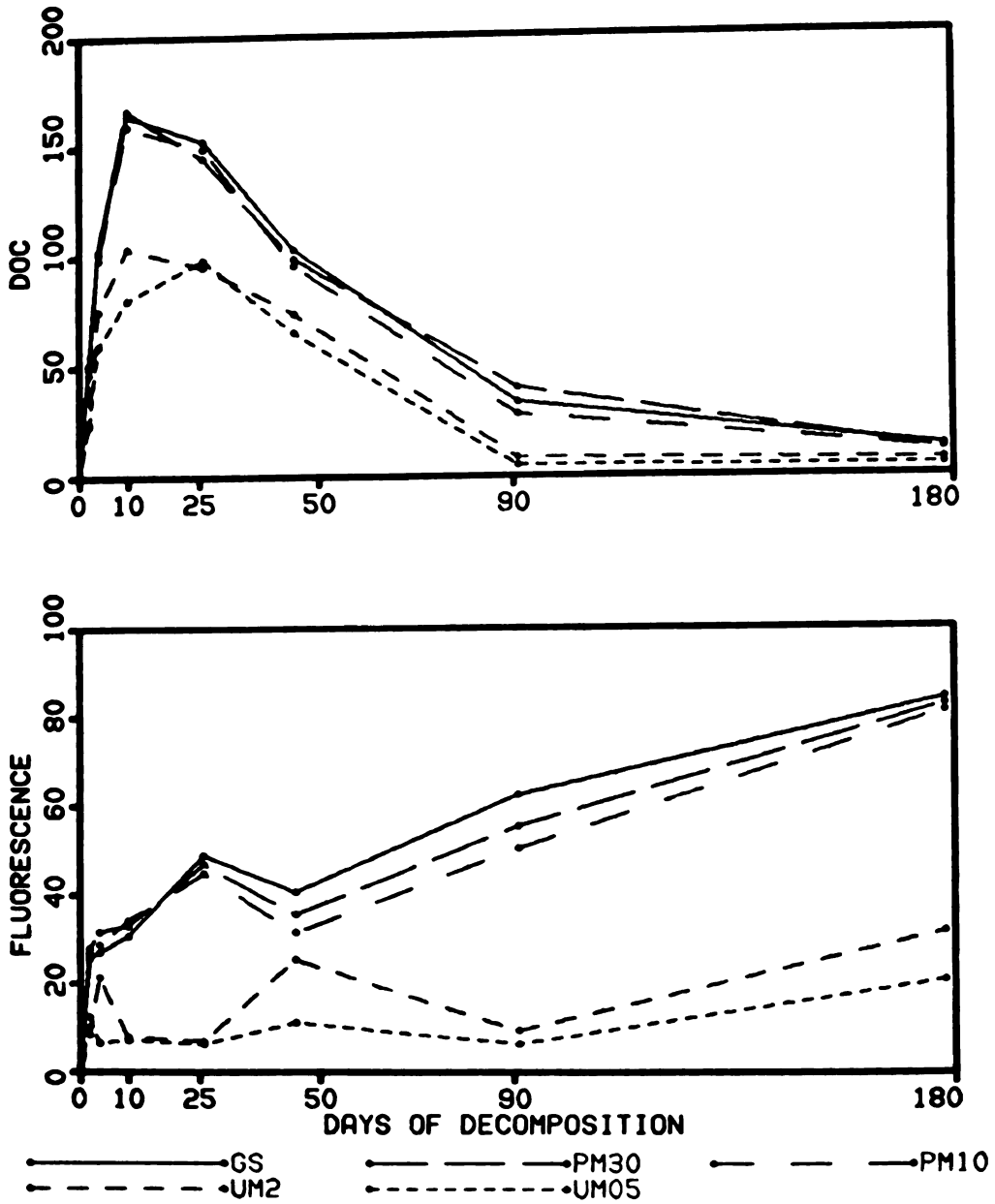
DOC
0
50
100
150
200
0 10 25 50 90 180
FLUORESCENCE
0
20
40
60
80
100
0 10 25 50 90 180
DAYS OF DECOMPOSITION
GS
PM30
PM10
UM2
UM05

Figure 3

Figure 4. UV absorbance and fluorescence activity of various molecular weight fractions of DOM from flasks containing Scirpus subterminalis during aerobic decomposition at 25°C.

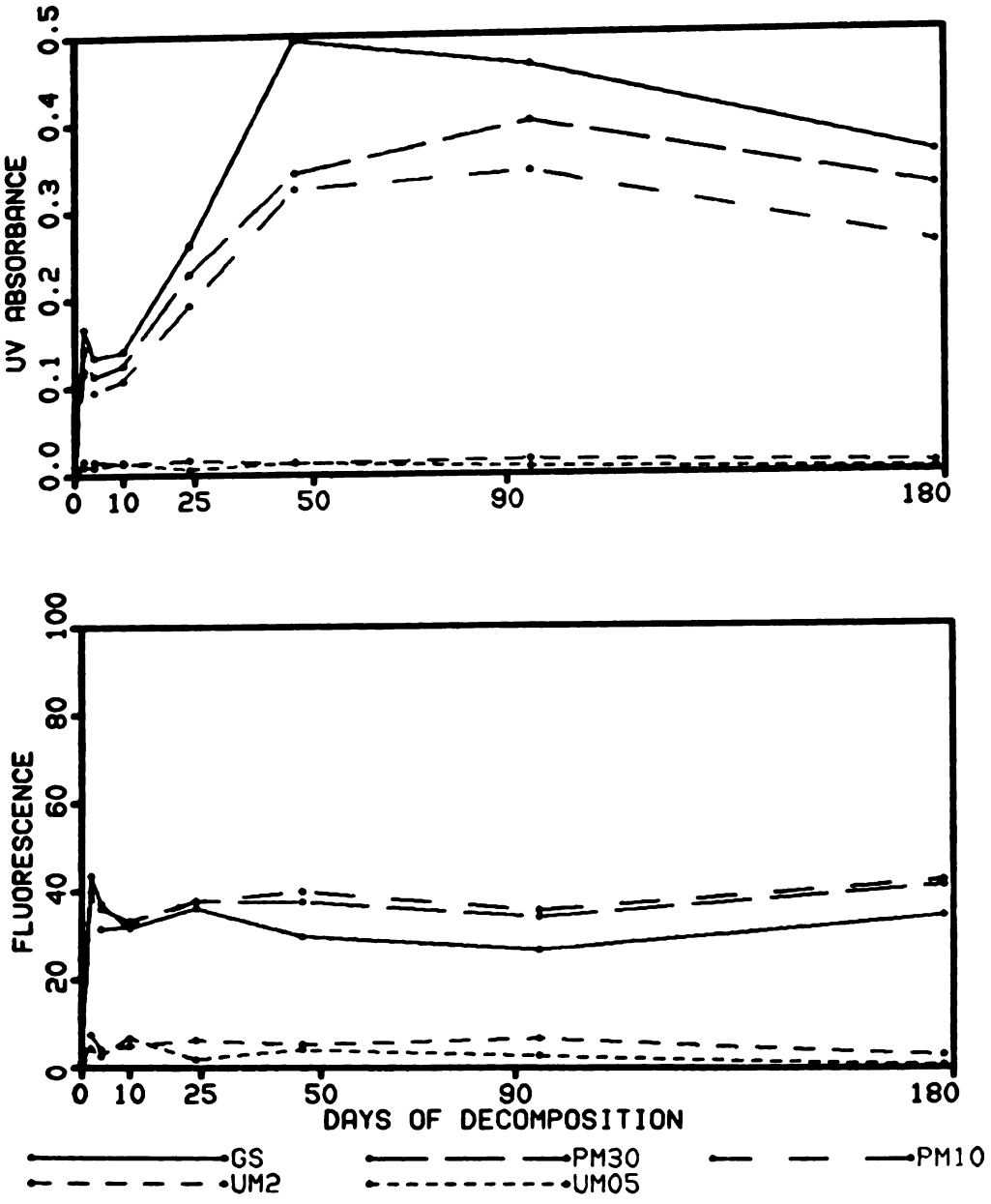
UV ABSORBANCE
0.0
0.1
0.2
0.3
0.4
0.5
0
10
25
50
90
180
FLUORESCENCE
0
20
40
60
80
100
0
10
25
50
90
180
DAYS OF DECOMPOSITION
GS
PM30
PM10
UM2
UM05

Figure 4

of absorption maxima but the intensity of fluorescence as well (Lévesque, 1972).

Both UV absorbance and fluorescence activity in natural waters are caused by the presence of dissolved humic substances or yellow organic acids, which are part of a large family of amorphous, colored substances of complex and highly variable structure (Schnitzer and Khan, 1972; Gjessing, 1976). These compounds, which exist in particulate form as well, are very important in sediment and soil processes (Davies, 1971). Terrestrial decomposition-soil humic matter questions have been well-studied (see reviews in Dickinson and Pugh, 1974).

Much evidence indicates that the phenolic and lignin compounds in plant tissue are the major precursors of humic substances (Christman and Ogelsby, 1961; Flaig, 1964). Many non-lignin phenolic compounds are present in plants as well (Bate-Smith, 1962, 1968; Ribéreau-Gayon, 1972). Many compounds obtained during destructive analyses of humic materials are known to be used in the cellular synthesis of lignin in plants (Christman and Ghassemi, 1966; Freudenberg and Neish, 1968). Flaig (1959) has shown the similar infrared (IR) spectra of lignin extracted from straw, humic acids from decomposing straw, and alkaline extracts of humic acids from marsh soil. IR spectra and comparison of chemical degradation products have been used to show that humic acids of Phragmites peat are made up in significant quantities by aromatic structures that were derived from Phragmites lignin (Farmer and Morrison, 1964). Thin-layer chromatrography of humic acids extracted from soils indicated the presence of relatively unaltered

lignin residues of oak and pine trees growing in those soils; lignin residues were not found in the humic acids of clumps of the lignin-free Antarctic moss Bryum argenteum (Burges et al., 1964). Lignin has reportedly been isolated from two species of Sphagnum (Lindberg and Theander, 1952) and the IR spectra of extracts of fresh plants, peat, and humic acids for another Sphagnum species were very similar to each other (Farmer and Morrison, 1964). Evidence also exists to show that lignin is not the only precursor (Christman and Minear, 1971) and that humic-like compounds can be derived from autochthonous and non-vascular plant sources (Otsuki and Hanya, 1967; Nissenbaum and Kaplan, 1972).

Several conclusions can be drawn from the data of the present study regarding the control of decomposition of detrital DOM in a lake by environmental conditions of temperature and oxygen concentration. Processing of DOM occurred faster at the higher temperature which generally caused declining or consistently low concentrations of measured DOC of all molecular weight fractions. In conjunction with the declining total DOC content during decomposition at the higher temperature, fluorescence and UV absorbance of the low molecular weight fractions declined and/or remained at low values. This relationship indicates that these smaller compounds with unsaturated bonds or ring structures were being taken out of solution, either by bacteria or by physico-chemical means such as complexing and adsorption. High molecular weight compounds, however, in spite of decreasing carbon content, exhibited increasing UV absorption and fluorescent properties, indicating an increased dominance in complex

humic-type compounds in the organic matter in solution. At the lower temperature decomposition did not proceed as rapidly, as indicated by rates of decline of DOC because of slow processing. Humic substances persisted in the low molecular weight fractions and did not accumulate in the larger molecular weight fractions.

Oxygen was the limiting factor for rapid disappearance of dissolved organic carbon at the low temperature; when oxygen was not present DOM was metabolized only slowly or not at all, and at 10°C even low molecular weight fractions accumulated carbon. The higher temperature eventually caused DOM to be processed despite the lack of oxygen. When oxygen was present, both small and large molecular weight fractions showed losses in total organic carbon at both temperatures. It is clear that dynamics of dissolved organic carbon in natural systems depends not only on quantitative aspects but on the qualitative characteristics of the substances as well (cf. Alexander, 1965).

Resistant Compounds

Humic compounds decompose slowly. Paul (1970) fractionated soil humus into nitrogen-rich materials that had an estimated residence time of 25 years and more resistant humic materials of aromatic structure that had residence times ranging from 200 to greater than 2,000 years. Fokin and Karpukhin (1974) theorize that the products of decaying plant tissue are to a large extent adsorbed by soil humus which is renewed not by formation of new molecules but by additions to currently present molecules. They believe that there is an inert

core or nucleus in humic molecules surrounded by more labile functional groups which are alternately lost and replaced.

The resistance of these recalcitrant compounds to microbial degradation results from their phenolic structure. Alexander (1975) has listed conditions under which microbes will not readily use organic compounds as substrates. Several of these situations are particularly applicable to humic compounds in aquatic environments. Microbes will not readily degrade the large amorphous polyphenolic structures that cannot pass into the cells. Compounds which require exoenzymes from more than one population will not be rapidly degraded. The heterogenity of the structure and functional groups of humic compounds may dictate that several different enzymes are needed to facilitate decomposition. However, microbes are fairly specific in the cabilities of their catabolic pathways (Dagley, 1971, 1975) and the need for different enzymes may translate to a need for several populations. This requirement has a retarding or inhibitory effect if not all of the necessary populations are present at the same place at the same time. In contrast, de Haan (1974) found that a fulvic acid fraction was stimulatory and was degraded by Pseudomonas using lactate as a primary carbon source; this response was attributed to co-metabolism of the two different organic compounds (cf. Horvath, 1972).

The diversity of humic compounds present in water is very high. Shapiro (1957) estimated by chromatographic methods that possibly as many as 42 distinct yellow acids could be isolated from ethyl acetate extracts of lake water. If the number of individual

compounds is high for a given concentration of resistant DOM, each compound may be present only in small quantities. Many microbes will not metabolize compounds present in concentrations too low to cause enzyme synthesis.

Finally, and most importantly, microbes cannot attack a compound for which no degradative enzymes exist. Some resistant organics may be the combination of so many biological and chemical reactions that no enzyme exists which can catalyze their breakdown. In addition, humics have an antagonistic deactivating effect on enzymes, e.g. lysozyme (Povoledo, 1972; see also Ladd and Butler, 1975).

Some of the resistance of these compounds to microbial degradation can be overcome by changes in the environment in which decay occurs. Waksman and Carey (1935a, 1935b) concluded that substrate resistance was partially a function of environmental conditions and could be ameliorated by creating optimal, albeit unnatural, conditions. Thus, the term "resistance" is truly relative and describes how readily macrophytic detritus might be decomposed.

Particulate Organic Matter

Weight Loss

Investigators of decomposition of natural products in both terrestrial and aquatic situations have often mathematically described the amount of material, nearly always in particulate form, that has "disappeared" or that remains over a period of time. Some decomposition data are fit well by a linear model where unit weight loss per unit time is constant, especially if weight loss due to leaching is ignored, giving a straight line (Mason and Bryant, 1975).

Most decay curves in which the leaching component is taken into account indicate that weight loss occurs much faster in the beginning of decomposition than later. For this reason, most often decay rates are fit well by an exponential function where a constant fraction of the material present at the beginning of a unit of time is lost during that time interval (e.g. Jewell, 1971; Saunders, 1972; Hodkinson, 1975). Reddy and Patrick (1975) used a quadratic equation.

Exponential decay is most frequently associated with the decay of radioactive material from one isotope to another by emission of a sub-atomic particle. Since in a given mass of isotope any one atom has just as much probability of decaying in any given period of time as any other atom, the amount of isotope disintegrating in a period of time is a constant proportion of the amount of isotope present. This model fits well, conceptually, the decomposition of physically homogeneous substances, but it is not valid to assume that most biotically-produced material would be subject to a constant rate of loss over time. Plant tissue, consisting of a complex of organic compounds from simple sugars and amino acids to very large and extremely stable structural polymers, certainly would be expected to decay more rapidly in the initial stages than later when the most labile compounds have been removed and only the resistant ones remain (cf. Minderman, 1968). The rate at which the remaining tissue becomes increasingly resistant is dependent on a multitude of factors: tissue structure, source, and physiological state prior to death, environmental conditions, organisms carrying out the degradation, etc.

There is no question that application of a simple exponential curve to experimental data and comparisons of resultant decay coefficients have value. Comparisons of such data for similar conditions are often very informative (e.g. Petersen and Cummins, 1974). However, care should be taken when extrapolating or predicting decay rates outside of the experimental conditions where the measurements were made. Often, a linear or exponential function is used for reasons of convenience; most computers and laboratory calculators are capable of least squares linear regression analysis of raw or logarithmically transformed data. However, this produces the best fit to the transformed data, not the raw data, in the case of an exponential function. A sophisticated least squares curve fitting computer program was used in testing the ability of virtually any selected function to accurately describe weight loss in these experiments.

Initially a simple exponential curve was fit to the macrophyte weight loss data with acceptable results (Table 2), the correlation coefficients (r; observed versus predicted weight remaining) ranging from 0.78 to over 0.99. However, examination of the functions plotted with the actual data pointed out a systematic poorness of fit, as exemplified in Figure 5a. Even though, in this example, $\underline{r}$ was 0.96, in this and most all other fits of a simple exponential model, the values of the function of best fit were consistently higher than the actual data points during the initial phase of decay, and continually lower than the weights measured during the latter portion of the experiments. This trend indicated that the rate of decay was not constant but was greater initially and then decreased. The simplest

Table 2. Decay rate constants of exponential functions of best fit to weight loss data of aquatic macrophytes under differing experimental conditions.

Species	Anaerobic	Aerobic
	25°C	
	0.060	0.085
	0.034	0.037
	0.028	0.026
	0.009	0.017
	0.005	0.011
	0.020	0.016
	0.009	0.006
	0.007	0.007
	0.002	0.004
	0.002	0.004

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Abstract

Table 2. Decay rate constants of exponential functions of best fit to weight loss data of aquatic macrophytes under differing experimental conditions.

Species	Anaerobic	Aerobic
	25°C	
Nuphar variegatum	0.060	0.085
Myriophyllum heterophyllum	0.034	0.037
Najas flexilis	0.028	0.026
Scirpus subterminalis	0.009	0.017
Scirpus acutus	0.005	0.011
	10°C	
Nuphar variegatum	0.020	0.016
Myriophyllum heterophyllum	0.009	0.006
Najas flexilis	0.007	0.007
Scirpus subterminalis	0.002	0.004
Scirpus acutus	0.002	0.004

Figure 5. Graphs of functions (solid lines) of weight remaining over time fit to actual data (triangles) for Najas flexilis during aerobic-to-anaerobic decomposition at 25°C: (a) simple exponential function, k = 0.028, correlation coefficient (observed vs. predicted weight remaining) r = 0.96; (b) exponential function where $\bar{k}$ is an exponential function as well, a = 0.063, b = 0.049, r = 0.99. See text for explanation of parameters.

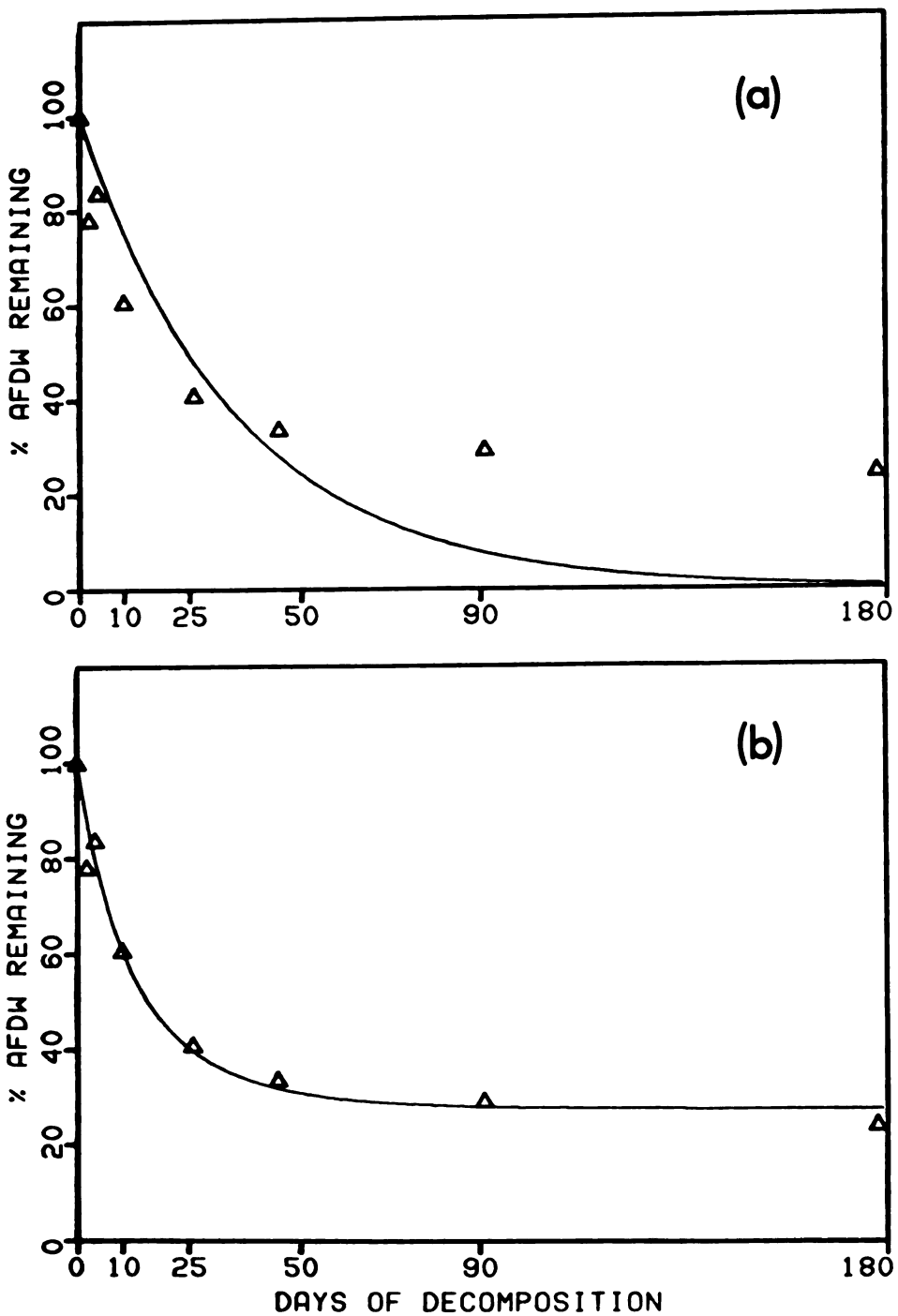
(a)
% AFDW REMAINING
0
20
40
60
80
100
0 10 25 50 90 180
(b)
% AFDW REMAINING
0
20
40
60
80
100
0 10 25 50 90 180
DAYS OF DECOMPOSITION

Figure 5

function to describe a declining decay coefficient would be a linear one ($k = a - bt$), but this was rejected because as t (days of decomposition) increases, the value of the decay coefficient, k, could theoretically become negative implying an increase in weight remaining. Obviously, while residual weight increases do occur, this characteristic of the model disqualifies it from being applicable in the general case. The next simplest model describing a regularly decreasing decay coefficient is the exponential. An overall weight remaining equation was derived as shown in Figure 6 and fitted to the weight data. Note that this function (Figure 5b) fits the data more closely than does the simple exponential in the example in Figure 5a. This situation was true for nearly all species-experiment combinations.

The predicted weight values of the model of best fit and the corresponding decay coefficients are plotted against time along with the actual data in Appendix Figures 97 through 140 for decomposition of macrophytes in both laboratory and field experiments. For comparative purposes the parameters of the functions of best fit for the aerobic-to-anaerobic and the aerobic experiments at both temperatures are listed in Table 3.

Parameter a is the decay coefficient at day 0, and parameter b is the constant proportion by which the decay coefficient is decreased in each time interval. If this model were fit to data for decay of a radioactive isotope, theoretically b would equal zero, and the proportion of isotope decaying in a unit of time would remain constant. Plant tissue does not decompose at a constant proportional rate: the values of parameters a and b vary with both species and

Figure 6. Derivation of exponential function fitted to weight loss data where the decay coefficient is itself an exponential function of time. W = percent of ash-free dry weight remaining; t = days of decomposition; a, b = constants obtained by least squares computer fit of function to actual data.

The model:

$$\frac{dW}{dt} = -kW, \text{ where } \frac{dk}{dt} = -bt \quad (\text{i.e. } k = ae^{-bt})$$

Substituting,

$$\frac{dW}{dt} = -(ae^{-bt})W$$

$$\frac{1}{W}\, dW = -ae^{-bt}\, dt$$

Integrating,

$$\ln W = \frac{a}{b}\, e^{-bt} + C$$

Solve for C when t = 0:

$$C = \ln W_0 - \frac{a}{b}$$

Substituting for C,

$$\ln W = \frac{a}{b}\, e^{-bt} + \ln W_0 - \frac{a}{b}$$

$$\ln W = \ln W_0 + \frac{a}{b}\,(e^{-bt} - 1)$$

Take antilog of both sides:

$$W = W_0\, e^{\frac{a}{b}(e^{-bt} - 1)}$$

Final form:

$$W = 100\, e^{\frac{a}{b}(e^{-bt} - 1)}$$

Table 3. Parameters of exponential functions of best fit to macrophyte weight loss data where the decay coefficient decreases exponentially with time. *a* is the initial rate of weight loss which declines exponentially through time at a rate of *b*. (From Godshalk and Wetzel, 1977b.)

Species	Anaerobic		Aerobic	
	a	b	a	b
	25°C			
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
	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

environmental conditions (see Table 3), and it is the interaction of these two constants that give the function its ability to fit the actual data. Initial decay rate, a, is correlated consistently with overall rate of weight loss, as determined by inspection of the curves and comparing constant decay coefficients, k, which were estimated by best fit of simple exponential functions (Table 2). The most rapidly decomposing plants had the highest values of a under all conditions. The values of b indicate how rapidly the tissue becomes more resistant to decay. The values of the b parameters are not directly comparable because they are related to the respective a parameter values. For example, in the case of Nuphar during aerobic decomposition at 25°C, the value of b is very high, but because a is also high, weight loss was the most rapid of all combinations studied. High a and b indicate rapid initial decomposition and moderate rates of continued loss during the latter stages. Moderate a and low b occurred when overall decay rates were fairly uniform for the entire period, i.e. in low leaching situations. Low a with high b, as in Scirpus acutus, indicate that leaching, though low compared to other species, was much more rapid than subsequent weight loss and occurred only for a short time. The only exception to the trend of greater values of a associated with greater overall weight loss rates was that of Scirpus subterminalis. Its values for a at 10°C were even lower than those of S. acutus, but because its b values were also extremely low, the average decay rate was greater than for the emergent species. The negative value of b for S. subterminalis

during anaerobic decomposition at 10°C indicates that the rate of decay actually increased with time (Appendix Figure 98).

It can be seen that values of b increased only slightly or decreased with progressively more conducive conditions for rapid decomposition (i.e. anaerobic at 10°C to aerobic at 25°C), implying that decay-resistance of tissue was partially overcome by environmental conditions causing decay rates to remain high for a longer time. The greatest increase in a and b resulted from increased temperatures, whether aerobic or anaerobic; oxygenation had less effect on the decay rate parameters at either temperature.

Weight loss was slowest during the 180-day laboratory decomposition period in the anaerobic flasks incubated at 10°C. Aeration did not appreciably increase particulate weight loss. However, decomposition was much faster at 25°C even under anaerobic conditions, and oxygenation accelerated weight loss somewhat. In most cases during the last half of the decomposition period further weight loss was minimal, and the curves approached very closely some asymptotic limit of minimal remaining weight. Conditions more conducive to decomposition lowered this asymptote but not so far as to result in total weight loss. Rates of plant decomposition for the five species were consistently ranked related to each other over the different experimental conditions: Nuphar was always fastest (i.e. greatest average weight loss per day and least weight remaining at the last sampling period), followed by Myriophyllum, Najas, S. subterminalis, and finally S. acutus.

No other studies are known where a decay model with an exponentially decreasing rate coefficient was fit to empirical data, so comparison of parameters is not possible. Few studies have determined simple exponential rates for aquatic decay of vascular plant tissue in the laboratory. Jewell (1971) decomposed 14 species of aquatic macrophytes in aerated cultures at about 18°C and calculated k values (as percent per day) ranging from 0.052 for Callictriche sp. to 0.18 for Rorippa sp. These values are somewhat higher than those of the present study (see Table 2), but his plants were of species probably with less structural tissue than the plants of this investigation.

Field studies showed trends similar to those observed in laboratory experiments. Weight loss from in situ litterbags over time was faster in summer where the response was similar for all species to the responses in laboratory aerobic experiments at 25°C, and slower in winter where in situ weight loss was slightly less than that of 10°C laboratory experiments. There were no discernible differences between the two Lawrence Lake incubation sites during the fall-winter experiments. Because curve fits are based on fewer samples in the field experiments, only Myriophyllum and Nuphar could be compared meaningfully between the littoral zone incubation sites (Appendix Figures 129 and 139, 130 and 140). In both instances decomposition was markedly faster in hypereutrophic Wintergreen Lake. This result is noteworthy because the littoral sediments of Wintergreen Lake are extremely heavily loaded with organics, and strongly reducing conditions always exist. In spite of the seemingly better

environmental conditions for decomposition in Lawrence Lake, the faster rates observed in Wintergreen Lake were possibly related to the very active microbial-detrital community of the sediments in this lake. Also, both of these macrophyte species grow abundantly at the incubation site in Wintergreen Lake, and they do not grow at the Lawrence Lake littoral site, so that specific bacteria required for decomposition of either species would be expected to be present in high concentrations in Wintergreen Lake and possibly not in Lawrence Lake.

The predicted in situ total weight loss during 180 days for the fastest decomposing species, Nuphar, was 60 to 90 percent and for the slowest, S. acutus, it was 20 to 40 percent of initial ash-free dry weight. Tissue of Spartina cynosuroides, Distichilis spicata, and Scirpus americanus all lost about 60 percent of their weight, and Juncus roemerianus leaves, most similar to those of S. acutus of the present study, lost about 40 percent of their initial dry weight during one year of incubation in litterbags in a Mississippi salt marsh (de la Cruz and Gabriel, 1974; de la Cruz, 1975). Leaves of J. tracyi lost 34 percent of their initial dry weight while decaying in litterbags in a Canadian beaver pond (Hodkinson, 1975). Wohler et al., (1975) incubated oven-dried tissue of Potamogeton diversifolius in glass jars with nylon mesh (1 mm openings) lids on the bottom of a pond and observed 57 percent loss in weight during a 100-day decomposition period. Mason and Bryant (1975) found no significant difference in rates of decomposition of Typha leaves in litterbags placed at the edge of reedswamps in two shallow productive English

lakes. Total weight loss was 70 to 80 percent over one year for Phragmites, 40 to 50 percent for Typha.

Carbohydrates, Fiber Components

The results of the carbohydrate and fiber constituent assays are presented in two ways. In Appendix Figures 141 through 184 the content of each component in the decomposing tissue is reported as the percent of the initial concentration, so that the actual gains and losses of each component can be followed during decomposition. In Appendix Figures 185 through 228 the proportion of recovered tissue that was found in each of the determined fractions is reported, thus making shifts in the dominance of one fraction over another more visible.

Total nonstructural carbohydrates (TNC; sugars, starches), present only in low concentrations even initially in these senescent plants, were expected to be susceptible to leaching; therefore, rapid loss of this fraction was anticipated. Anaerobically at 10°C, most TNC levels gradually declined to values about one-half of initial content, sometimes after an early increase over the original content (see Appendix Figures 141-184). Aeration at 10°C caused much more rapid decline of the original TNC content in all species, and losses of TNC during these experimental conditions were very similar to those of anaerobic decomposition at 25°C. Aerobic decay at 25°C did not result in the expected rapid decrease to immeasureable levels, and the continued absence of these compounds for the duration of the experiment. Instead, the trends were very similar to those seen in previously described experiments: gradual but continual decline

through time and much dependence of rate on species. Under all experimental conditions, Nuphar continually lost its TNC faster than did the other species. Losses of TNC by Myriophyllum and Najas were also rapid and usually faster than occurred in the Scirpus species. However, in many instances the two bulrushes were devoid of measurable TNC sooner than were the two submersed plants, particularly under aerated conditions. The initial high levels of TNC in Najas were probably concentrated in the many nearly mature seeds in the axils of the leaf material.

Changes from initial TNC content in the field-incubated samples showed the same species-dependent rate characteristics, but overall losses occurred more slowly and, except during summer incubation, TNC levels did not drop as low as in the flask experiments. TNC contents of winter field samples were much like those of the 10°C anaerobic samples.

Structural carbohydrates constituted the majority of the biomass of the plants and were nearly always present in large amounts at the end of the incubation period. The material that was assayed as lignin was very resistant to decomposition, and this fraction usually showed an increase over initial content during at least the beginning of the decomposition period. Under aerobic-to-anaerobic conditions at 10°C the proportions of hemicellulose, cellulose, and lignin in the recovered plant material remained approximately constant in all species. Structural carbohydrates gradually decreased through time. The lignin fraction increased by as much as two to five times over the initial concentration in the two Scirpus species and Nuphar,

while the proportion of lignin in Najas and Myriophyllum increased only slightly. Greater increases in the lignin fraction and less overall loss of hemicellulose and cellulose were observed from S. subterminalis and Myriophyllum in the strict anaerobic experiment at 10°C. Aeration at 10°C caused a more rapid loss of the structural carbohydrates, and the proportion of lignin in the recovered plant tissue subsequently increased through time. This increased concentration was the result of the presence of nearly constant masses of lignin fraction, at or above initial levels (except in Najas) for the entire experiment. Hemicellulose and cellulose decayed to about one-third their original contents in Nuphar, Myriophyllum, and Najas, and to one-half in both species of Scirpus. At 25°C during anaerobic decomposition, the lignin fraction decreased very little during the entire 180 days, and real increases in this component above original levels were not substantial. Under these experimental conditions, however, cellulose and hemicellulose decayed much more quickly than at 10°C. Aerobically at 25°C, hemicellulose and cellulose decreased to less than half of their initial amounts within 25 days in Nuphar, Myriophyllum, and Najas, and decreased only very slowly thereafter. These constituents in both species of Scirpus did not decline as fast initially and continued to be decomposed over the entire time of the experiment. Even under these conditions, the lignin fraction was exceptionally resistant, and there was always nearly as much or more than the original amounts of lignin-like material in all species except Najas. Thus, the lignin component dominated the fiber constituents of the recovered macrophytes by the end of decomposition

under warm aerobic conditions in all species except S. subterminalis and S. acutus. Lignin-like materials made up over 30 percent of the ash-free dry weight of Myriophyllum and over 20 percent in Najas and Nuphar, in the last samples that had enough tissue to analyze for fiber.

Field-incubated samples exhibited trends similar to those of the laboratory samples. There were no discernible differences in structural constituents between the three sites of fall-winter incubation; rates of change of component concentrations were greater during the spring-summer experiment for most species.

The data from TNC and fiber assays, when reported either as percent of initial content or percent of recovered ash-free dry weight often appear erratic. Surely in some cases there was much random variability in the plant tissue that was used as substrate, the organisms responsible for decomposition, subsampling and assay procedures, etc. However, the data were often remarkably consistent. All fiber data, reported as percent of sample weight, for Scirpus acutus samples incubated in litterbags are presented in Figure 7. The magnitudes and trends through time of each of the four components were very similar for all incubation conditions. The consistency of such subtle responses under widely diverse conditions of decay is an indication of the importance of considering species effects in decomposition studies. Presumably some of the uniformity of this particular species during decomposition is because of its decay-resistant structure and resultant slower alteration.

Figure 7. Total nonstructural carbohydrates (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) components, as percent of recovered AFDW, of Scirpus acutus during in situ decomposition under four conditions: (a) Lawrence Lake littoral zone, summer; (b) Lawrence Lake littoral zone, winter; (c) Lawrence Lake pelagial zone, winter; (d) Wintergreen Lake littoral zone, winter. See text for explanation.

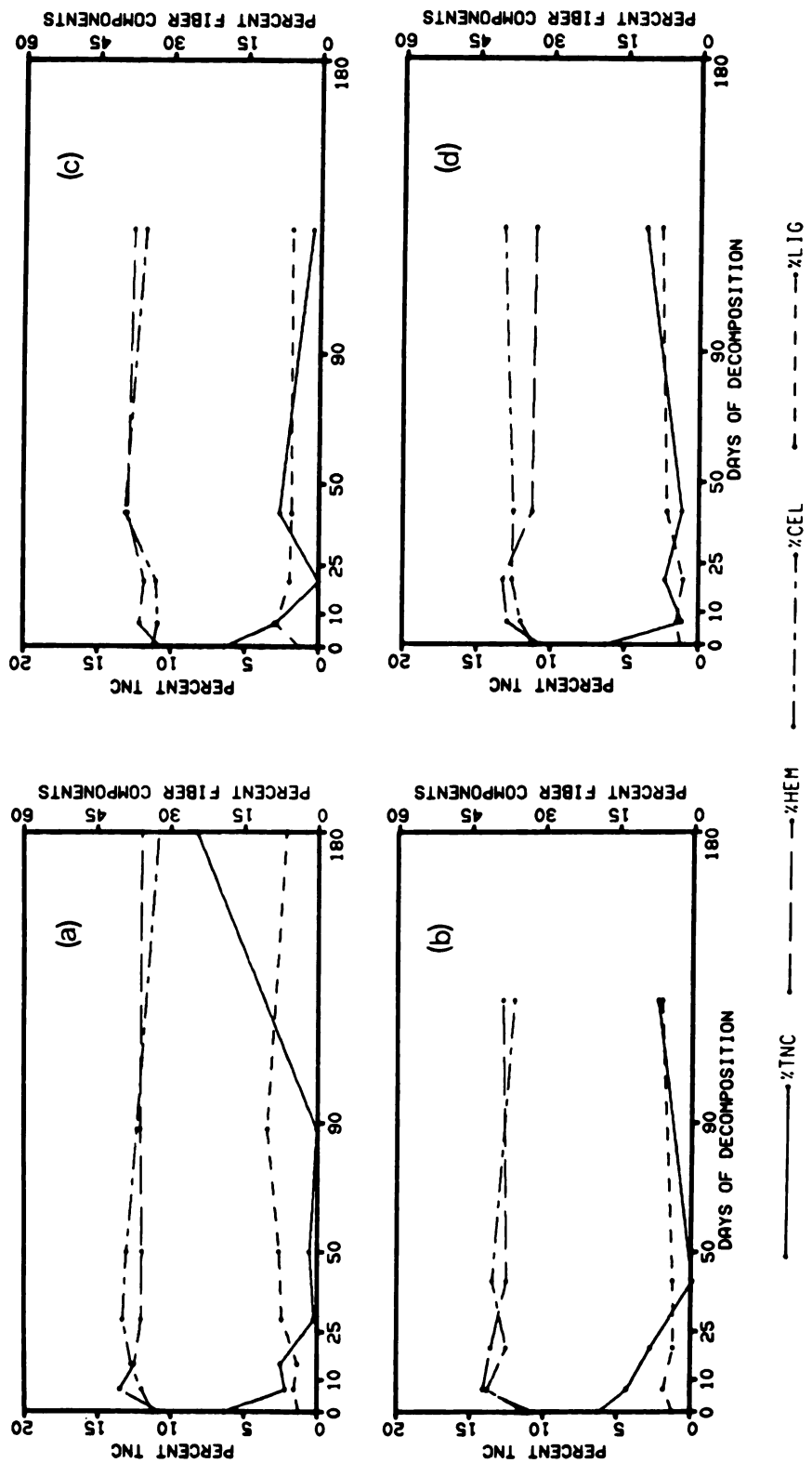
(a)
(b)
(c)
(d)
PERCENT TNC
PERCENT FIBER COMPONENTS
DAYS OF DECOMPOSITION
%TNC
%HEM
%CEL
%LIG

Figure 7

The conclusion to be drawn from these data on the decomposition of macrophytic fiber is that plant decay dynamics are unique to each species. The initial content of hemicellulose, cellulose, and lignin, and the sum of these individual concentrations are listed in Table 4 by species in order of decreasing rate of plant decomposition. The high fiber content of Najas, which decomposed at rates similar to those of Myriophyllum samples, was probably the result of high content in the leaf material of many seeds whose protective coats were resistant to breakdown during fiber analysis and caused an overestimation of the cellulose fraction. It is noteworthy that Scirpus subterminalis, which grows totally submersed for its entire life cycle, did not decompose as the other submersed plants did but apparently retained the structural characteristics of its genus of emergent bulrushes and decayed much as did Scirpus acutus.

These data concur exactly with those of Polisini and Boyd (1972) who measured the non-cell wall material in 21 species of aquatic macrophytes and obtained these averages for the three major growth forms: submersed 53.4, floating-leaved 66.6, and emergent 33.7 g non-cell wall material/100 g dry weight of plant tissue. By subtraction, the average percentages of the cell-wall material in the respective forms are obtained as 46.6, 33.4, and 66.3. These data indicate that the floating-leaved plants contain the least amount of structural tissue, followed by submersed and then emergent plants.

It can be seen that the concentration of no single component correlates as well with decomposition rates as does the total fiber content. In spite of the high resistance of lignin to degradation,

Table 4. Initial content of fiber components (as percent of ash-free dry weight) of senescent macrophytes. (From Godshalk and Wetzel, 1977b.)

Species	Hemi-cellulose	Cellulose	Lignin	Total
Nuphar variegatum	12.3	17.6	4.8	34.7
Myriophyllum heterophyllum	10.3	17.3	4.7	32.3
Najas flexilis	20.0	31.6	8.4	60.0
Scirpus subterminalis	34.6	26.4	2.6	63.6
Scirpus acutus	32.3	33.7	3.8	69.7

its concentration apparently did not totally regulate the decomposition of plant material. Hence, the fiber components which constitute the major part of macrophytic biomass are probably the most resistant components of this tissue, and rates of decomposition of whole plant material may be a function of the amount of these components initially present. Not only is the polymeric and/or aromatic structure of these individual compounds less readily broken down, but also some compounds affect the decomposition of others by the way they are associated with each other in the tissue (Cowling and Brown, 1969).

Microbes will not readily degrade compounds in which the substrate or bond to be attacked is not accessible. The highly cross-linked structure of lignin (Schubert, 1965:34), and presumably of its derivatives, makes them less vulnerable to enzymatic attack.

Nickerson (1971) suggested that degradability of a compound such as lignin may be related to the geological time it has been available as a substrate, comparing relatively old and degradable cellulose with the more recent and resistant lignin. Lignin is decomposed by some organisms, mostly basidiomycete fungi (cf. Christman and Ogelsby, 1971). The two enzymes most implicated in the degradation are phenolase and laccase, both oxidases that catalyse the oxidation of their substrates by molecular oxygen; they will not function in anaerobic conditions (Schubert, 1975:79). Recent studies using radioactively-labelled lignins demonstrated decomposition of lignin to carbon dioxide in numerous aerobic habitats and the rates of oxidation were related to temperature and concentration of carbon, nitrogen, calcium,

and potassium at the incubation site (Crawford and Crawford, 1976; Hackett et al., 1977).

Few investigators have examined the dynamics of the fiber fractions of decomposing aquatic macrophytes. de la Cruz and Gabriel (1974) reported that the crude fiber fraction of Juncus roemerianus declined from 39.4 percent of ash-free dry weight of "standing dead" plants to 9.1 percent during various stages of decomposition. Carbohydrates (measured as nitrogen-free extract by an unnamed solvent) decreased from 52.4 to 11.3 percent. In a similar study (de la Cruz, 1975) it was found that crude fiber decreased from 34.2 to 12.5, 31.5 to 10.0, and 29.9 to 6.4 percent, respectively, in Spartina cynosuroides, Distichlis spicata, and Scirpus americanus during decomposition for 12 months in litterbags. Corresponding changes in carbohydrate for the same species were 49.6 to 35.0, 53.1 to 39.8, and 50.8 to 11.3 percent respectively.

These carbohydrate values were determined by a method different from the one used in the present study and are not comparable. McIntire and Dunstan (1976) used the same enzymatic assay for carbohydrate as was used in this study to analyze living tissue of Spartina alterniflora. They measured values in the range of 4 to 10 percent of total dry weight as TNC. The measurements are only slightly higher than those found for senescent freshwater plants of the present study. The low concentrations of TNC observed in the present study may be partially due to incomplete degradation of the carbohydrates during analysis. When this enzymatic assay was performed on lotic allochthonous leaf litter, the enzyme was found to complex with humic

compounds present, severely reducing the effective enzyme concentration (M.J. Klug, Kellogg Biological Station, pers. comm.). Such an effect is likely to have occurred in the analysis of TNC of decomposing macrophytes as well.

Other investigations by Fleischer and Larsson (1974), Park (1974), and Kormondy (1968), and others have examined the decomposition of various forms of pure cellulose. These studies have limited value since the decomposition of filter paper, cotton thread, or cellophane in natural waters bears little relationship to the degradation of natural plant materials.

Microbial Metabolism

Monitoring the concentrations of various components of decomposing macrophytes and the related production of DOM is informative of the fate of plant tissue in the littoral zone but not of the means by which this fate is achieved. Measurement of the ATP content and the dehydrogenase activity of the detrital-microbial complex were used as direct assessments of the activity of the decomposition processes occuring under the various experimental conditions. The data obtained from these measurements are presented in Appendix Figures 229 through 272.

ATP Content

Theoretically, the ATP content of detritus is an approximation of living microbial biomass associated with the detrital material since ATP is not stored in significant amounts by living cells, and it breaks down very quickly upon cell death (Holm-Hansen and Booth,

1966). Although ATP determinations have been performed mostly in natural waters on planktonic organisms, investigators have applied the technique to measure the ATP of microorganisms associated with the detritus and sediments (e.g. Lee et al., 1971; Holm-Hansen and Paerl, 1972; Asmus, 1973; Karl and LaRock, 1975; Bancroft et al., 1976; see review by Laake, 1976).

The ATP content of the microflora associated with decaying Nuphar, Myriophyllum, and Najas attained maximum values after about 25 days and then declined slowly during the remainder of anaerobic incubation at 10°C. Both Scirpus species maintained only very low contents of ATP for the entire period. At 25°C and under anaerobic conditions, ATP levels were somewhat greater among all plant species than at 10°C. Aerobic decomposition resulted in greater concentrations of ATP. In Nuphar, Myriophyllum, and Najas, ATP levels again reached maxima at about day 25 and then declined; levels associated with S. subterminalis and S. acutus were low initially but continued to increase for the duration of the experiment. Levels in aerobic flasks were higher than those in anaerobic flasks at 25°C, and highest levels often occurred in a sharp peak within the first ten days of decomposition.

Only during aerobic decomposition at 25°C were differences in ATP content detectable among plant species. Najas and Myriophyllum exhibited maximal ATP contents about four times greater than those of S. subterminalis and Nuphar, but the latter two species maintained substantial levels over the entire study period so that ATP contents for the four species were probably not different if averaged over

time of decomposition. S. acutus, the most fibrous and slowly decaying plant, consistently had much higher ATP content than the other species, implying a higher microbial biomass associated with this resistant plant.

Litterbag samples were characterized by having very constant ATP levels compared to laboratory samples during the entire incubation period. Values for laboratory and lake incubation were generally of the same magnitude, and no consistent differences between species were observed. Except in the spring-summer series where samples taken after day 25 usually did not contain sufficient tissue for ATP extraction, ATP levels rose slightly from the beginning to peak amounts at about day 40 and then declined before the last sampling on day 128.

The dependency of the results of this assay on sample type and efficiency of extraction and enzymatic determination preclude comparison to absolute quantities of ATP found by other investigators. Also, both laboratory and field samples were exposed to abundant supplies of calcium carbonate and humic compounds, both of which have been found to interfere with the determination of ATP (Cunningham and Wetzel, 1977). For this reason, present ATP values are not comparable to those of other studies, and may vary within this study because of the variations in humic matter content of samples of differing plant species and incubation conditions.

Pamatmat and Skjoldal (1974) measured ATP in marine coastal sediments and found consistently lower ATP content at greater depths of sediment. Presumably, the implied decrease in microbial biomass in

the lower layers of sediments is caused by the concentration of dissolved oxygen and the proportional reducing conditions there, accumulation of end products because of poor flushing and impeded diffusion, increased predominance of resistant organic substrates, etc. These are all conditions that were probably occurring in the decomposition flasks in this study and might explain the consistent decline in ATP during the latter stages of incubation among the rapidly decomposing species. In flasks containing resistant species of macrophytes, these conditions were established only slowly, thus allowing microbial ATP levels to increase for a longer time. Oláh (1972) observed an increase in ATP during the first five days of laboratory decomposition of ground Phragmites and then decreasing values.

ETS Activity

Whereas ATP has been proposed as an estimate of microbial biomass, assays of the activity of microbial electron transport systems have been used to estimate the actual respiratory activity of cells. The assay supposedly is a measure of the activity of dehydrogenase enzyme which is a participant in a portion of the metabolic electron transport system that is common to aerobic and anaerobic organisms alike (Curl and Sandberg, 1961; Zimmerman, 1975). Ecologists have used this assay to estimate respiratory activity of both planktonic and benthic aquatic and marine organisms.

In this study, under anaerobic decomposition at 10°C, ETS activity increased throughout the decomposition period among all species except for S. acutus which decreased after 50 days. ETS activity was lower for S. subterminalis, Myriophyllum, and Najas under

aerated conditions at 10°C, but activities for Nuphar and S. acutus reached very high levels after 50 days and then declined. High ETS activity was observed intermittently during anaerobic decay at 25°C, but there were no trends in the changing values. Again, Nuphar had the greatest maximal activity of all species. The ETS levels of aerated samples at 25°C were lower than the anaerobic ones and approximately the same as those from 10°C aerobic conditions. For all species, ETS activity was greatest during the first 25 days and then declined steadily. In the study of Oláh (1972) mentioned above, dehydrogenase increased initially (to day 9) and then declined.

Interpretation of the results of the ETS assay is particularly difficult. In all species, ETS activity was considerably higher under anaerobic conditions than aerobic, thus implying a chemical reduction that was not necessarily dependent on biotic respiratory activity (see also Pamatmat, 1975). It has also been shown that reduced humic compounds, which obviously are present in large amounts in decomposing plant tissue (especially anaerobically), have the potential to provide electrons and thereby reduce the tetrazolium salt used as the colorimetric alternate electron acceptor in this assay (Schindler et al., 1976). Because of this interference and the role of humic compounds, which can be reversibly oxidized and reduced and thus participate in aquatic electron transport systems, the ability of the ETS assay to assess strict biological respiratory activity has been questioned (A. Zimmerman, Univ. Toronto, pers. comm.).

In the present study ATP content did not correlate with ETS activity, and the values obtained by each assay varied independently.

Pamatmat and Skjoldal (1974) also measured ETS activity in their investigation of sediments and found it to decrease with increasing sediment depth as well. The ratio of ETS/ATP increased significantly with sediment depth, suggesting to the authors the possible existence of a gradient of microbial species or metabolic types in the sediments.

Knowledge of the quantiative aspects of microbial metabolism in aquatic ecosystems is crucial to understanding them, and certainly much more effort must be applied toward accurately obtaining such information.

Nitrogen and Decomposition

Nitrogen serves in several critical processes of the metabolism of the littoral zone. Various inorganic forms of nitrogen are present in different proportions depending on redox conditions and pH. Organic nitrogen exists mostly as protein or protein subunits. Interconversion of these forms is mediated by several groups of microorganisms which variously oxidize or reduce nitrogen compounds. Despite the abundance of molecular nitrogen in the atmosphere, low concentrations of dissolved nitrogen can limit productivity in aquatic ecosystems. Nitrogen is needed by living organisms as a protein constituent; unavailability of nitrogen, either by total lack of the element or by its being present predominantly in a form that is difficult to metabolize, limits protein synthesis and, in the case of microorganisms, results in declining populations over time.

Much of the decomposition of polymerized carbon of macrophytic origin undoubtedly occurs by extracellular enzymes, requiring a large

synthesis and secretion into the habitat of organic nitrogen by microbes (cf. Kim and ZoBell, 1974). Because of the importance of nitrogen to the metabolism of lakes in general (Kuznetsov, 1975:259; Wetzel, 1975:186) and its role in decomposition processes in particular, changes in the amounts of total nitrogen, both in particulate and dissolved forms, were monitored during decomposition of macrophytes. Particulate nitrogen and carbon, as percentages of total dry weight, of recovered macrophyte tissue are shown in Appendix Figures 273 through 316. The percentages by weight of nitrogen and carbon in the residue of lyophilized media (i.e. inorganic salts plus DOM) are reported in Appendix Figures 317 through 340.

Particulate Nitrogen

During anaerobic decomposition at 10°C, the proportions of nitrogen and of carbon in the plant tissue remained fairly constant in the two species of Scirpus, yielding constant C:N ratios through time. The less resistant species, especially Nuphar, exhibited increased percentages of nitrogen associated with the POM as decomposition proceeded. At the same time, C:N values decreased as carbon levels remained constant. Aeration of the 10°C flasks caused increases in nitrogen in all species except S. acutus; the greatest increase was again in Nuphar and the least in S. subterminalis. Under these conditions, as in the 10°C anaerobic experiments, the overall net increases in percentage nitrogen followed temporary losses of nitrogen in the first two to ten days of incubation of Nuphar, Myriophyllum, and Najas. The Scirpus species attained minimal levels of nitrogen

only after a longer period of up to 50 days. These results indicate that the two species of bulrush lost less nitrogenous DOM by leaching than the other species which contained greater proportions of non-cell wall tissue.

Aerobic incubation at 25°C resulted in overall increases in nitrogen in both the Scirpus tissues similar to those of the more flaccid species during cold incubation. These less resistant species, however, showed very steep increases in percent nitrogen during the first 25 days of decomposition at 25°C, and then declines of particulate nitrogen. Thus, the C:N ratio continually decreased in S. subterminalis and S. acutus, but in Nuphar, Myriophyllum, Najas the ratio reached minimal levels at about day 25 and then increased. The proportions of nitrogen in the particulate detritus increased very rapidly to maximal levels within four to ten days in all species except S. acutus which increased continuously. Following these rapid increases, nitrogen levels remained constant or declined, and the resultant C:N ratios were stable once minimal values were reached.

The response of particulate nitrogen in litterbag samples incubated in summer behaved as for the 25°C aerobic flask samples: percentage nitrogen increased for the first 10 to 50 days and then declined in all species except S. acutus which showed an increase in the latter 150 days of decomposition. During fall-winter incubation, percentage nitrogen in all species usually increased to maximal values within the first 10 to 25 days and then decreased, but the changes in both Scirpus species were smaller than in the other plants. Percentage nitrogen values were generally higher for plant samples

incubated in eutrophic Wintergreen Lake than those in oligotrophic Lawrence Lake. This difference was attributed again to the greater microbial activity of Wintergreen Lake sediments at the incubation site. No apparent differences in response were found between the two Lawrence Lake incubation sites.

Dissolved Nitrogen

Without exception by any species, the proportion of nitrogen in the dissolved matter of the media decreased rapidly to very low levels during decomposition at 10°C (dissolved nitrogen data are in Appendix Figures 317-340). Under anaerobic conditions Myriophyllum, Nuphar, and S. acutus either showed slight increases or no change over initial concentrations after the first two days of decomposition, but in the other two species nitrogen began to decrease immediately. Anaerobically, the percentage dissolved nitrogen remained low in media of all species. Aeration caused levels of dissolved nitrogen in S. subterminalis and S. acutus flasks to be continually slightly higher than at 10°C and in Nuphar, Myriophyllum, and Najas the percentage nitrogen showed increases later in the incubation period although initial levels were never reached again. During anaerobic decomposition at 25°C, percentage dissolved nitrogen again decreased quickly and was maintained at constant levels which were lower than those of aerobic flasks at 10°C. Highest proportions of dissolved nitrogen were found in the 25°C aerated flasks. Flasks of both species of Scirpus had the greatest proportions of nitrogen in the dissolved matter, followed closely by Nuphar, Myriophyllum, and Najas

during anaerobic conditions. Aerobically, S. acutus had the most dissolved nitrogen, and again Najas the least.

Discussion

It might be expected that a negative relationship would have existed between dissolved and particulate forms of nitrogen based on leaching and microbially mediated conversions. The data however do not necessarily support such a conclusion. Increases in particulate nitrogen were not necessarily accompanied by decreases in dissolved nitrogen, and vice versa. These data are reported as percentages of the dry weights of the particulate and dissolved fractions rather than actual masses of nitrogen, and are not corrected for ash content. Values of percent nitrogen in the residue of the media could change drastically without changes in the actual content of dissolved nitrogen just by variations in the mass of other substances, particularly DOM. No attempt was made to convert these proportional data to absolute units. These data represent the net result of several processes occurring between sampling days and do not reflect the magnitude of total nitrogen flux among the many pools present (inorganic, organic, particulate, dissolved, gaseous). For example, values of particulate nitrogen rarely exceeded 100 percent of the amount present initially. That is, in almost all cases, peaks in percentage nitrogen of recovered particulate macrophyte tissue do not represent absolute increases in nitrogen content. This does not mean that particulate nitrogen was not added to the detrital material; it does indicate that there was a net removal of nitrogen from particulate form, even

when this removal was less than the net loss in weight, i.e. when percentage nitrogen was increasing. In other words, whole tissue often decomposed at a greater rate than the particulate nitrogen fractions of the tissue.

Many investigators have encountered increases of nitrogen in decaying plant tissue in soil decomposition studies (e.g. Tenney and Waksman, 1930; Sowden and Ivarson, 1959; Anderson, 1973), studies of decay of allochthonous plant tissue in streams and rivers (Kaushik and Hynes, 1968, 1971; Hynes and Kaushik, 1969; Mathews and Kowalczewski, 1969; Iversen, 1973, Triska et al., 1975), and aquatic macrophytes in lakes and marshes (Odum and de la Cruz, 1967; Boyd, 1970; de la Cruz and Gabriel, 1974; de la Cruz, 1975; Mason and Bryant, 1975; Hodkinson, 1975; Hunter, 1976). Consistent losses of nitrogen from decomposing plant tissue have been reported as well (e.g. Tenney and Waksman, 1930; Kaushik and Hynes, 1968; Harrison and Mann, 1975a, 1975b).

Nearly always the increase in nitrogen in the detritus is attributed to accumulation of protein in the form of microbial biomass. Kaushik and Hynes (1971), using anitbacterial and antifungal antibiotics in cultures of decomposing leaf tissue determined that nearly all of the protein increase that occurred was the result of fungal biomass and little was in the form of bacteria. However, there was an increase in total percentage nitrogen (protein plus other) even in the treatments receiving either antifungal or antibacterial antibiotic or both, indicating that there was another source of nitrogen partly responsible. Gosselink and Kirby (1974) calculated the

increase in mass of microorganisms associated with decomposing Spartina alterniflora based on probably invalid assumptions that nitrogen as percent of ash-free dry weight remained constant during decay in each of the microbial and plant fractions. Nevertheless, as Spartina lost weight over time the biomass of microorganisms, computed from particulate nitrogen data, increased, and respiratory measurements (i.e. oxygen consumption) correlated well with estimated microbial biomass values. de la Cruz and Gabriel (1974) also observed parallel increases in proportional nitrogen content and oxygen consumption in finely ground detrital tissue of Juncus decaying in the laboratory.

The assumption that observed increases in nitrogen content occur as microbial protein is often made without corroborative data, and there is evidence that associated microbial biomass may not account for all increases in detrital nitrogen during decomposition. Harrison and Mann (1975a) determined both total nitrogen and trichloroacetic acid-insoluble nitrogen. In dead, fallen Zostera marina leaves non-protein nitrogen accounted for over half of the total nitrogen. Green and living senescent leaves contained greater proportions of non-protein nitrogen.

Iversen (1973) studied the decomposition of beech leaves in a stream and found that in the first month of decomposition nitrogen (percent of AFDW), bacterial numbers, fungal and algal biomasses, and oxygen consumption all increased. By converting bacterial numbers and fungal volumes to units of mass he estimated the absolute amount of nitrogen in the microbial community associated with the leaf material, and it amounted to only 1 to 4 percent of the total leaf nitrogen.

Iversen suggested that the majority of the nitrogen increase was "released and deposited" by microorganisms. A similar conclusion was made by Suberkropp et al. (1976) who measured absolute and proportional increases over time in nitrogen content of the lignocellulose fraction of decomposing oak and hickory leaves. Since true lignin compounds theoretically contain no nitrogen, such increases in the presence of nitrogen in this fraction were attributed to complexing ("tanning") of microbial exoenzymes by phenolic compounds abundant in both the plant tissue and the surrounding water. Úlehlová (1971) discovered significant increases in C:N values of humic fractions of decomposing tissue of the macrophyte Stratiotes aloides. There is much biochemical evidence to justify the idea of such complexation of nitrogenous and polyphenolic-lignin compounds (e.g. Handley, 1954; Flaig, 1964; Feeny, 1969; Haslam, 1974; see review by Ladd and Butler, 1975).

Data of the present study can be interpreted as supporting the microbial biomass explanation of increasing nitrogen content. The consistent increase in the proportion of particulate nitrogen during anaerobic decomposition at 10°C paralleled accumulations of DOM and slow weight loss. Under conditions more conducive to decay the proportion of particulate nitrogen increased faster, particularly in the faster decomposing plant species. Particulate nitrogen decreased again at about the same time that weight loss rates began to decrease, implying a decline of microbial populations as the plant substrates became more resistant to microbial conversion.

It should be remembered that most described increases in nitrogen are actually increases in the proportion of nitrogen in residual substrate. This may be the result merely of differential decomposition rates where weight loss is due more to mineralization of non-nitrogenous constituents in the detritus (cf. Minderman, 1968). There are many cases of increases in absolute nitrogen content of detritus and these, as well as increases in the mass of the lignin-like fraction of POM, might be explained together by complexing of protein and phenolic compounds. Surely both microbial biomass and complexation account for increased predominance of nitrogen in the biomass of decomposing plant material.

It is important that future studies deal with both of these processes as they have very different implications in the ecosystem. If accumulated nitrogen occurs largely in the form of microbial protein it is indicative that conversion of both carbon and nitrogen are occurring via microbial catabolism of plant tissue. Further, the microbial protein associated with the detritus is usually considered a significant food source for aquatic detritivores. On the other hand, complexed enzymes represent a dead-end or at least a severe obstacle to complete mineralization of organic matter and a wasted expenditure of energy and nitrogen by decomposers.

A complicated relationship exists between the abundance and form of available nitrogen and decay rate of plant biomass. Waksman and Carey (1935b) discovered that the decomposition of glucose in seawater was controlled by the amount of nitrogen (added as ammonium sulfate) in the water, to a certain point where excess nitrogen no

longer accelerated decay. If more glucose was added at this point, both bacterial numbers and oxygen consumption increased. Addition of glucose without excess nitrogen did not increase microbial activity.

Hynes and Kaushik (1969) found that elm leaves, which gain nitrogen during decomposition (Kaushik and Hynes, 1968), showed increased weight loss when any form of nitrogen was added (i.e. nitrate, ammonia, or animal protein). More resistant leaves of oak and alder, which had decreasing nitrogen concentrations in the earlier study, required either more of the reduced form of nitrogen or higher temperatures in order to show faster weight loss. Greater concentrations of nitrogen in solution increased apparent protein associated with the elm leaves, but did not always do so for oak and alder leaves. Triska and Sedell (1976) fertilized replicate experimental streams with different levels of nitrate-nitrogen and observed no significant differences in decay rates or nitrogen accumulation of the leaves in the different streams. Addition of nutrients (nitrogen, phosphorus, potassium) to cultures of decomposing crop-plant tissues always accelerated weight loss (Waksman and Tenney, 1928). Many other examples exist in the literature of agricultural and woodland soil decomposition studies where plant species behave oppositely with respect to nitrogen gain or loss during decomposition.

It is generally agreed that the initial content of nitrogen of plant tissue itself has much to do with how fast it will be decomposed and that plant tissues with higher initial levels of nitrogen will be broken down faster. Polisini and Boyd (1972) determined that floating-leaved and submersed macrophytes had greater content

of nitrogen than emergent plants. Hodkinson (1975) observed that after a month of incubation an inverse correlation existed between the C:N values, which had stabilized by then, and the rates of decomposition of five species of plant tissue in a pond. Initial nitrogen content also influences whether nitrogen will be consumed or liberated in the decomposition process. Tissues with a low initial C:N release nitrogen on decomposition and tissues with high C:N ratios require nitrogen from a source other than the substrate (Waksman and Renn, 1936).

Parnas (1975) developed a mathematical model to describe decomposition of organic matter with special emphasis on nitrogen fluxes. The conclusions reached were that nitrogen is not needed and has no effect on the decay of materials already containing relatively high amounts of nitrogen (C:N less than critical value of 20 to 30), and that nitrogen will be released as a result of decomposition. Materials with initial values of C:N greater than the critical value will respond to outside additions of nitrogen with increased decay rates and decreasing C:N values during decomposition.

Based on the obviously complex and sometimes seemingly contradictory interactions of nitrogen and plant decomposition, the results of this study are best generalized as follows. The fastest decomposing plant, Nuphar, had the greatest initial concentration of nitrogen in its tissues, as seen in Table 5. Over all environmental conditions investigated, tissue weight loss rates were correlated with initial nitrogen content. Correspondingly, faster decomposing plants had lower C:N ratios. The nitrogen and carbon content of senescent

Table 5. Initial nitrogen and carbon content (as percent of total dry weight) and the C:N ratio of senescent macrophytes. (From Godshalk and Wetzel, 1977b.)

Species	Nitrogen	Carbon	C : N
Nuphar variegatum	2.4	39.3	16.6
Myriophyllum heterophyllum	2.0	24.7	12.2
Najas flexilis	1.8	31.2	17.8
Scirpus subterminalis	1.2	30.4	25.7
Scirpus acutus	1.5	43.6	29.9

macrophyte tissue, along with the C:N ratios, are listed in Table 5 by species in decreasing order of rate of weight loss.

All species showed increases in nitrogen during decay but the rates and magnitudes varied by species in the conditions necessary to promote the increases. Among flaccid, fast decomposing plants, proportional nitrogen concentrations increased even under cold, anaerobic conditions when no changes in the proportional nitrogen of the resistant bulrushes were observed. Warm aerated conditions were found to be necessary to promote nitrogen increases in the resistant Scirpus species, and these conditions were so conducive to rapid early decomposition of the softer species that in them particulate nitrogen rapidly increased and then declined. The decline must reflect die-back of microbial populations after the labile substrates in the plant tissue had been utilized.

In spite of the fact that all species used in these experiments had initial C:N values below or in the range of the "critical C:N" (= 20 to 30) of Parnas (1975), all species apparently utilized inorganic nitrogen available in dissolved form in the media during decomposition. Further, the species with the lowest initial C:N values maintained the highest levels of dissolved nitrogen, and the least resistant species showed the greatest loss of dissolved nitrogen. Aeration at either temperature caused higher dissolved nitrogen concentrations. This increase was probably the result of greater rates of mineralization of nitrogen during rapid weight loss and is in agreement with the generally declining levels of particulate nitrogen

and corresponding increases in particulate C:N ratios during decomposition at 25°C.

In summary, among the macrophytes studied, weight loss rates correlated with initial levels of nitrogen in the plant tissue. During rapid decay, the microflora utilized dissolved nitrogen and all tissues showed decreasing C:N values. However, once decay rates slowed, particulate C:N ratios again increased and often so did dissolved nitrogen. Dissolved nitrogen concentrations were probably never limiting to decomposition, and they changed according to environmental conditions and rates of tissue decay, not according to low tissue nitrogen content. All species showed similar trends over time in proportional concentrations of nitrogen in particulate and dissolved form. The temperature and oxygen conditions that were necessary for these trends to occur varied with species.

The Importance of Decomposition Rates

Decomposition is the antagonist to production in ecosystems. Both processes are continually occurring, and the balance between them influences the eventual fate of the ecosystem. Knowledge of the controls of decomposition and of comparative rates will compliment the substantial information that exists on production, providing better understanding of the metabolism of ecosystems.

As explained previously, many mathematical approaches have been taken toward explaining rates of decomposition of natural material, mostly plant tissue, in the environment. Most often the simple exponential is used, probably because it is easy to use and adequately fits many observed data; there usually is no biological

justification given for its application. Saunders (1972, 1976) has provided a conceptual model which results in an exponential function when converted to mathematical form. His and two other meaningful functions explaining decay rates are compared in Table 6.

The essence of Saunders' model (Table 6 [1]) is that weight loss of the substrate over time is a function of the amount of substrate present, the concentration of enzymes capable of degrading the substrate, and a constant coefficient accounting for environmental constraints on decay rate. On a short term basis, necessary enzymes may be limiting, causing a lag in decomposition of specific compounds until enzyme concentrations increase sufficiently. But, in the entire lake on a seasonal basis the microbes necessary for degradation are present and can increase in a relatively short time to levels promoting decay of the newly available substrates. As Saunders points out, enzyme concentration may be assumed to be constant and is included in the decay coefficient. An exponential function results upon integration.

A flaw in this model is that the decay coefficient cannot be considered constant. Because tissues are heterogeneous mixtures of interacting components, various fractions of the whole substrate are converted at different rates. Even under constant environmental conditions (usually obtained only in the laboratory) decay rates will be greater in early stages when labile components are being metabolized and will be lessened as more resistant fractions of the tissue become more concentrated in the residue. It was based on this observation that an exponential function utilizing an exponentially

Table 6. Summary of conceptual models used to explain rates of natural decomposition of biological tissues, modified slightly from original forms for comparative purposes.

Model*	Reference
[1] $\frac{dW}{dt} = -cWE$	Saunders, 1971
[2] $\frac{dW}{dt} = -a(e^{-bt})W$	Present study
[3] $\frac{dW}{dt} = \sum_{i=1}^{n} -k_i w_i$	Bunnell et al., 1977, after Minderman, 1968

* W = proportion of whole tissue remaining
t = time
E = effective absolute enzyme concentration
w_i = proportion of tissue component i remaining
k_i = decay constant of tissue component i
n^i = number of components in whole tissue
a, b, c = decay constants

decreasing decay coefficient was used to describe weight losses in the present study (see earlier discussion of weight loss, Figure 6, Table 6 [2]).

The idea of exponentially decreasing decay rates, developed independently in this work, incorporates many of the conclusions of Minderman (1968). In addition, such a model accounts for interactions of individual components, for example, complexation of protein and lignin fractions, in retarding decomposition. The problem with this model involves its further development. The constants a and b each represent such a multitude of both environmental and tissue-specific variables that mathematical elaboration of these factors will very quickly make the model too unwieldy to be practical.

For this reason, the model of Minderman (1968), as furthered by Bunnell et al. (1977) (Table 6 [3]), though too oversimplified to be acceptable conceptually, is of greatest potential use in decomposition studies. Only as biological information is obtained can realistic decay coefficients, whether they are constants or functions of several variables, be determined and assembled together to make a model which is truly descriptive, and predictive, of the complex processes of natural decomposition.

CONCLUSIONS*

Fates of Decomposing Organic Matter

From the preceding discussions it is apparent that the products of decomposition form a continuum of chemical substances from high molecular weight stable ring structures to short-chain fatty acids to carbon dioxide and other gases. As heterogeneous substrates such as vascular plant tissue decompose, the several individual constituents are differentially subject to microbial attack. Basically, there are four alternative, or sequential, fates for decomposing macrophytic tissue: (a) Complete and efficient decomposition of organic materials to carbon dioxide and water would cause little or no particulate material to remain, and there would not be a large concentration of dissolved organic matter in the media. Less complete decay would involve a smaller loss of particulate plant material and production and accumulation of dissolved organic matter, with relatively small amounts of the dissolved organic compounds being oxidized. This pool of dissolved organic matter can be subdivided into (b) relatively refractory high molecular weight compounds and (c) relatively labile low molecular weight compounds. Solubility of substrate is crucial for its decomposition. The majority of heterotrophic

*Much of the following text is taken from manuscripts currently in press (Godshalk and Wetzel, 1977a, 1977b).

utilization of organic matter involves uptake of dissolved materials. The substrate can either be dissolved in water or solubilized enzymatically. Vallentyne (1962) has discussed the solubility aspect of decomposition from a biogeochemical point of view. (d) The final possible fate of plant material in lakes is to remain largely undecomposed; some or nearly all of the plant tissue, depending upon the species and its morphology, may not be converted significantly to any other form and is permanently interred in the sediments.

The composite results of this study are summarized in Figure 8. A temperature of 18°C is equidistant between the experimental temperatures of 10°C and 25°C used in the laboratory experiments and therefore is an arbitrary separation of relatively cold and warm conditions. The influence of temperature and oxygen conditions on rates and completeness of degradation are elaborated for the four general fates of organic matter: complete decomposition to carbon dioxide, conversion to refractory or labile DOM, or sedimentation of particulate matter in relatively unaltered form. The lengths of the vectors denote the relative importance of the respective fates under the four general conditions of decomposition. Large amounts of plant tissue are expected to stay in particulate form as a result of cold or anaerobic decomposition. Refractory DOM is produced especially under anaerobic conditions. The most conspicuous features of the results are the direct proportionalities of (a) decomposition of POM to DOM with temperature, and (b) decomposition of DOM to carbon dioxide with oxygen concentration. While both of these findings were anticipated from general knowledge of controls of decomposition of

Figure 8. Relative importance, with respect to rates and total accumulation, of the four possible fates of macrophytic tissue observed during decomposition under various conditions of temperature and oxygen concentration. See text for further explanation. (From Godshalk and Wetzel, 1977a.)

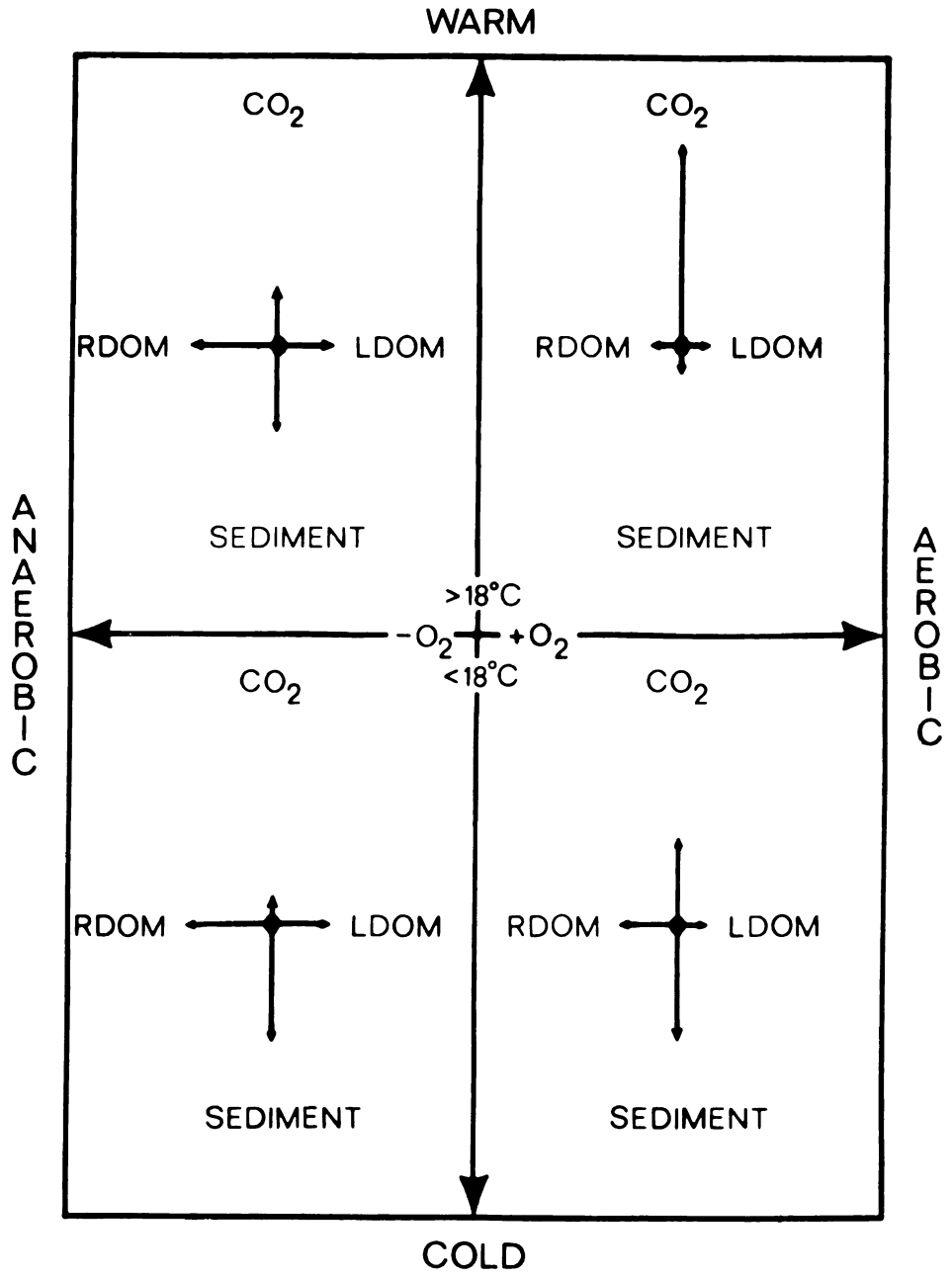
WARM
CO_2
CO_2
RDOM
LDOM
RDOM
LDOM
SEDIMENT
SEDIMENT
ANAEROBIC
AEROBIC
>18°C
$-O_2$
$+O_2$
<18°C
CO_2
CO_2
RDOM
LDOM
RDOM
LDOM
SEDIMENT
SEDIMENT
COLD

Figure 8

organic matter, they have not been evaluated previously for aquatic angiosperms.

Decomposition in Lakes

Temperature and Oxygen in Lakes

The seasonal behavior of oxygen concentrations and temperature with depth in lakes of various productivities is discussed in detail by Wetzel (1975:126). Temperature and oxygen concentrations at two depths in the pelagial zone of Lawrence Lake (maximum depth 12.5 m) for the year 1975 are diagrammed in Figure 9. Data for the 12 m depth are indicative of environmental conditions at the pelagial sediment-water interface; temperatures at 3 m just above the sediments in the littoral zone were quite close to those measured biweekly in the pelagial zone, but littoral oxygen at this depth was probably less than pelagial concentrations in winter and greater than pelagial concentrations in summer (daylight) conditions (cf. Wetzel, 1975:134).

Warm aerobic conditions exist for extended periods of time in temperate lakes only in the pelagial zone during summer. At other locations in the lake where temperatures are relatively high but where water is not subject to continual mixing, absolute oxygen concentrations, already limited somewhat by lowered solubility at higher temperatures, are likely to be rapidly depleted. Among dense stands of plants in the littoral zone, oxygen consumption, particularly at night, is very high and because of the impeding effect of the plants to water circulation, there is little influx of oxygenated water to these areas. Thus, once initial littoral oxygen supplies are consumed,

Figure 9. Distribution of temperature and oxygen at depths of 3 and 12 m in the pelagial zone of Lawrence Lake, 1975. Hatching on upper abcissa denotes period of ice cover; hatching on center abcissa indicates periods of isothermal conditions during spring and fall turnover. See text for further explanation.

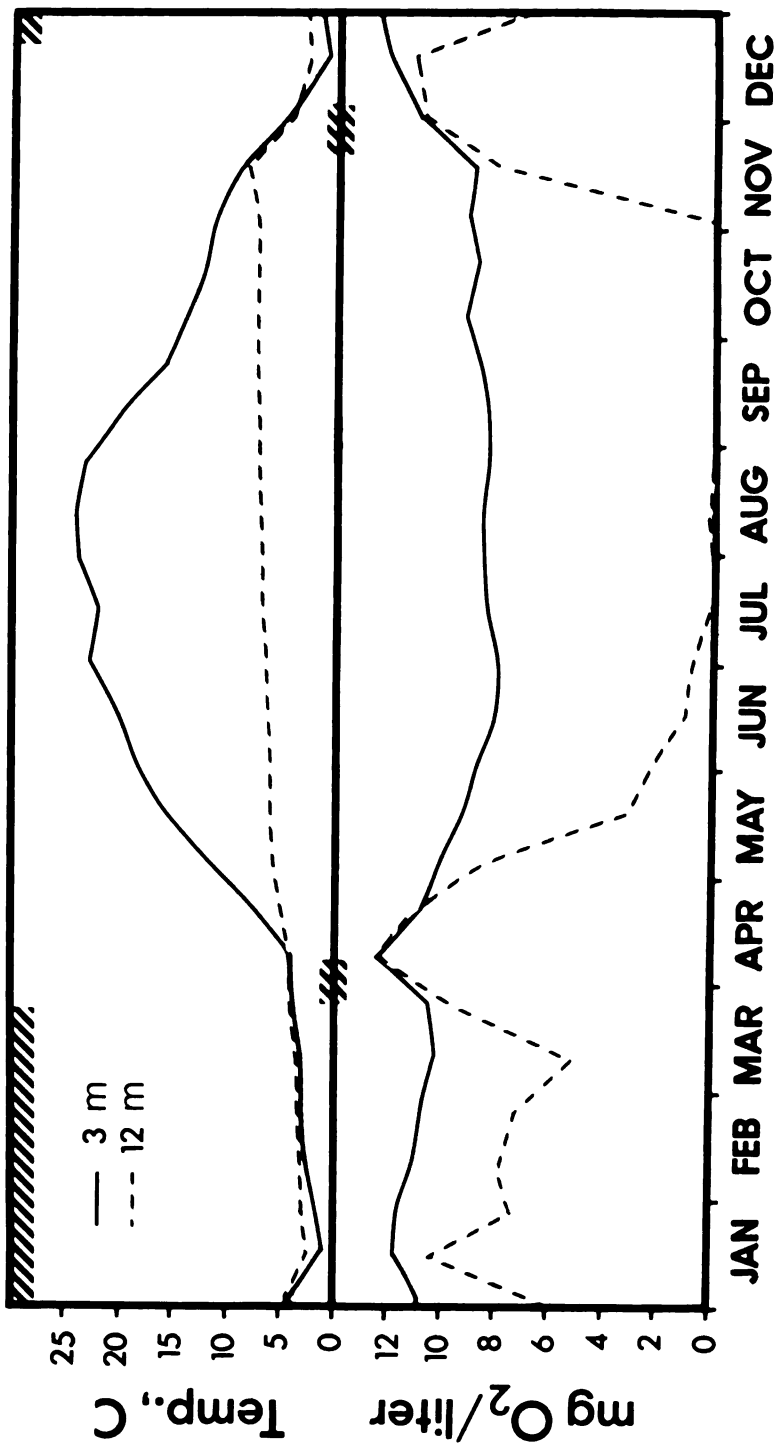
Temp., C
25
20
15
10
5
0
3 m
12 m
mg O2/liter
12
10
8
6
4
2
0
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC

Figure 9

further input of this important oxidant is limited to that produced locally by photosynthesis until the next severe mixing of the epilimnion. Little is known of the relative redox conditions of littoral waters and sediments in the microzones close to the sediment-water interface or of the effects of seasons, wind, plant density, and photosynthetic activity on littoral oxygen conditions. It is suspected that, except in the pelagial zone, warm aerobic decomposition occurs only minimally in temperate lakes, and the faster decomposition initially proceeds under these conditions the sooner oxygen will become limited and anaerobic decay processes will be established.

Annual Cycle of Decomposition

All combinations of temperature and oxygen simulated in the laboratory experiments of this study are found during one year in the different zones of this typical temperate, dimictic, mesotrophic lake. Decomposition of macrophytic tissue is proceeding under one or more of these situations at all times. How these conditions occur seasonally in a lake like Lawrence Lake, are depicted in Figure 10a-10f, along with some important aspects of carbon metabolism in the ecosystem.

In late summer and early fall (Figure 10a), the growing season for most annual macrophytes ends, and the plants begin to senesce. The actual beginning of decomposition is difficult to define, but certainly some plant parts remain viable while other parts begin to lose their integrity, lose dissolved organic matter (Otsuki and Wetzel, 1974), and begin to be colonized by microflora. If the plants collapse to the sediment-water interface when the water of the littoral zone has not yet greatly cooled and contains high dissolved oxygen

Figure 10. General diagrammatic representation of seasonal conditions of carbon metabolism of particulate and dissolved organic carbon of macrophytic origin in a typical temperate, dimictic lake of intermediate productivity. See text for explanation. (From Godshalk and Wetzel, 1977a.)

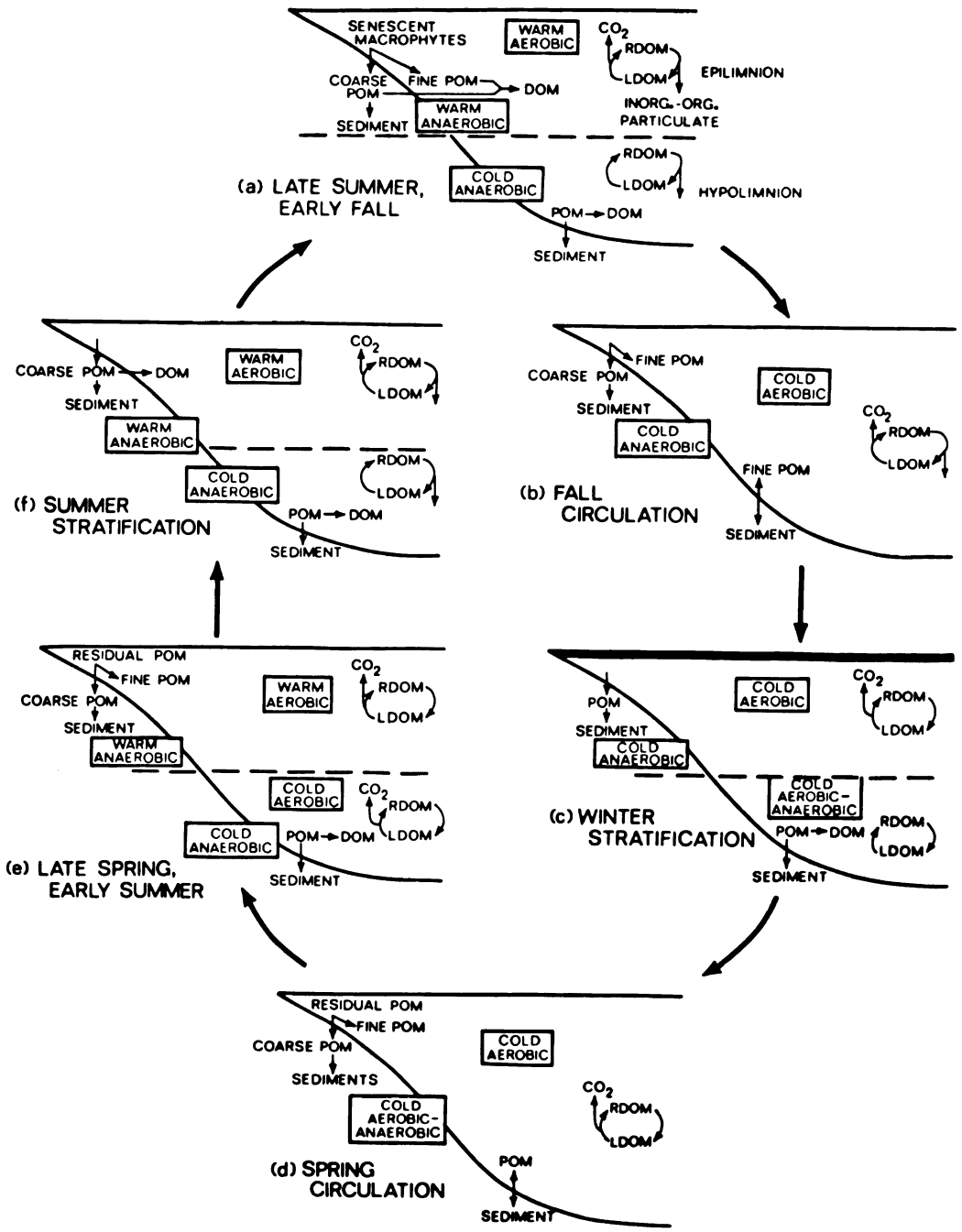
SENESCENT MACROPHYTES
WARM AEROBIC
CO_2
RDOM
LDOM
EPILIMNION
COARSE POM
FINE POM
DOM
INORG.-ORG. PARTICULATE
SEDIMENT
WARM ANAEROBIC
(a) LATE SUMMER, EARLY FALL
COLD ANAEROBIC
HYPOLIMNION
POM→DOM
SEDIMENT
(b) FALL CIRCULATION
COLD AEROBIC
(c) WINTER STRATIFICATION
COLD AEROBIC-ANAEROBIC
(d) SPRING CIRCULATION
RESIDUAL POM
SEDIMENTS
(e) LATE SPRING, EARLY SUMMER
(f) SUMMER STRATIFICATION

Figure 10

concentrations, decomposition will result in the rapid conversion of POM to DOM and of DOM to carbon dioxide. However, in most small temperate lakes the temperature of the water will already be significantly lowered at this time and, from the results of this study, slow degradation of macrophytic POM can be predicted. Boylen and Brock (1973) studied decomposition processes in lake sediments during winter and observed much reduced glucose uptake rates; the same bacteria isolated at 4°C grew better when the incubation temperature was raised to 25°C.

Meanwhile, in the colder hypolimnion of the lake, which commonly has, at least to some degree, become anoxic from decomposition of organic materials associated with the bottom sediments, an accumulation of DOM has been taking place. Data from deep-water samples of Lawrence Lake at this time of the year show an increase in absorbance of ultraviolet light and in fluorescence activity, implying an accumulation of refractory dissolved organic compounds of plant origin. Lack of oxygen in the hypolimnetic waters prevents rapid conversion of this DOM to carbon dioxide. It has been shown that DOM from ocean surface waters is relatively easily decomposed, but that from greater depths is quite resistant (Barber, 1968). The age of some resistant deep ocean DOM has been estimated by carbon dating to be 3400 years (Williams et al., 1969).

At fall turnover (Figure 10b), mixing of the total lake volume accomplishes two things. First, the entire water body is aerated. which allows the DOM that had been accumulating as a result of anaerobic decomposition to be further oxidized to carbon dioxide and

water. Second, recently sedimented POM is resuspended. Particles that had previously been confined to the anaerobic conditions of the sediment-water interface are brought into contact with oxygenated water. While decomposition is slow because of low water temperatures, further conversion of POM to carbon dioxide is made possible.

During the cold winter stratification (Figure 10c), decomposition continues both in the water and at the sediments of all depths. Depending on the types and amounts of organic matter present at the sediment-water interface, and the degree of oxygenation accomplished by fall circulation, the sediment surface often rapidly becomes anoxic at increasing water depths. Most POM lies at the sediment surface without being appreciably degraded; what decomposition does occur results in the production of DOM with further conversion to carbon dioxide being dependent on available dissolved oxygen. Dissolved compounds that are produced at the sediment-water interface can escape that stratum by diffusion or in water currents and become part of the pool of potential substrates for many aquatic organisms (Sepers, 1977).

Spring turnover (Figure 10d) causes aeration of the water mass and resuspension of fine POM from the sediments again. At this time of the year the water is constantly warming and consequently, as long as dissolved oxygen is present, microbial conversion of the DOM which accumulated over winter and of the POM brought up from the sediments will be accelerated and be more complete than under winter conditions.

As the epilimnetic waters and littoral sediments begin to warm, more of the heavier, coarser, non-resuspended material may be degraded (Figure 10e). As the rates of decomposition increase because of higher temperatures, oxygen demand increases. By midsummer (Figure 10f), littoral sediments are commonly anaerobic, and complete oxidation of organic matter is greatly reduced. DOM is continually generated from macrophytic detritus at these warmer temperatures, and as it diffuses or is flushed to oxygenated waters of the pelagial zone a greater conversion to carbon dioxide can result. The hypolimnion is in large part sealed off physically from oxygen renewal and becomes increasingly anaerobic, allowing an accumulation of DOM that is being degraded at rates less than those of inputs.

Effects of the Decomposition Cycle

The implications of the variety of conditions under which decomposition occurs in a lake are great. Influxes of readily metabolizable carbon into the system can be largely decomposed in the fall when many macrophytes senesce in the littoral zone, but lower water temperatures in autumn prevent rapid conversion of particulate organic materials to dissolved forms. Constantly low temperatures at the sediment-water interface where particulate matter comes to rest cause this material to be metabolized gradually. Periodic oxygenation of the entire lake allows accumulated labile and, more importantly, refractory dissolved organic matter produced at the sediment-water interface to be converted to carbon dioxide. Resistance to decomposition by refractory compounds displaces carbon metabolism in time.

The effect of seasonal mixing is to bring fine particulate material out of conditions of incomplete decomposition for further degradation while suspended periodically in oxic waters. Vallentyne (1962) points out that the influence of gravity "selects" for eventual decomposition of dissolved and particulate materials which are less dense than water by keeping them in or on top of the water column. As long as less dense POM remains suspended it has the potential of being dissolved and therefore the possibility of being acted upon as a microbial substrate. More dense particles eventually sink to the sediments where the liklihood of permanent preservation is higher because of colder and less oxygenated conditions. Many studies have demonstrated the importance of particle size to decomposition. In most cases decomposition of smaller particles is faster than that of larger particles. As particle size decreases, rate of weight loss, oxygen consumption, and numbers of microbes per unit weight of detritus all increase (Odum and de la Cruz, 1967; Fenchel, 1970; Gosselink and Kirby, 1974; Hargrave, 1972).

During the course of decomposition of macrophyte tissue to DOM and/or carbon dioxide, the size of the macrophyte fragments will decrease. As particle size decreases, the surface area:volume ratio increases, providing greater area for microbial attack. At the same time, as the more labile constituents of the particles are utilized, the residual material becomes proportionately more resistant to further decay. These two processes have opposite effects on overall decomposition rates. In addition, the production of large amounts of fine particles may affect subsequent decomposition rates as the fine

particles will compact more densely, thus limiting diffusion of oxygen and waste products and thereby causing more severe reducing conditions (cf. Acharya, 1935). Coarse, heavy particles are not resuspended and are not removed from the littoral zone where they are more effectively decomposed under warmer and more frequently oxygenated conditions. This provides that only the most refractory particulate organic materials will be permanently buried in the sediments of the basin. The extent of transport of particulate material of littoral origin to other regions of a lake is unknown.

Thus, the metabolism of the large amounts of carbon that become available as senescent macrophytic tissue in the fall is delayed by intermittent decomposition of POM to DOM, and the conversion of this DOM to carbon dioxide is further buffered through time. Pulsed decomposition provides stable levels of continual carbon metabolism.

Response of Decomposition to Eutrophication

The most common perturbation to natural lacustrine ecosystems is eutrophication, the acceleration of nutrient input. The response of major groups of primary producers in lakes of increased fertility is explained in detail elsewhere (Wetzel and Hough, 1973; Wetzel, 1975:416). Present data on decay of plant tissue allow general predictions to be made regarding the response of decomposition in such systems to increased inputs of detrital carbon.

Increased bacterial activity in response to higher concentrations of substrates can be expected immediately. In a comparison of

seven lakes of varying trophic state, Godlewska-Lipowa (1975) found increased bacterial numbers, biomass, and oxygen consumption in more eutrophic lakes. The oxygen consumption of lake water samples to which additional organic substrates were added, compared to controls without added substrate, was greater in samples from more eutrophic lakes, an indication of higher gross decomposition rates. However, this relationship does not mean that increased respiration will balance the increased photosynthesis. The amount of material that sediments to the bottom of the lake and becomes less likely to be decomposed increases as the amount of carbon available for decomposition increases and as mean lake depth, or mixed-layer depth, decreases (Ohle, 1956; Hargrave, 1975). Hence, as primary production increases, absolute rates of decomposition also will increase, but efficiency of decomposition (i.e. decomposition/production) will decrease and accumulation of organic matter will be accelerated.

Increased loading of sediments generally will increase the rate at which reducing redox conditions are establsihed, and the effect that this has on regeneration of nutrients has already been mentioned. Mixed-layer depth is important in this regard also and Oláh (1975) has described the function of the metalimnion in isolating sources of nutrients, particularly phosphorus, from oxidation-induced chemical precipitation and promoting "self-accelerated eutrophication."

The presence of organic carbon in the sediments does not necessarily imply strong reducing conditions or high oxygen consumption. The quality of that carbon, i.e. whether it is susceptible or resistant to microbial degradation controls the demand for oxidants.

In deeper oligotrophic systems (oceans, huge lakes) sedimented carbon is predominantly resistant and reducing conditions are weak, but in shallower, more productive systems (coastal waters, eutrophic lakes) more labile carbon reaches the sediments and oxidation demands are greater (cf. Rybak, 1969; Pamatmat, 1973; Bordovskiy, 1974).

Sedimentation of undecomposed biological material in lakes has long term effects on the filling of the basin. As emergent macrophytes dominate primary production in increasingly eutrophic situations, there will be a corresponding increased loading of the littoral sediments with greater amounts of tissue. Also, the tissue from these rigid, erect plants which contain greater amounts of structural tissue will be more resistant. Accumulating organic matter may cause filling of the basin by encroachment of the littoral zone toward the center of the lake. How fast this process occurs depends on the morphometry of the basin and where sediments accumulate most rapidly (Lehman, 1975). Comparison of sediment characteristics at different depths in shallow ponds has demonstrated that inorganic, and presumably organic, average particle size decreases at greater depths, probably as a result of the sieving effect of resuspension and subsequent settling of fine-grained materials (Boyd, 1976). This finding lends support to the idea of coarser, bulkier pieces of macrophyte tissue remaining in the littoral. Increased littoral zone productivity in a hypereutrophic situation has been implicated as a cause for the very rapid extinction of the lake (Manny et al., 1977).

SUMMARY

The decomposition of aquatic macrophytes of the littoral zone is an important part of the total metabolism of carbon in a lake, especially in small lakes where littoral production is of similar or greater magnitude than pelagial planktonic production.

Temperature and oxygen concentration are two environmental parameters that were found to strongly influence aspects of decomposition. Temperature primarily affected the rate of conversion of particulate tissue to dissolved organic matter. If oxygen was present, the dissolved detrital carbon was metabolized to carbon dioxide and water, but DOM accumulated, at least initially, under anaerobic conditions.

The floating-leaved plant decomposed faster than submersed plants, which decomposed faster than the emergent plant. Decay rates were related to initial tissue nitrogen and fiber contents, with high-nitrogen, low-fiber plants decomposing more rapidly than plants with low initial nitrogen and high fiber. Under environmental conditions more conducive to decomposition (i.e. warmer and more oxygen), resistance to decay was at least partially overcome. Hence, all species showed similar trends in decomposition, but the species were different in the conditions of temperature and oxygen that were required to promote those trends.

One class of products of decomposition is resistant organic compounds. These compounds are derived mostly from phenolic and lignin plant constituents. One of their roles in the aquatic ecosystem is as carbon substrates which are not readily assimilable by bacteria. The delayed metabolism of these energy sources represents a buffering of the input of detrital organic matter to the lake ecosystem. The variations in oxygen and temperature in various zones of a temperate dimictic lake during an annual cycle provide for pulsed decomposition, and, therefore, further contribute to stable rates of metabolism of organic carbon from aquatic macrophytes of the littoral zone.

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APPENDIX

APPENDIX

Graphs of Parameters of Decomposition of Macrophytes

Graphs are numbered consecutively from 1 through 340 and are arranged in groups according to data type. To locate a specific graph, first find the listing of the parameter of interest in the Guide to Appendix Tables on the following page, and then go to the indicated index. All Appendix Figure numbers of the selected parameter are listed in tabular form, plant species against experimental condition, in each index. Specific figures in the pages following the indices are referenced by the tabulated Appendix Figure numbers.

GUIDE TO APPENDIX TABLES

Parameter	Table	Page
ATP	H	137
Carbohydrates (TNC), percent of initial content	F	135
Carbohydrates (TNC), percent of recovered weight	G	136
Carbon, dissolved organic (DOC)	B	131
Carbon:nitrogen ratio, dissolved	J	139
Carbon:nitrogen ratio, particulate	I	138
Carbon, total dissolved	J	139
Carbon, total particulate	I	138
Cellulose, percent of initial content	F	135
Cellulose, percent of recovered weight	G	136
E_h (Redox potential)	A	130
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Lignin, percent of initial content	F	135
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Appendix Table A. Index of Appendix Figure Numbers.

pH and Eh (redox potential) of media.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	1	2	3	4	5
Anaerobic, 10 C		6		7	
Aerobic, 10 C	8	9	10	11	12
Aerobic-to-anaerobic, 25 C	13	14	15	16	17
Anaerobic, 25 C		18		19	
Aerobic, 25 C	20	21	22	23	24

Appendix Table B. Index of Appendix Figure Numbers.

DOC in various molecular weight fractions of DOM.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	25	26	27	28	29
Anaerobic, 10 C		30		31	
Aerobic, 10 C	32	33	34	35	36
Aerobic-to-anaerobic, 25 C	37	38	39	40	41
Anaerobic, 25 C		42		43	
Aerobic, 25 C	44	45	46	47	48

Appendix Table C. Index of Appendix Figure Numbers.

UV absorbance by various molecular weight fractions of DOM.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	49	50	51	52	53
Anaerobic, 10 C		54		55	
Aerobic, 10 C	56	57	58	59	60
Aerobic-to-anaerobic, 25 C	61	62	63	64	65
Anaerobic, 25 C		66		67	
Aerobic, 25 C	68	69	70	71	72

Appendix Table D. Index of Appendix Figure Numbers.

Fluorescence activity by various molecular weight fractions of DOM.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar varicgatum
Aerobic-to-anaerobic, 10 C	73	74	75	76	77
Anaerobic, 10 C		78		79	
Aerobic, 10 C	80	81	82	83	84
Aerobic-to-anaerobic, 25 C	85	86	87	88	89
Anaerobic, 25 C		90		91	
Aerobic, 25 C	92	93	94	95	96

Appendix Table E. Index of Appendix Figure Numbers.

Percent of initial AFDW remaining and decay coefficients.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	97	98	99	100	101
Anaerobic, 10 C		102		103	
Aerobic, 10 C	104	105	106	107	108
Aerobic-to-anaerobic, 25 C	109	110	111	112	113
Anaerobic, 25 C		114		115	
Aerobic, 25 C	116	117	118	119	120
Lawrence L. littoral, summer	121	122	123	124	125
Lawrence L. littoral, winter	126	127	128	129	130
Lawrence L. pelagial, winter	131	132	133	134	135
Wintergreen L. littoral, winter	136	137	138	139	140

Appendix Table F. Index of Appendix Figure Numbers.

Percent of initial content of carbohydrates and fiber components.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	141	142	143	144	145
Anaerobic, 10 C		146		147	
Aerobic, 10 C	148	149	150	151	152
Aerobic-to-anaerobic, 25 C	153	154	155	156	157
Anaerobic, 25 C		158		159	
Aerobic, 25 C	160	161	162	163	164
Lawrence L. littoral, summer	165	166	167	168	169
Lawrence L. littoral, winter	170	171	172	173	174
Lawrence L. pelagial, winter	175	176	177	178	179
Wintergreen L. littoral, winter	180	181	182	183	184

Appendix Table C. Index of Appendix Figure Numbers.

Percent of carbohydrates and fiber components of recovered tissue weight.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	185	186	187	188	189
Anaerobic, 10 C		190		191	
Aerobic, 10 C	192	193	194	195	196
Aerobic-to-anaerobic, 25 C	197	198	199	200	201
Anaerobic, 25 C		202		203	
Aerobic, 25 C	204	205	206	207	208
Lawrence L. littoral, summer	209	210	211	212	213
Lawrence L. littoral, winter	214	215	216	217	218
Lawrence L. pelagial, winter	219	220	221	222	223
Wintergreen L. littoral, winter	224	225	226	227	228

Appendix Table H. Index of Appendix Figure Numbers.

ATP content and ETS activity of plant tissue.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	229	230	231	232	233
Anaerobic, 10 C		234		235	
Aerobic, 10 C	236	237	238	239	240
Aerobic-to-anaerobic, 25 C	241	242	243	244	245
Anaerobic, 25 C		246		247	
Aerobic, 25 C	248	249	250	251	252
Lawrence L. littoral, summer	253	254	255	256	257
Lawrence L. littoral, winter	258	259	260	261	262
Lawrence L. pelagial, winter	263	264	265	266	267
Wintergreen L. littoral, winter	268	269	270	271	272

Appendix Table I. Index of Appendix Figure Numbers.

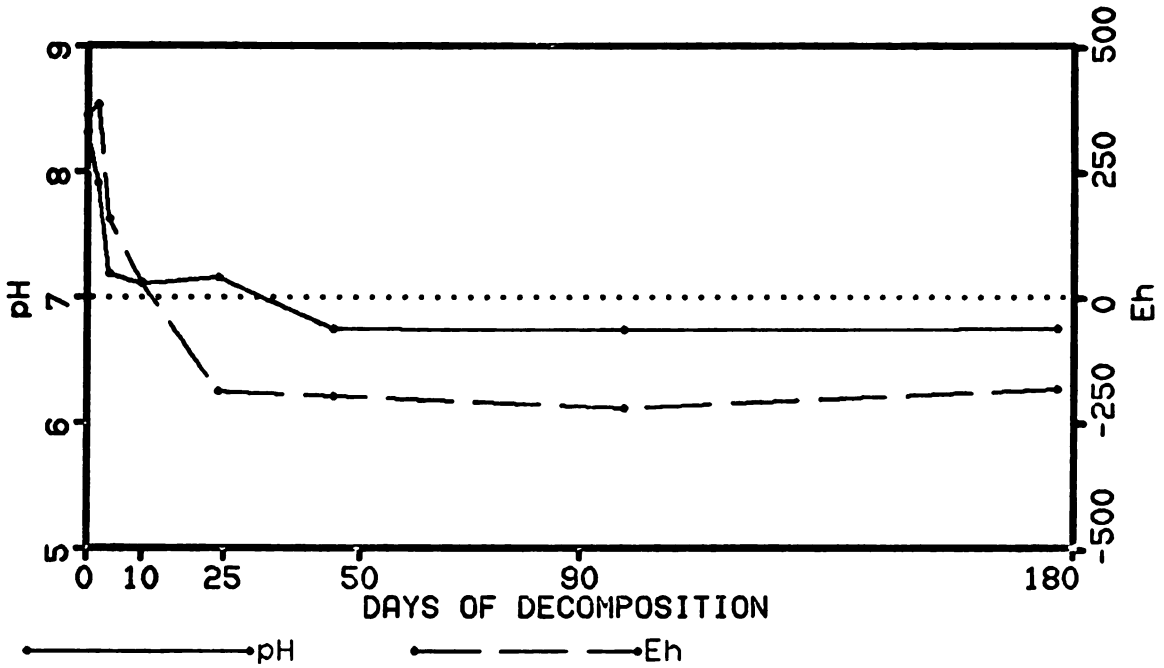
Percent carbon and nitrogen and C:N ratio of plant tissue.

EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	273	274	275	276	277
Anaerobic, 10 C		278		279	
Aerobic, 10 C	280	281	282	283	284
Aerobic-to-anaerobic, 25 C	285	286	287	288	289
Anaerobic, 25 C		290		291	
Aerobic, 25 C	292	293	294	295	296
Lawrence L. littoral, summer	297	298	299	300	301
Lawrence L. littoral, winter	302	303	304	305	306
Lawrence L. pelagial, winter	307	308	309	310	311
Wintergreen L. littoral, winter	312	313	314	315	316

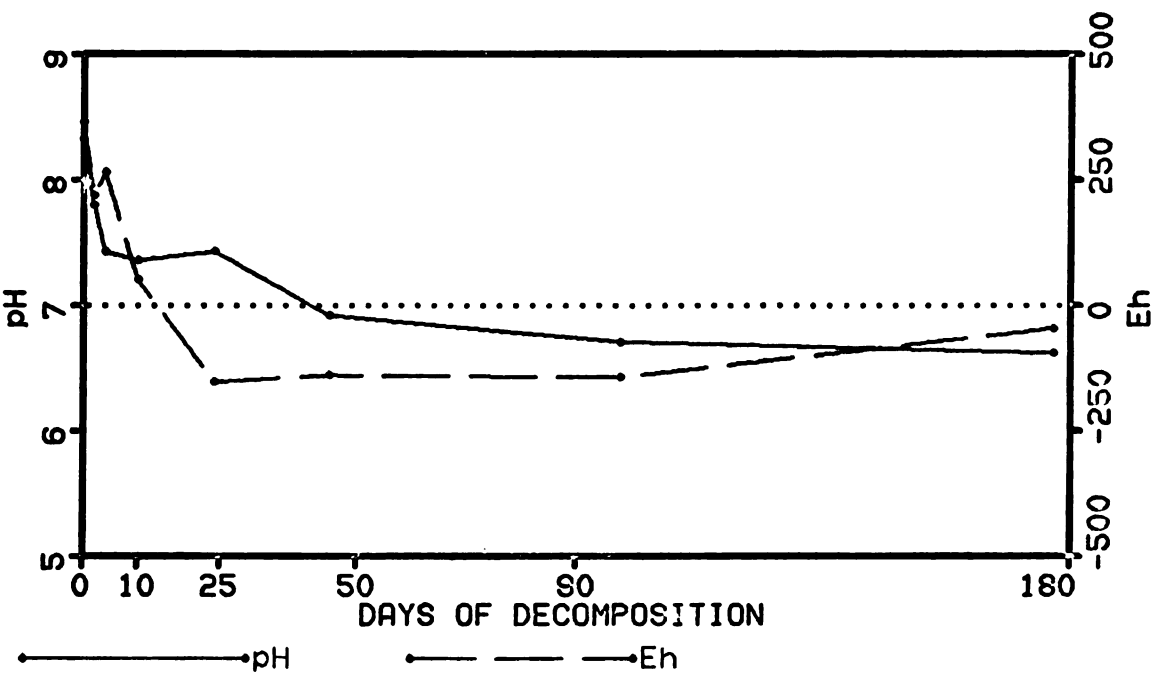
Appendix Table J. Index of Appendix Figure Numbers.

Percent carbon and nitrogen and C:N ratio of media.

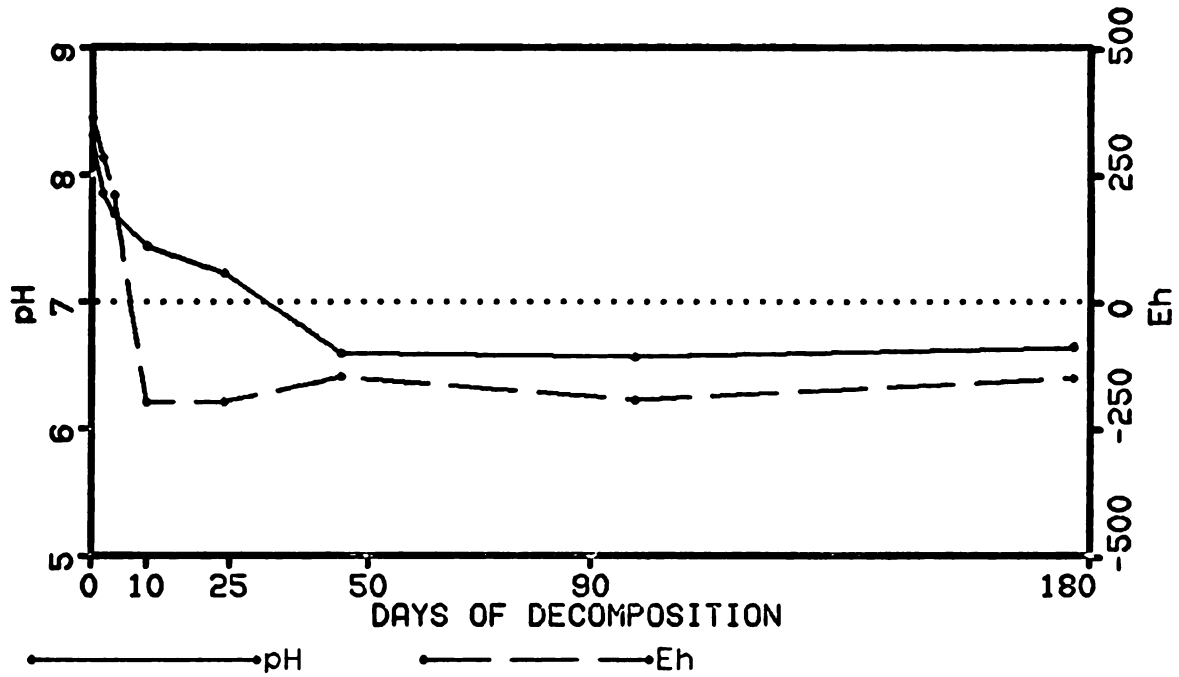
EXPERIMENTAL CONDITIONS	Scirpus acutus	Scirpus subterminalis	Najas flexilis	Myriophyllum heterophyllum	Nuphar variegatum
Aerobic-to-anaerobic, 10 C	317	318	319	320	321
Anaerobic, 10 C		322		323	
Aerobic, 10 C	324	325	326	327	328
Aerobic-to-anaerobic, 25 C	329	330	331	332	333
Anaerobic, 25 C		334		335	
Aerobic, 25 C	336	337	338	339	340



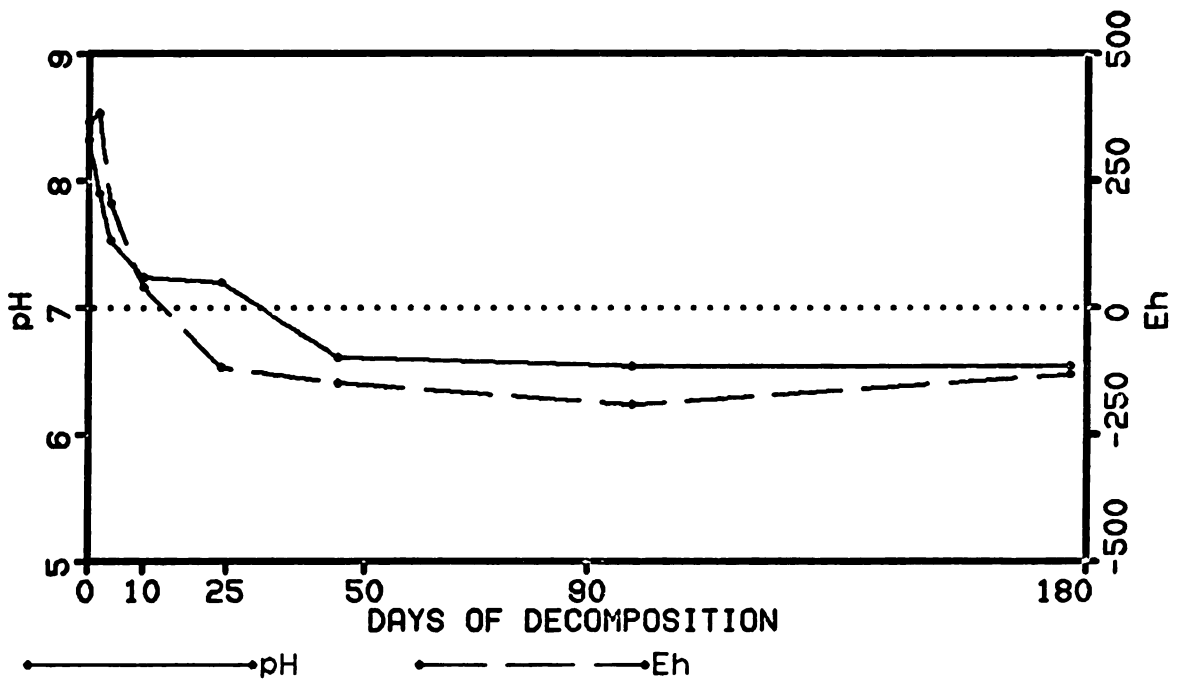
Appendix Figure 1. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. pH and Eh (millivolts) of media.



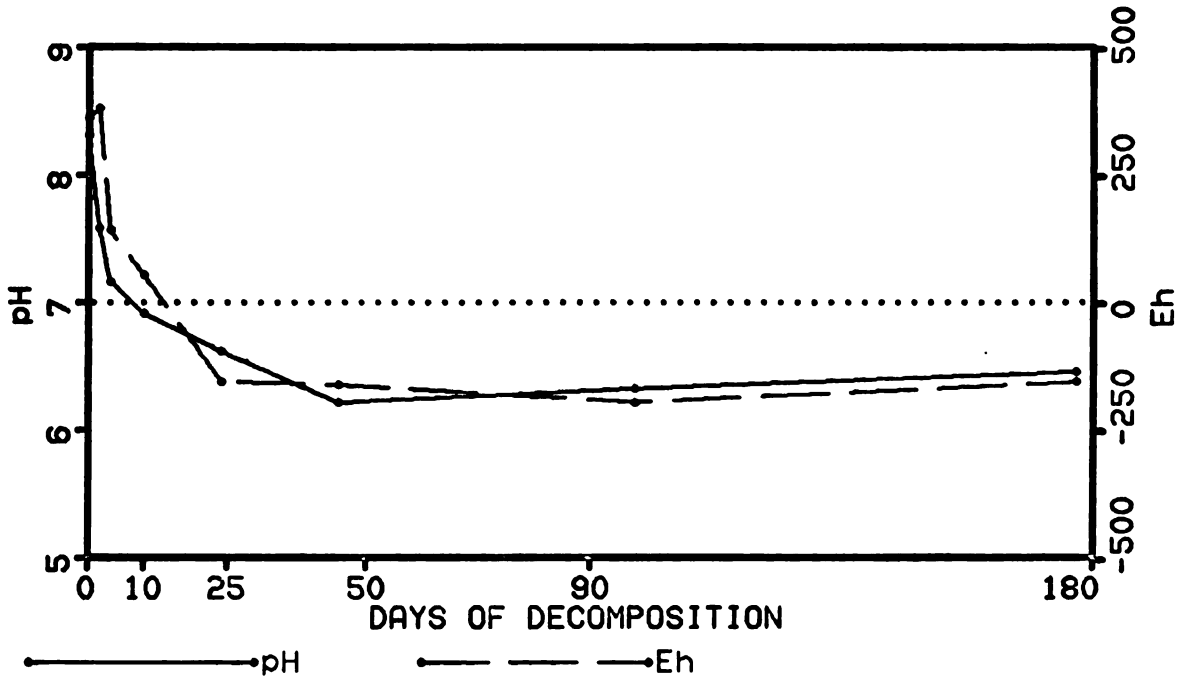
Appendix Figure 2. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. pH and Eh (millivolts) of media.



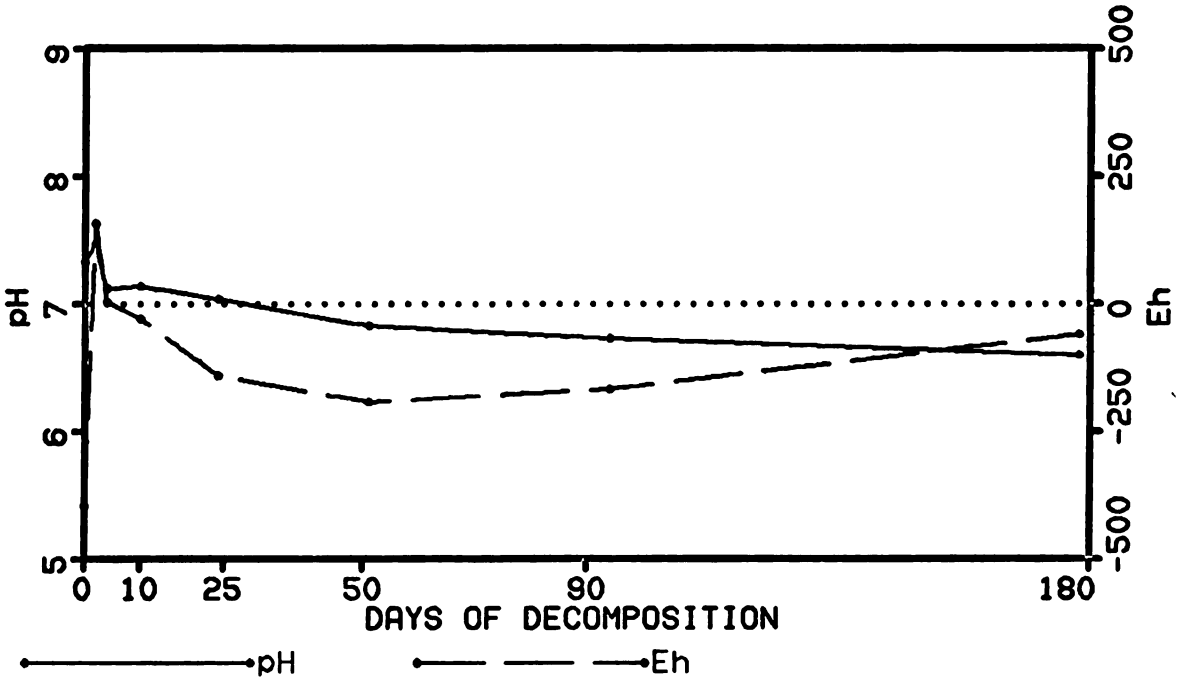
Appendix Figure 3. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. pH and Eh (millivolts) of media.



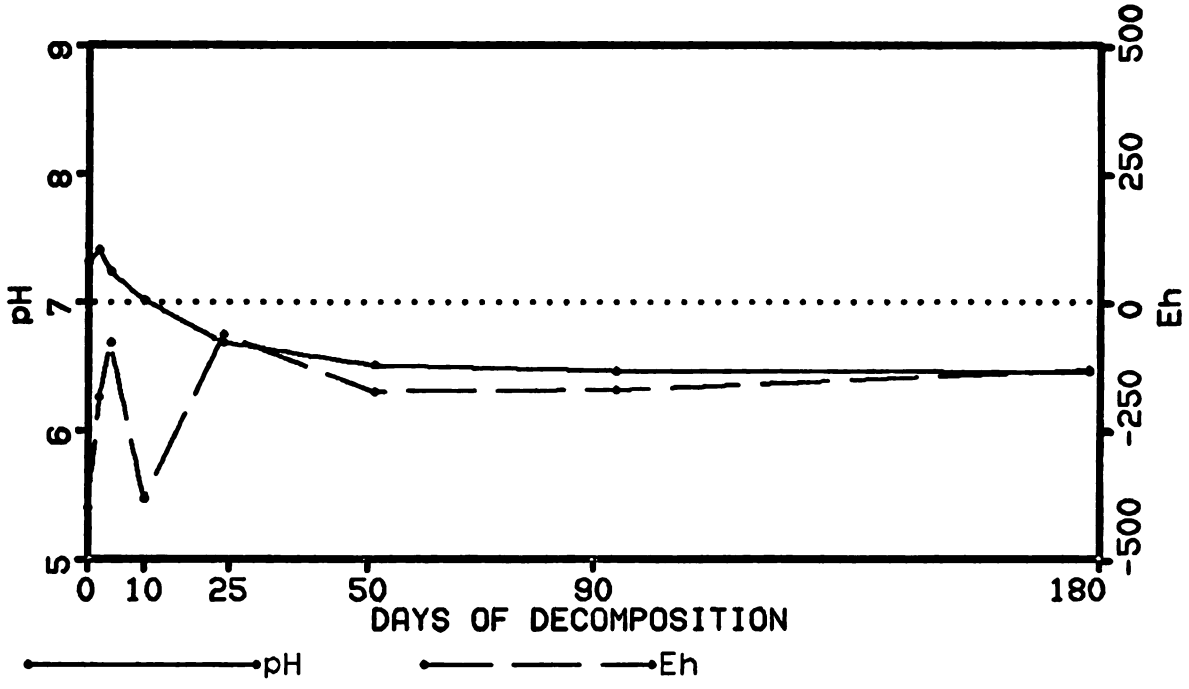
Appendix Figure 4. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. pH and Eh (millivolts) of media.



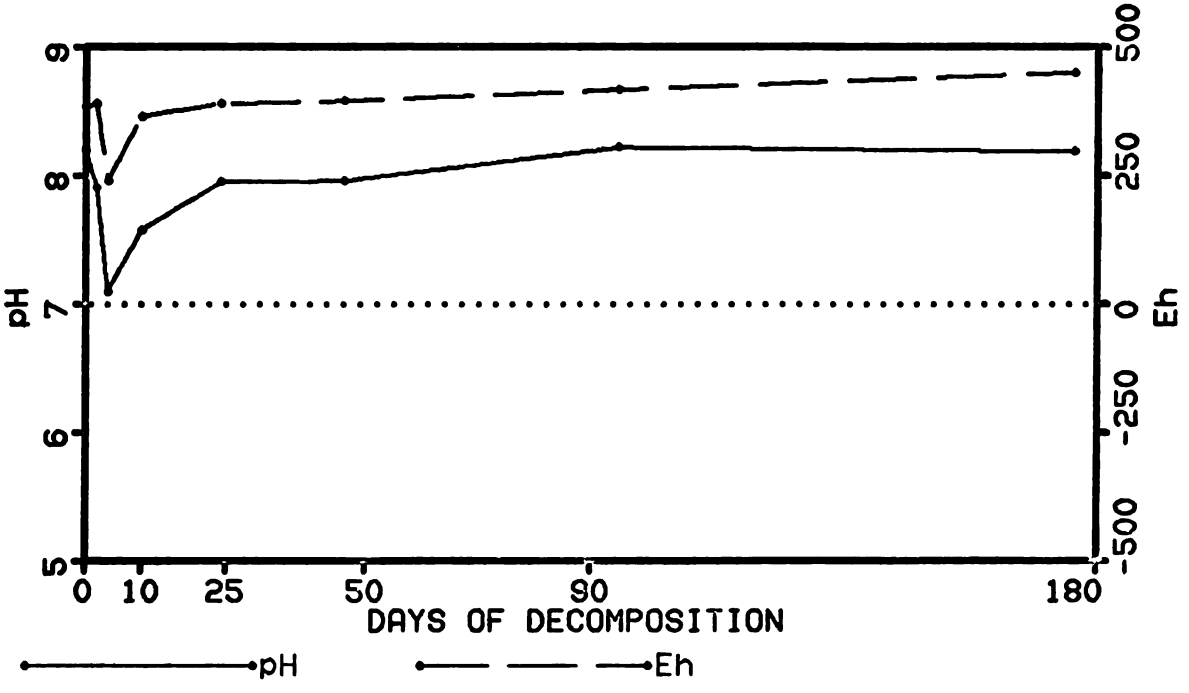
Appendix Figure 5. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. pH and Eh (millivolts) of media.



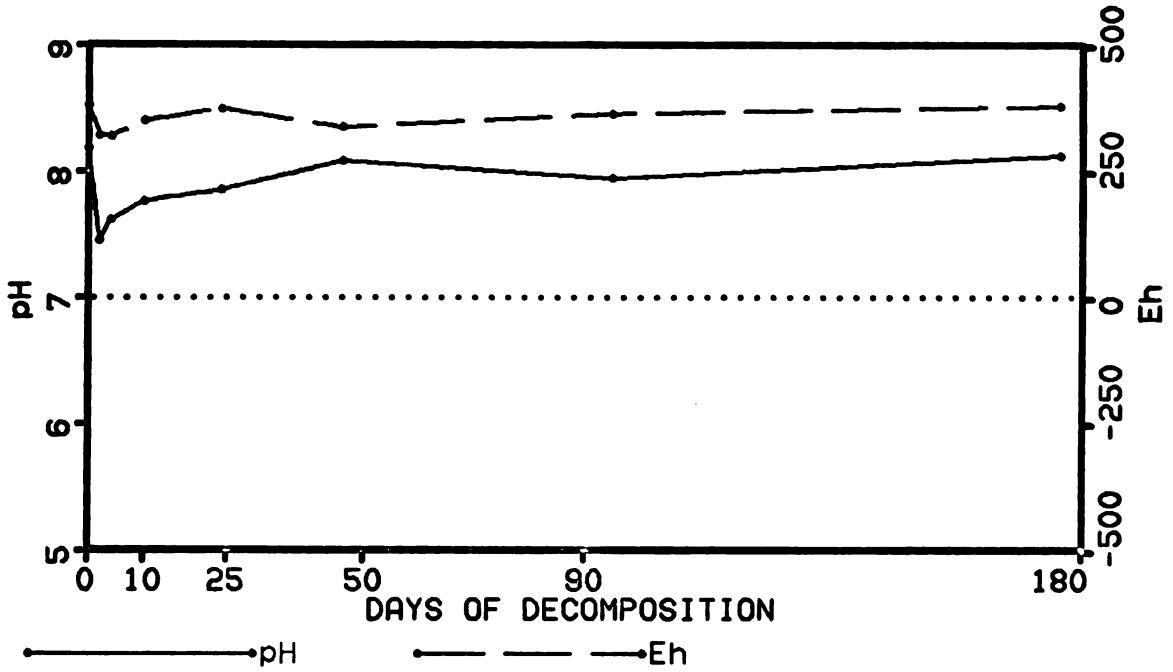
Appendix Figure 6. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. pH and Eh (millivolts) of media.



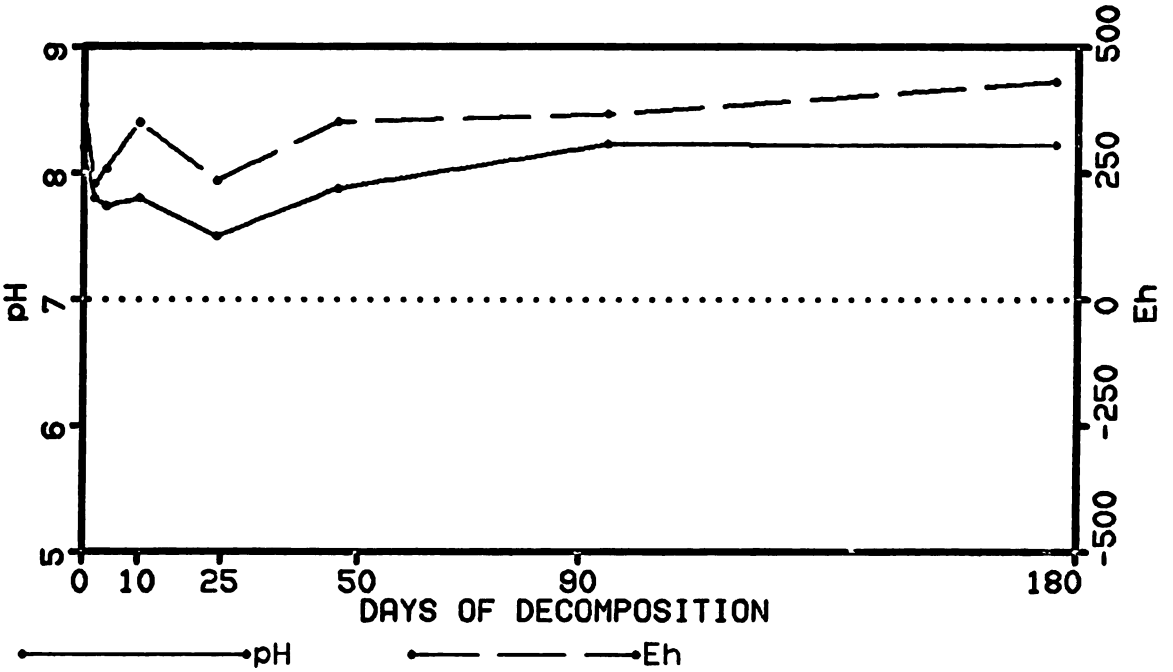
Appendix Figure 7. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. pH and Eh (millivolts) of media.



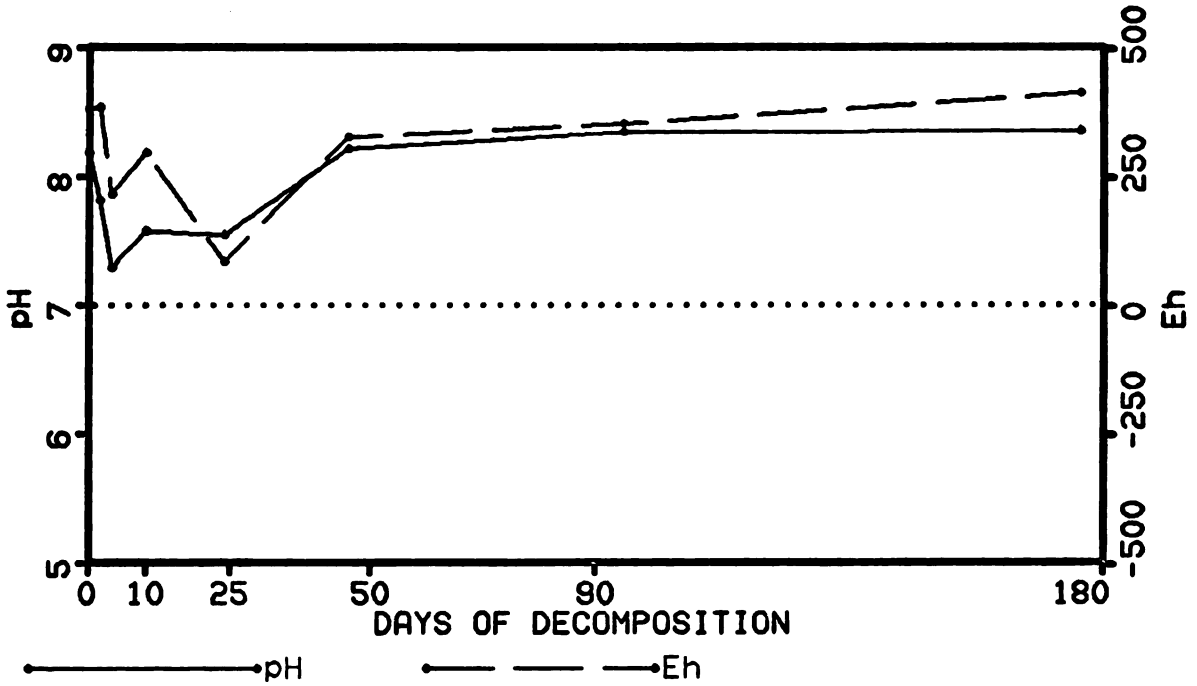
Appendix Figure 8. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. pH and Eh (millivolts) of media.



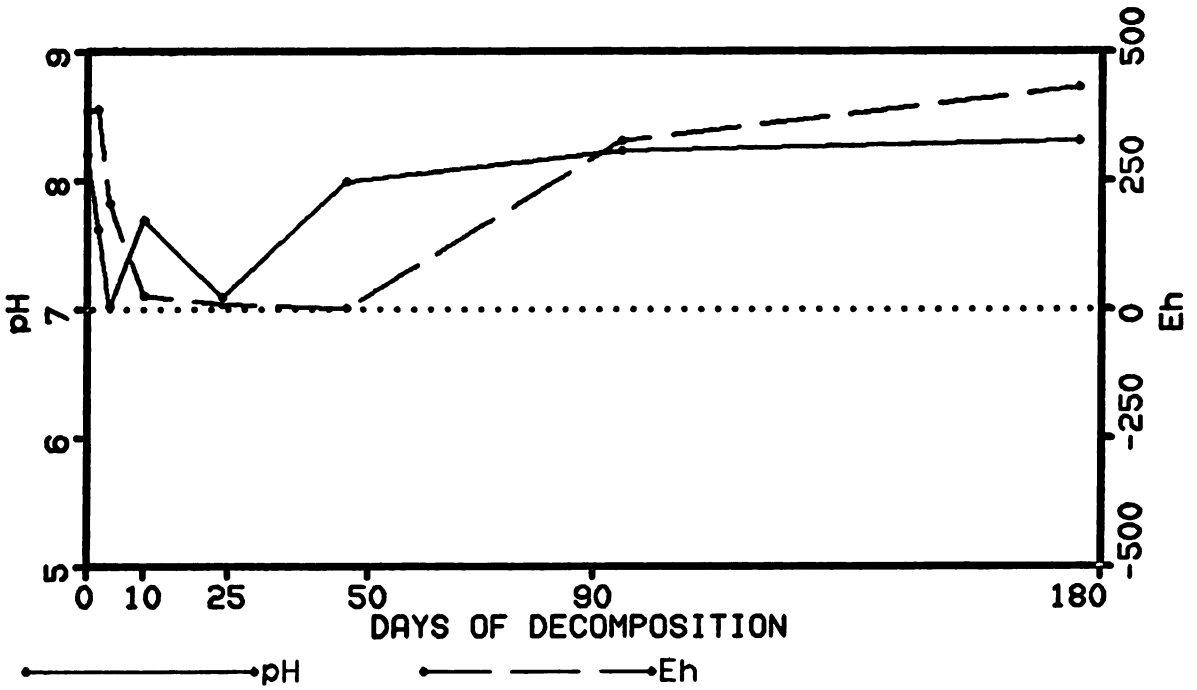
Appendix Figure 9. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. pH and Eh (millivolts) of media.



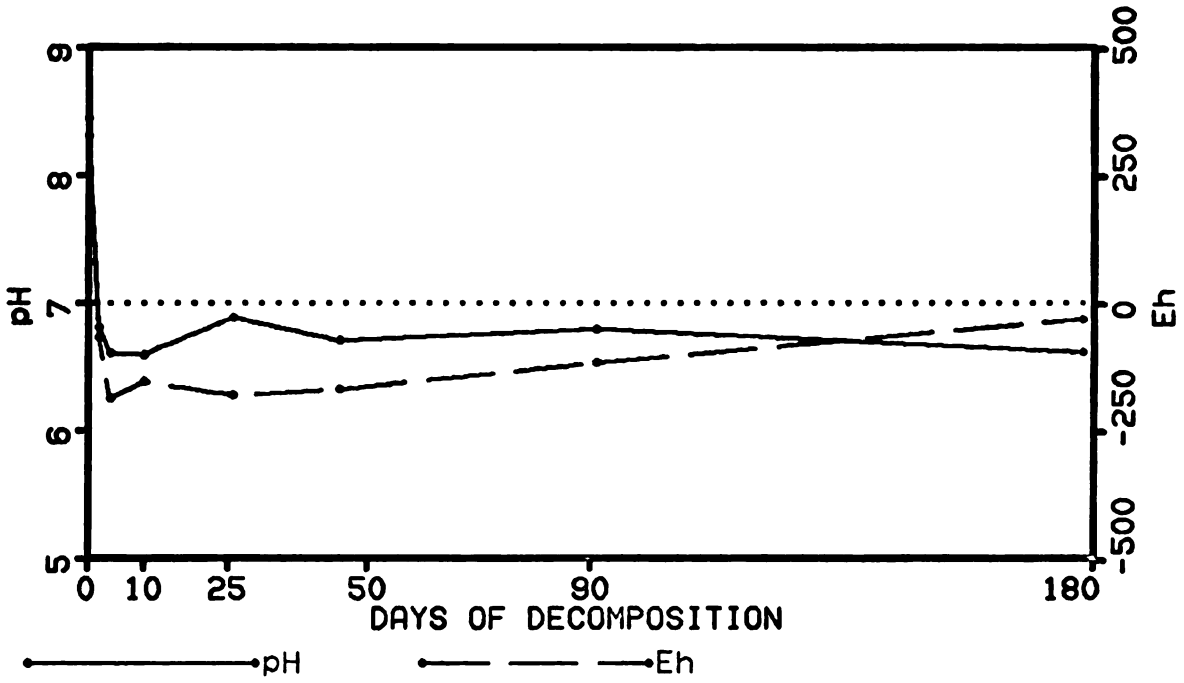
Appendix Figure 10. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. pH and Eh (millivolts) of media.



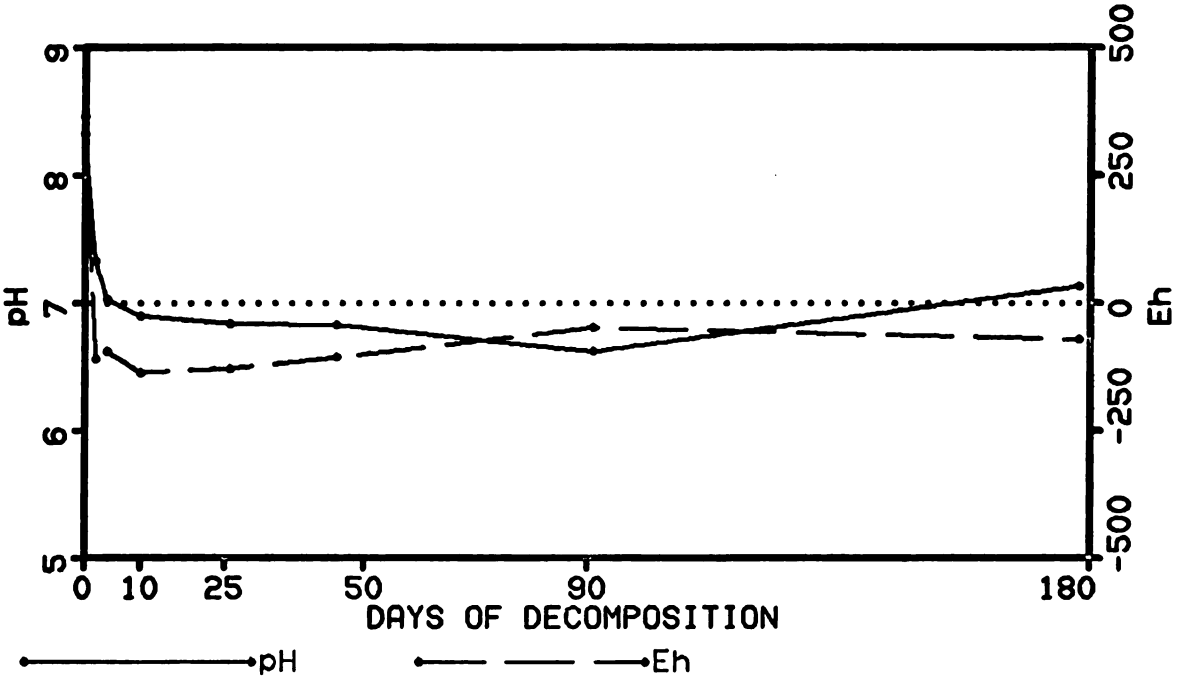
Appendix Figure 11. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. pH and Eh (millivolts) of media.



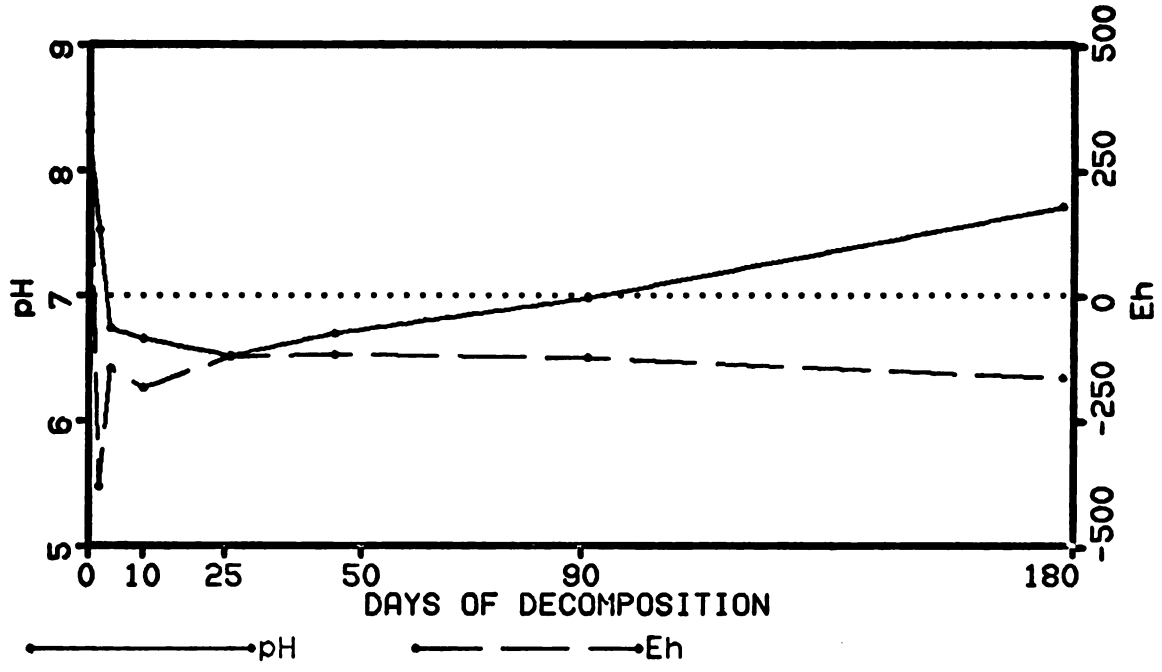
Appendix Figure 12. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. pH and Eh (millivolts) of media.



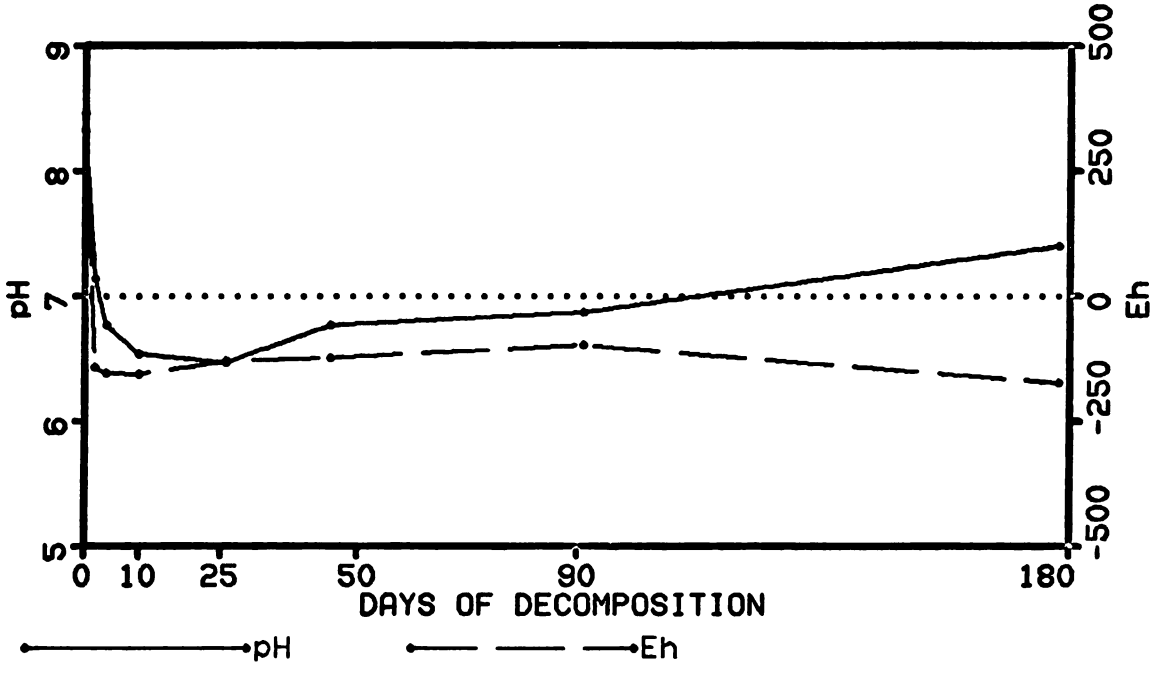
Appendix Figure 13. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. pH and Eh (millivolts) of media.



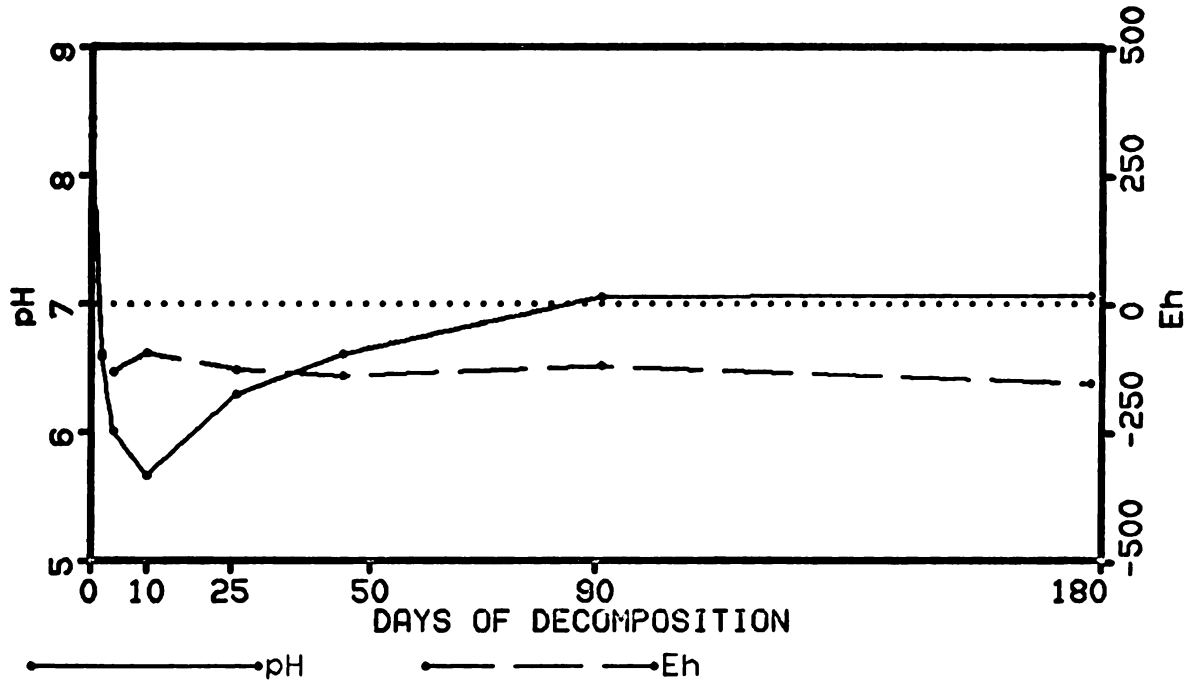
Appendix Figure 14. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. pH and Eh (millivolts) of media.



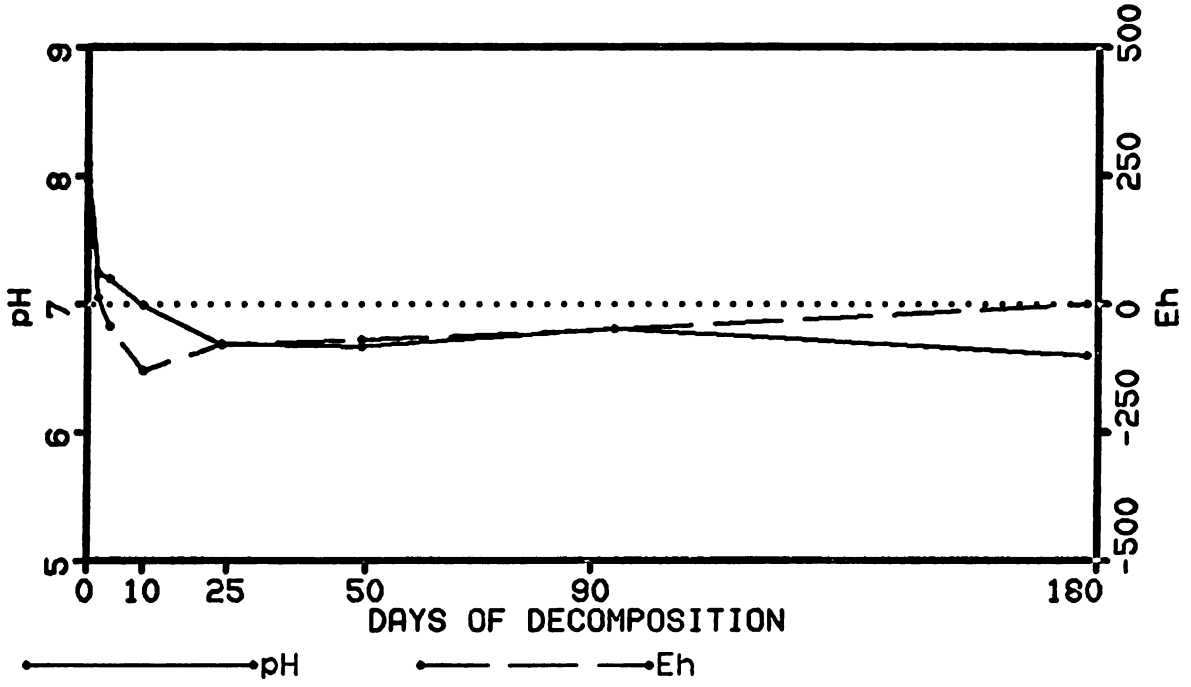
Appendix Figure 15. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. pH and Eh (millivolts) of media.



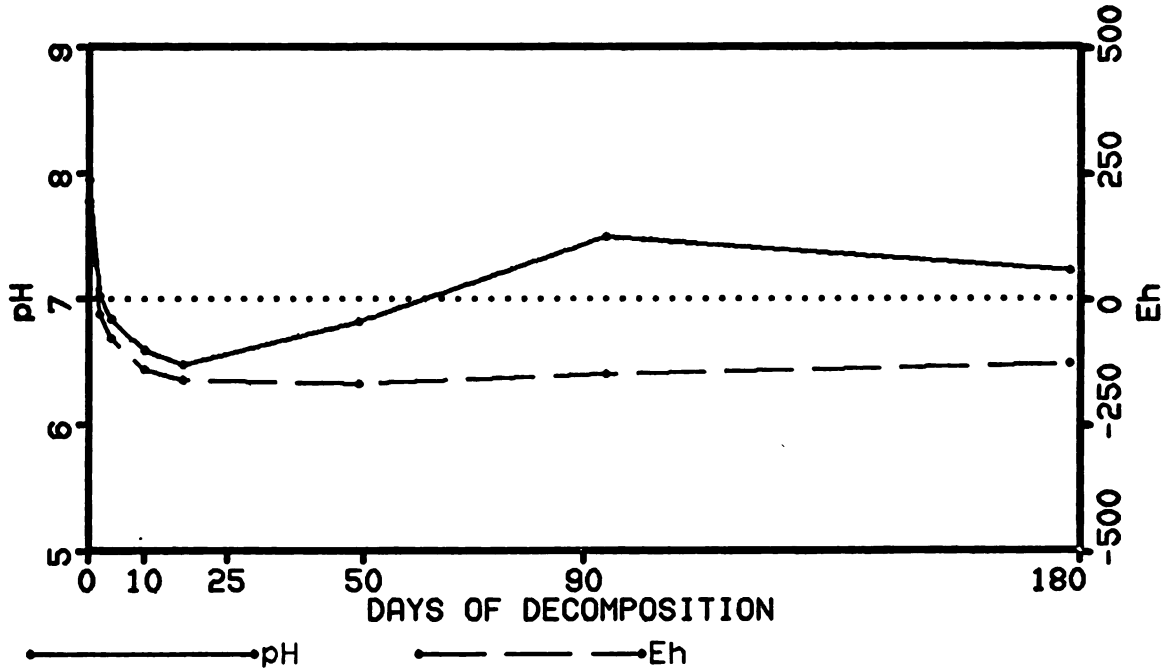
Appendix Figure 16. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. pH and Eh (millivolts) of media.



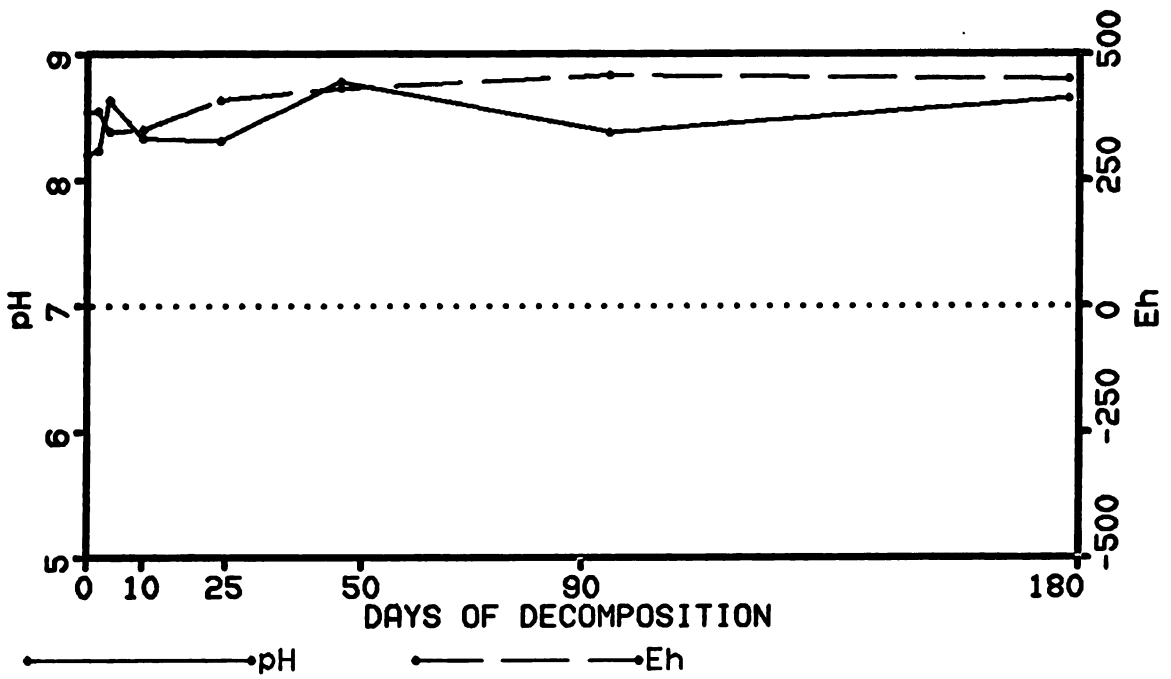
Appendix Figure 17. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. pH and Eh (millivolts) of media.



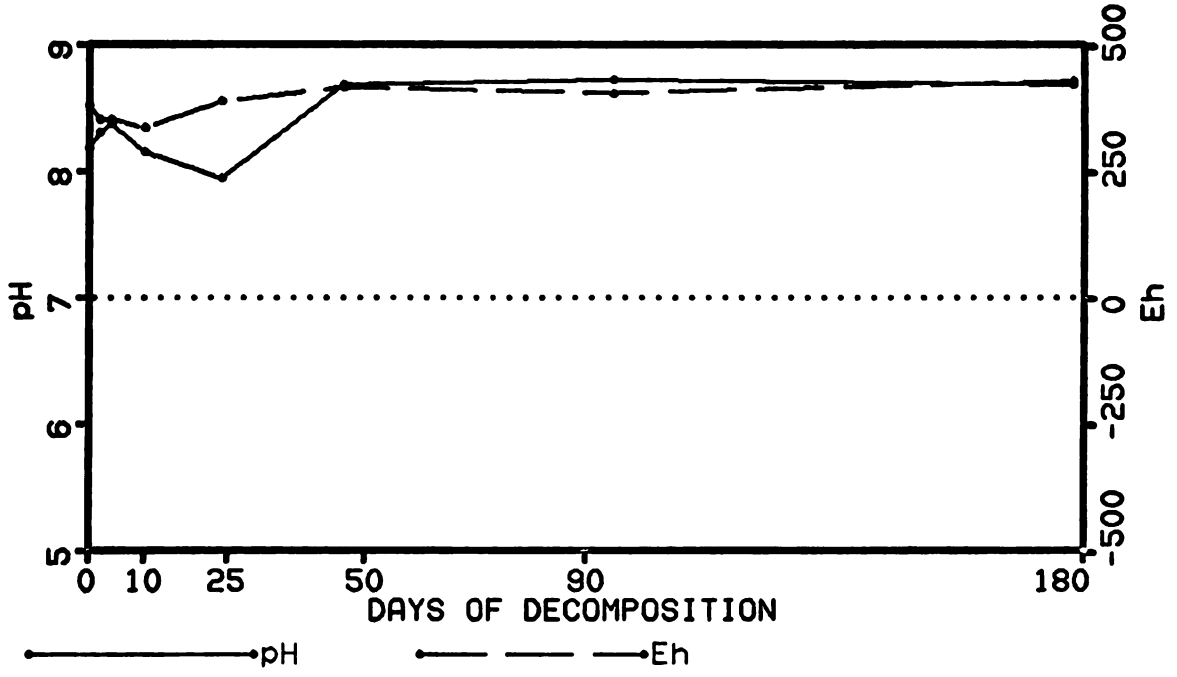
Appendix Figure 18. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. pH and Eh (millivolts) of media.



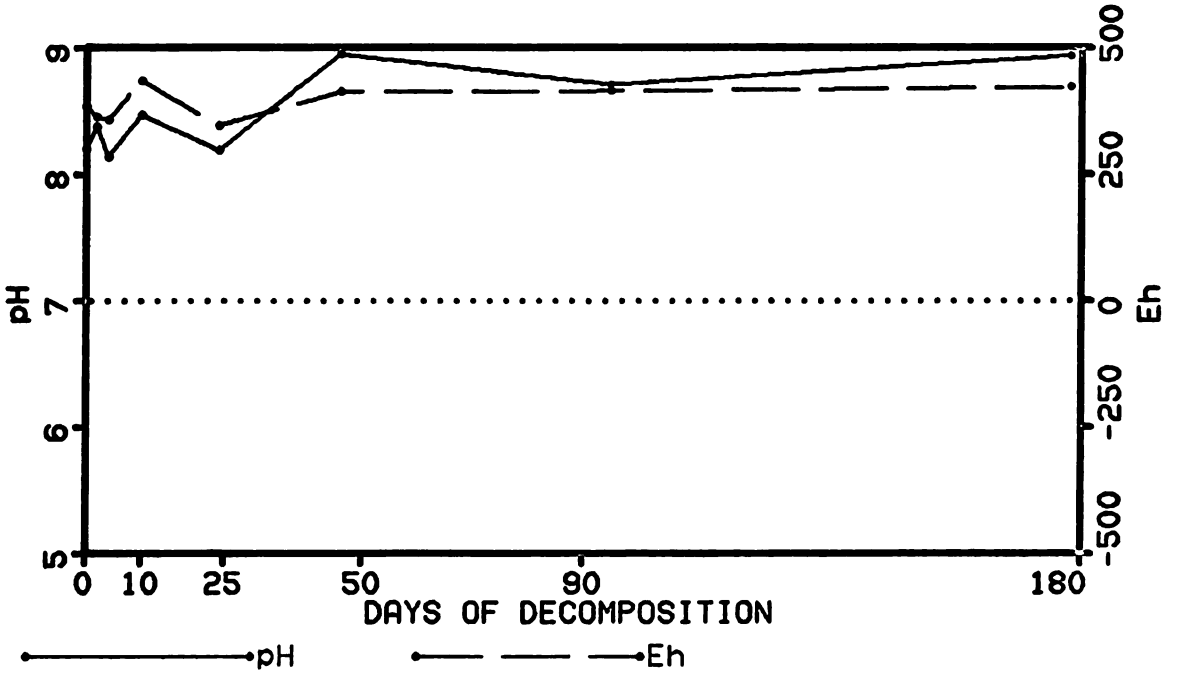
Appendix Figure 19. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. pH and Eh (millivolts) of media.



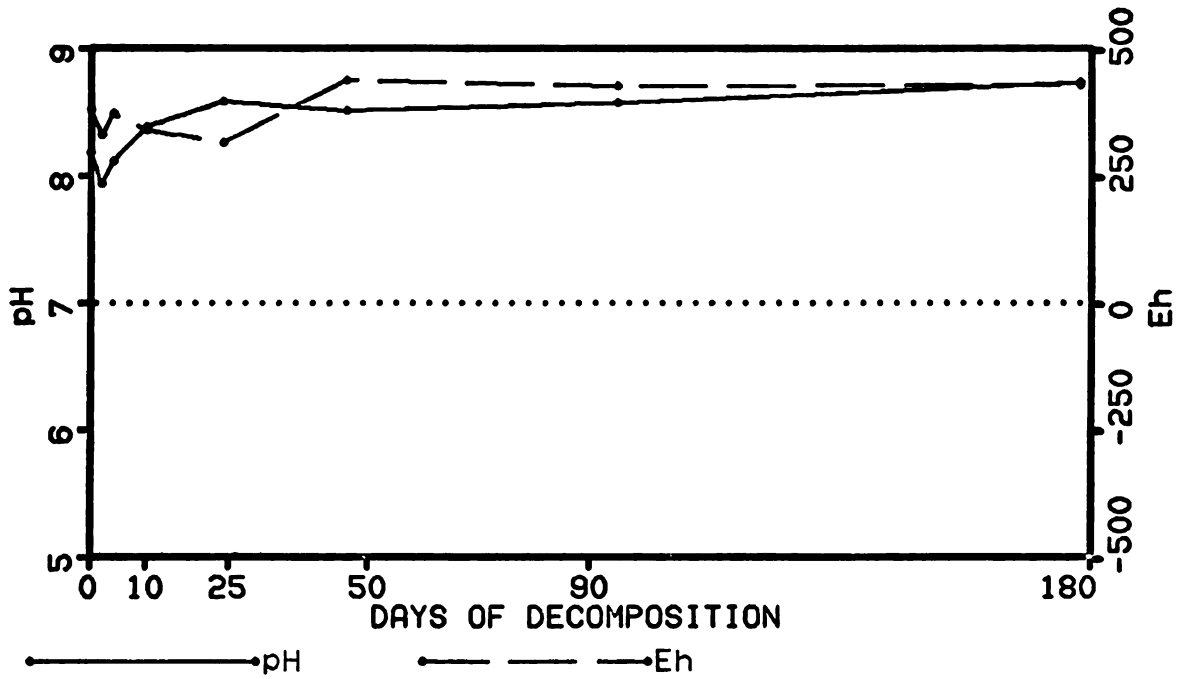
Appendix Figure 20. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. pH and Eh (millivolts) of media.



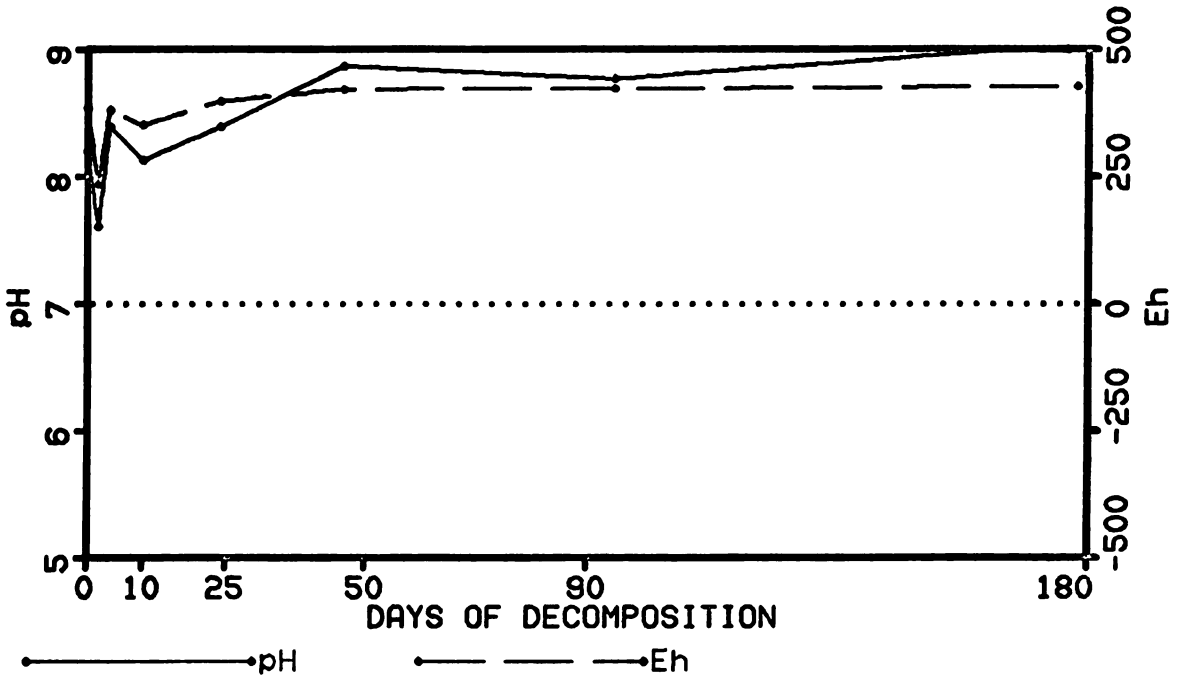
Appendix Figure 21. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. pH and Eh (millivolts) of media.



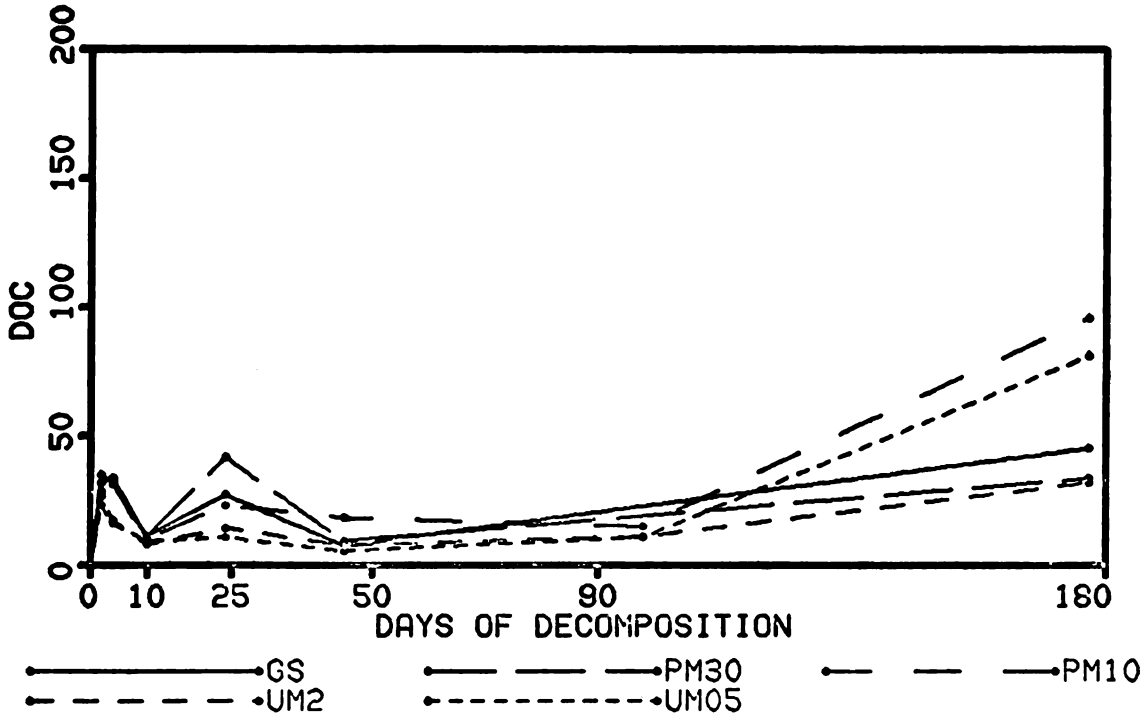
Appendix Figure 22. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. pH and Eh (millivolts) of media.



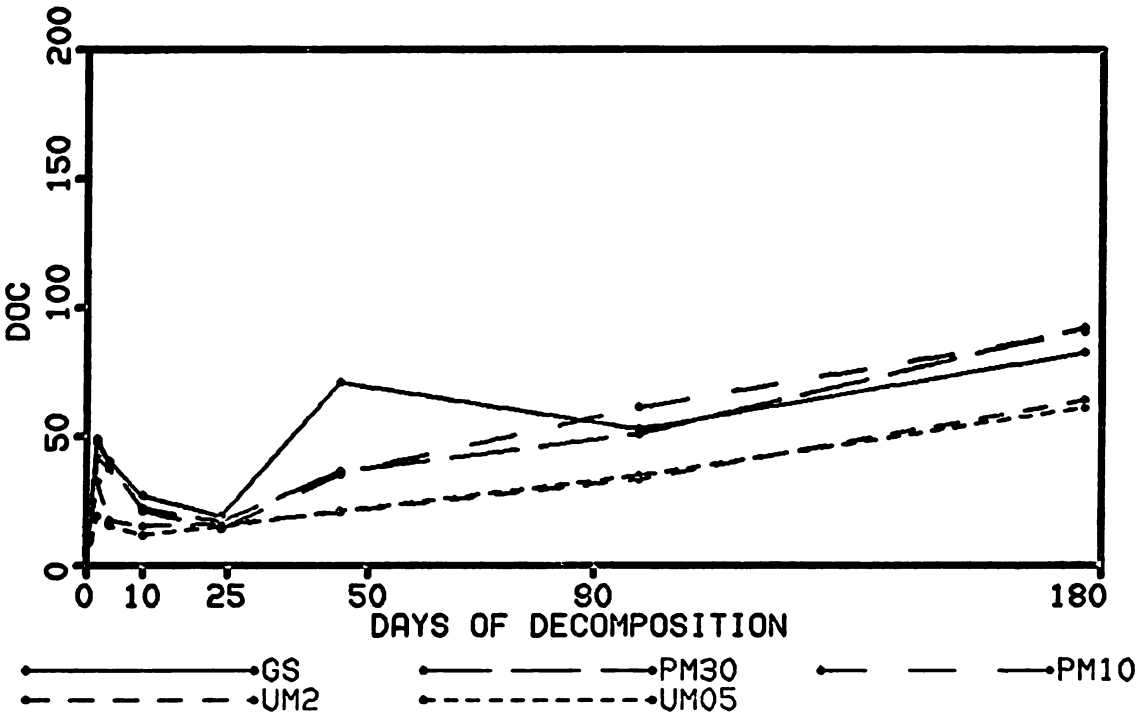
Appendix Figure 23. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. pH and Eh (millivolts) of media.



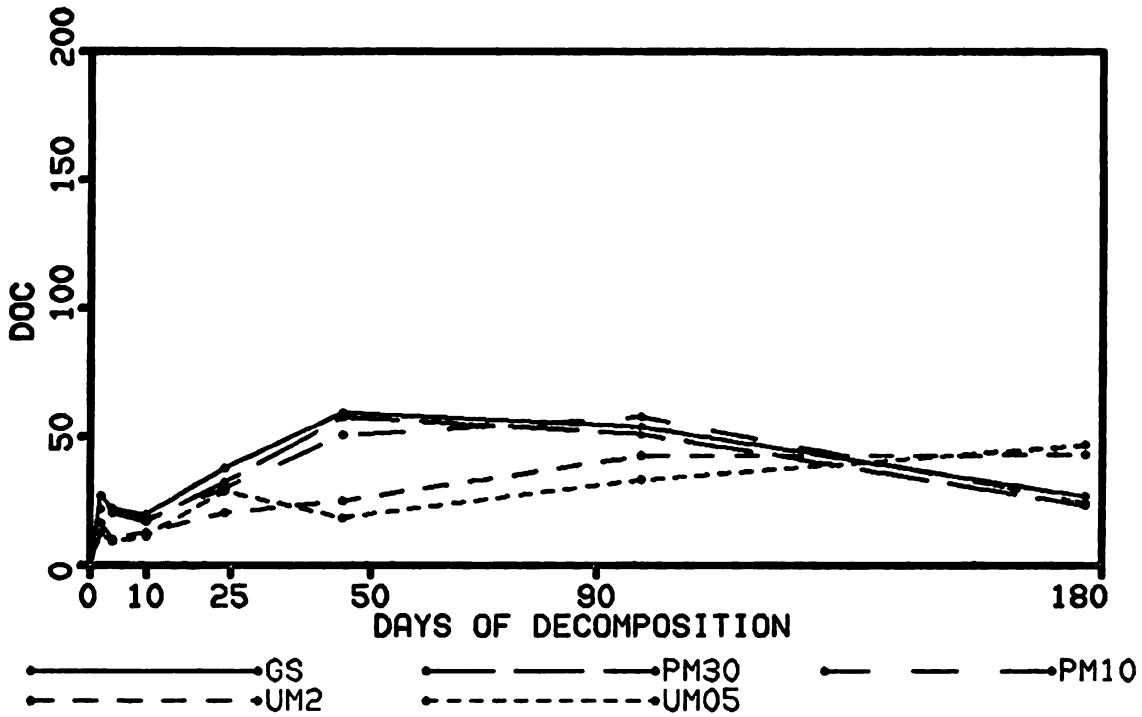
Appendix Figure 24. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. pH and Eh (millivolts) of media.



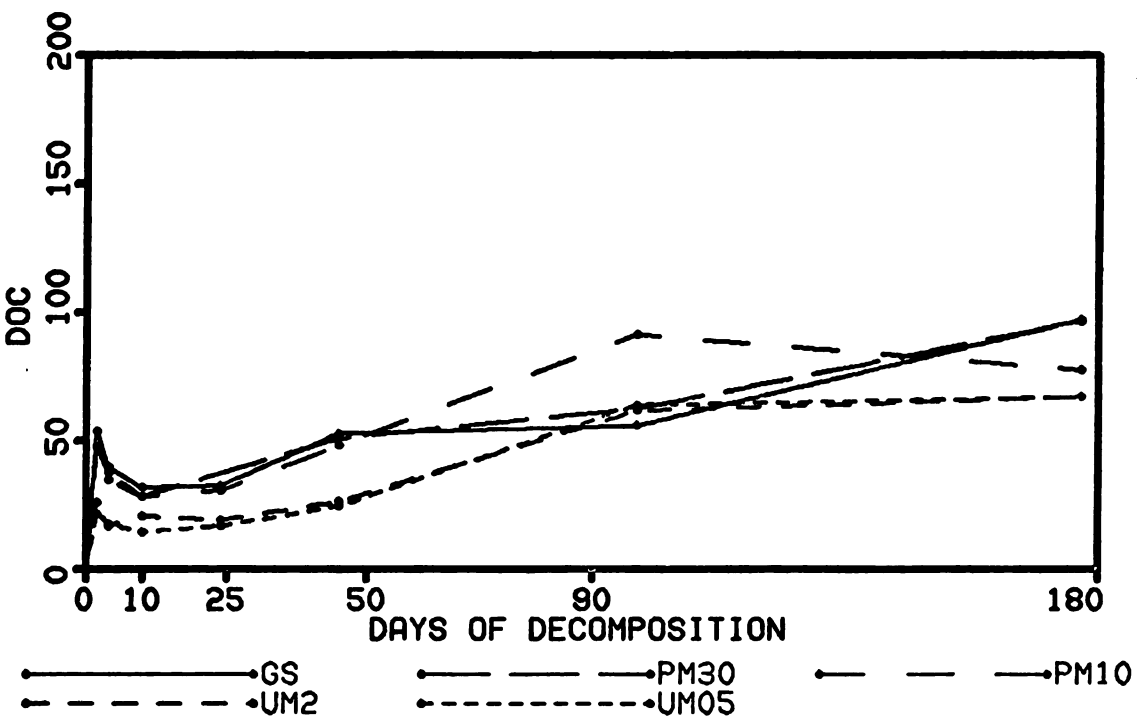
Appendix Figure 25. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



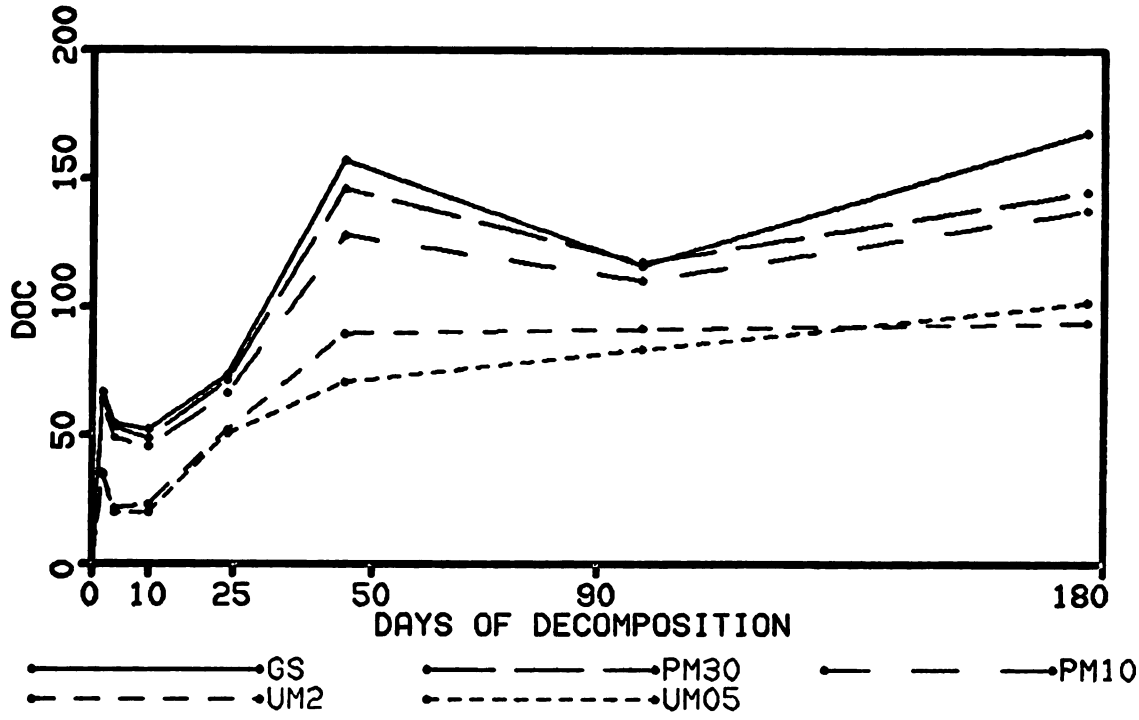
Appendix Figure 26. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



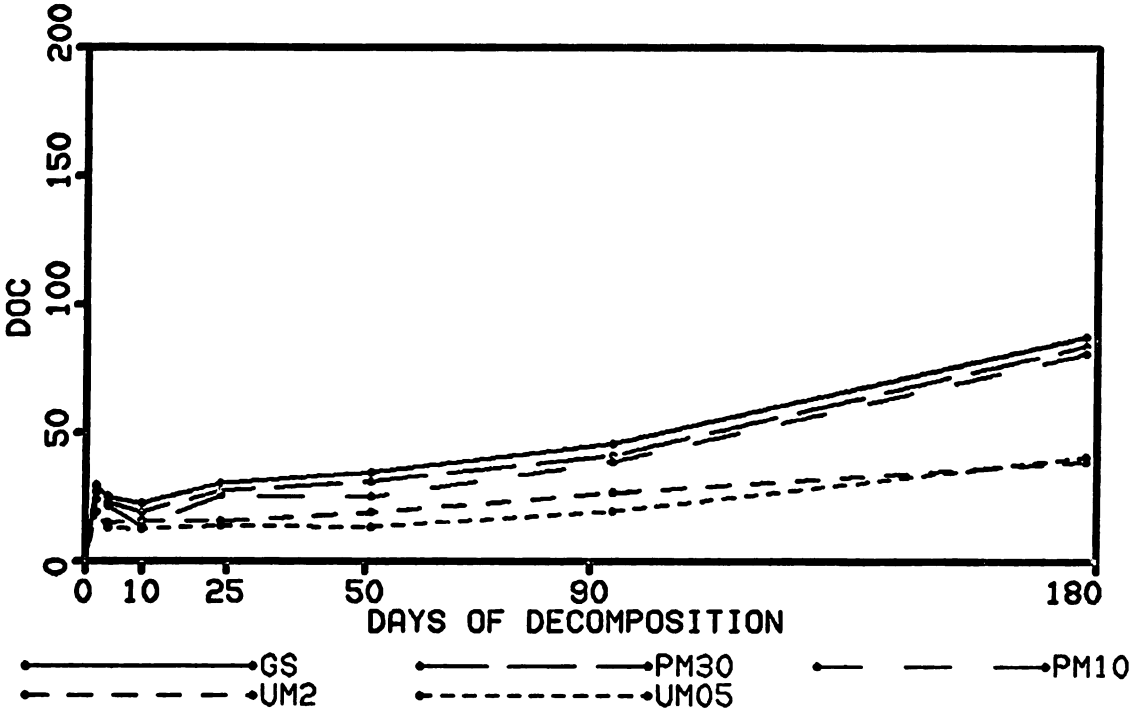
Appendix Figure 27. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



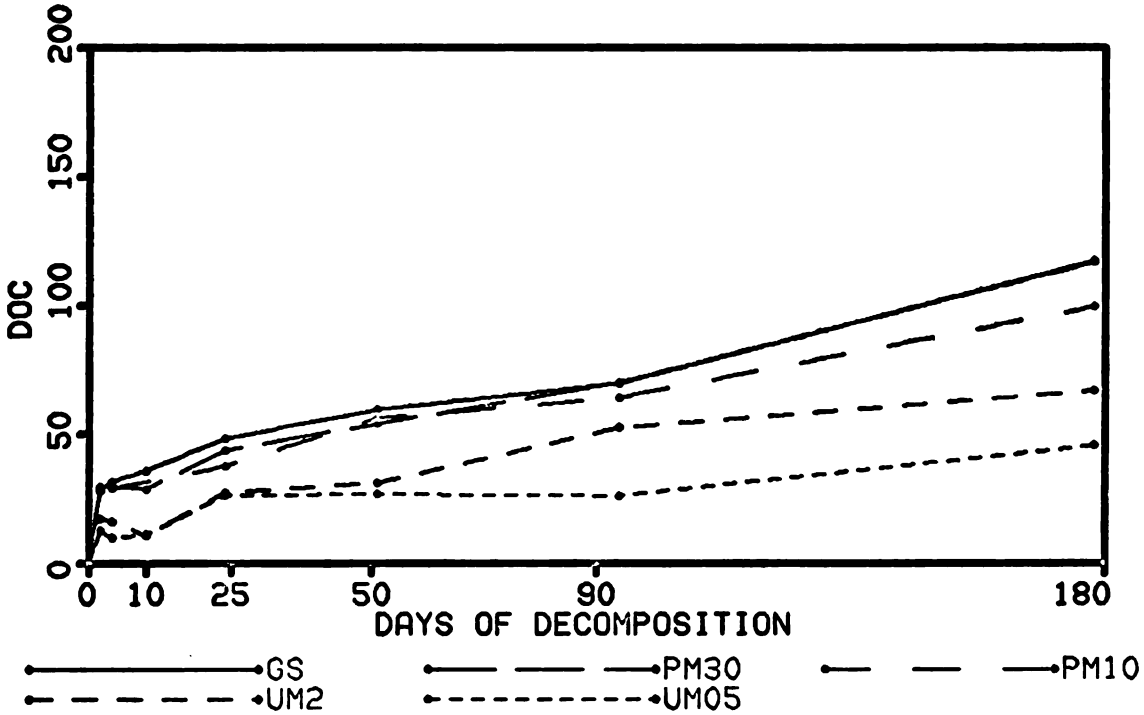
Appendix Figure 28. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



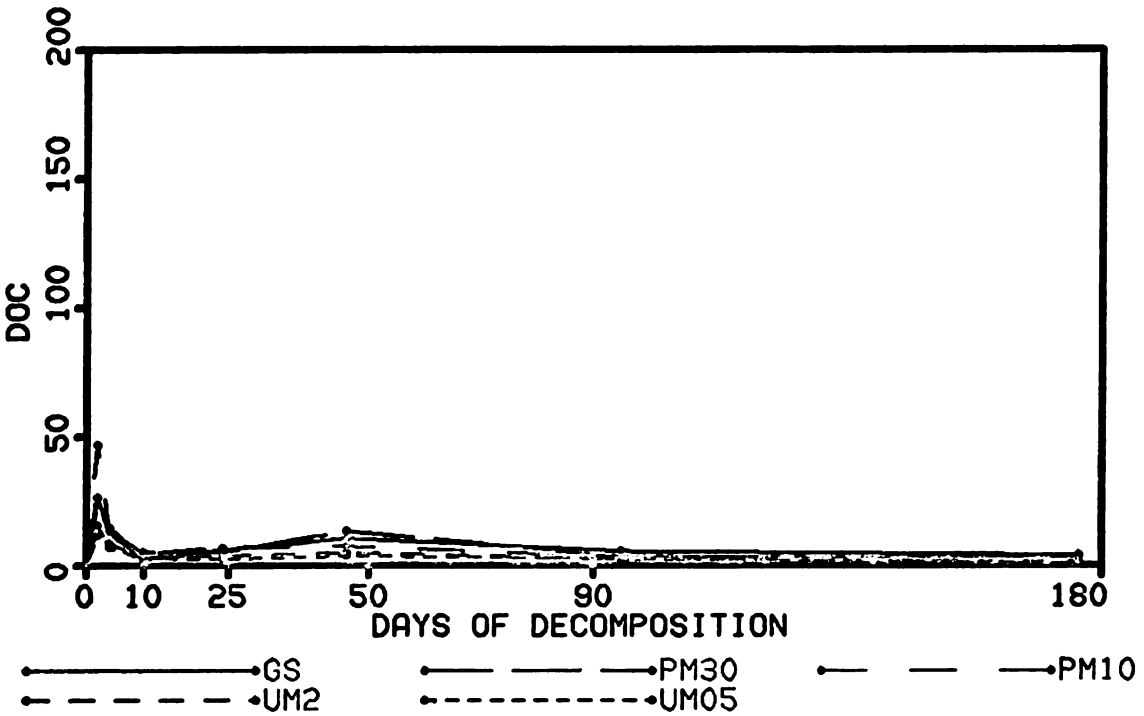
Appendix Figure 29. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



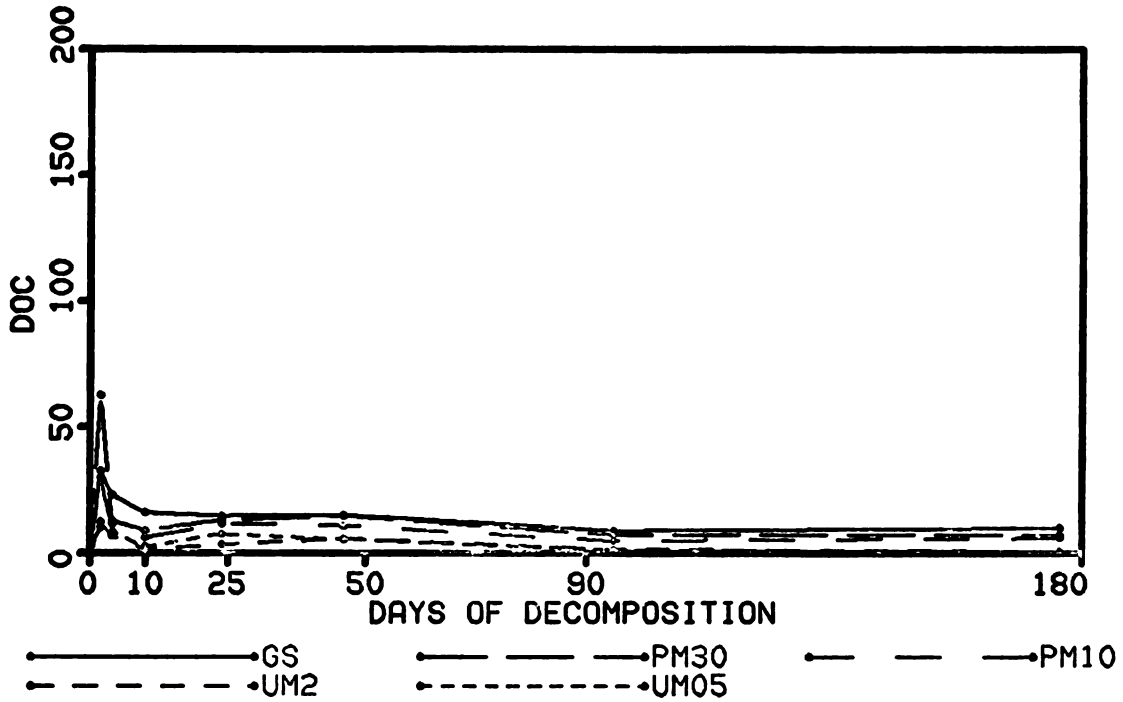
Appendix Figure 30. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



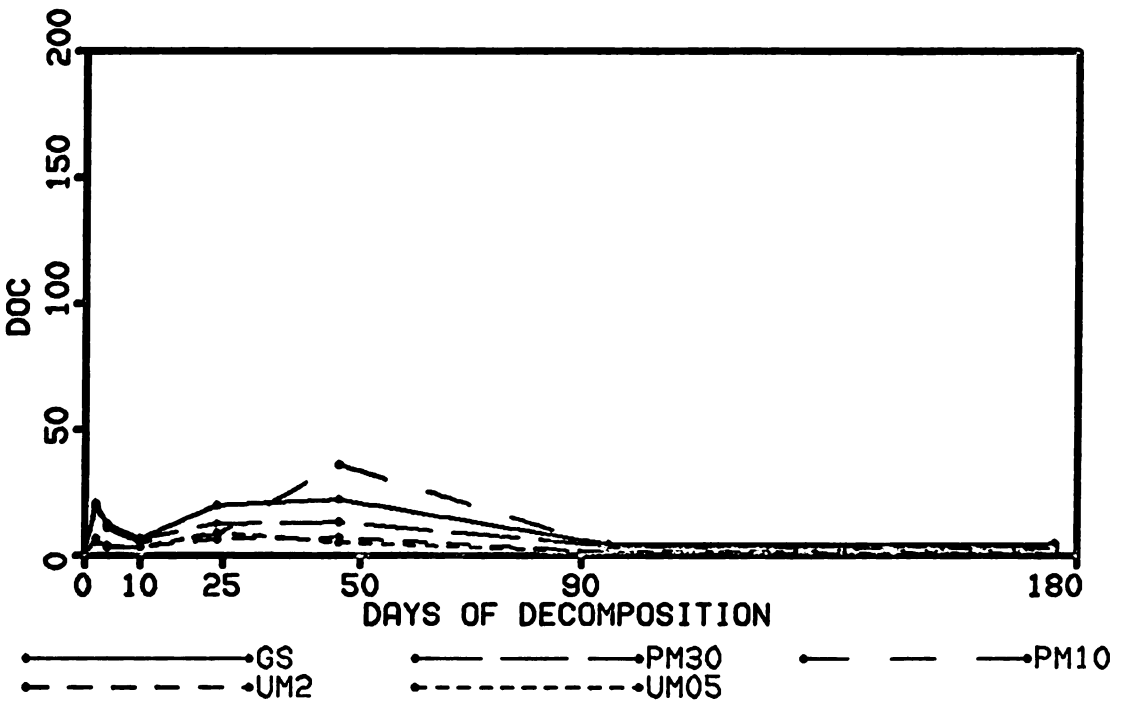
Appendix Figure 31. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



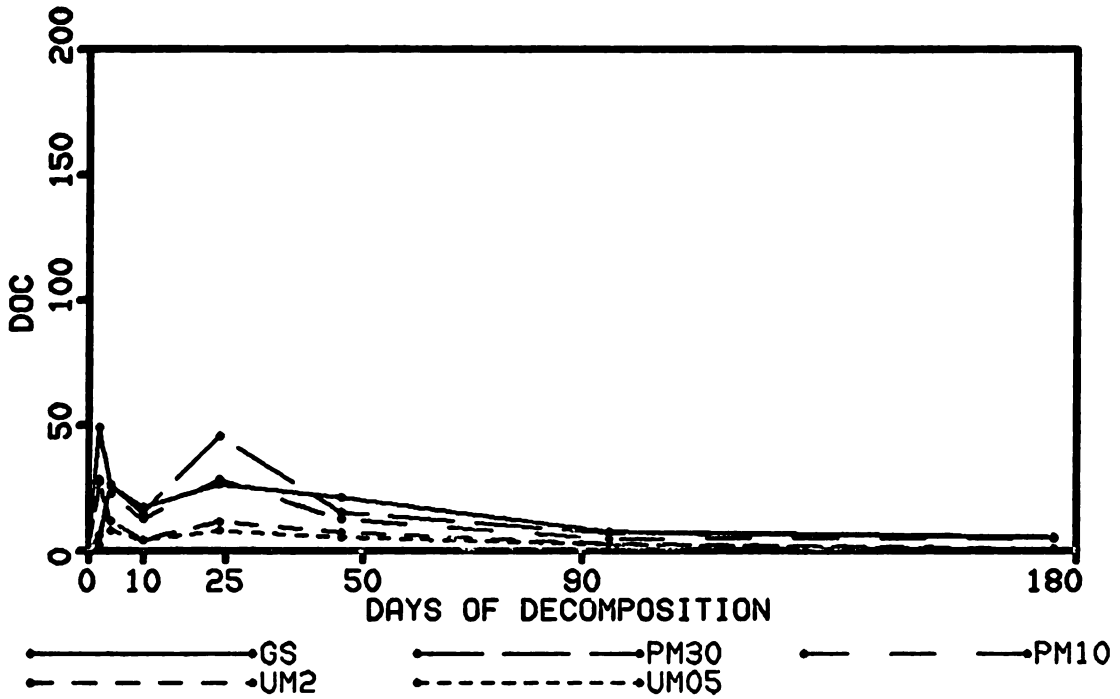
Appendix Figure 32. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



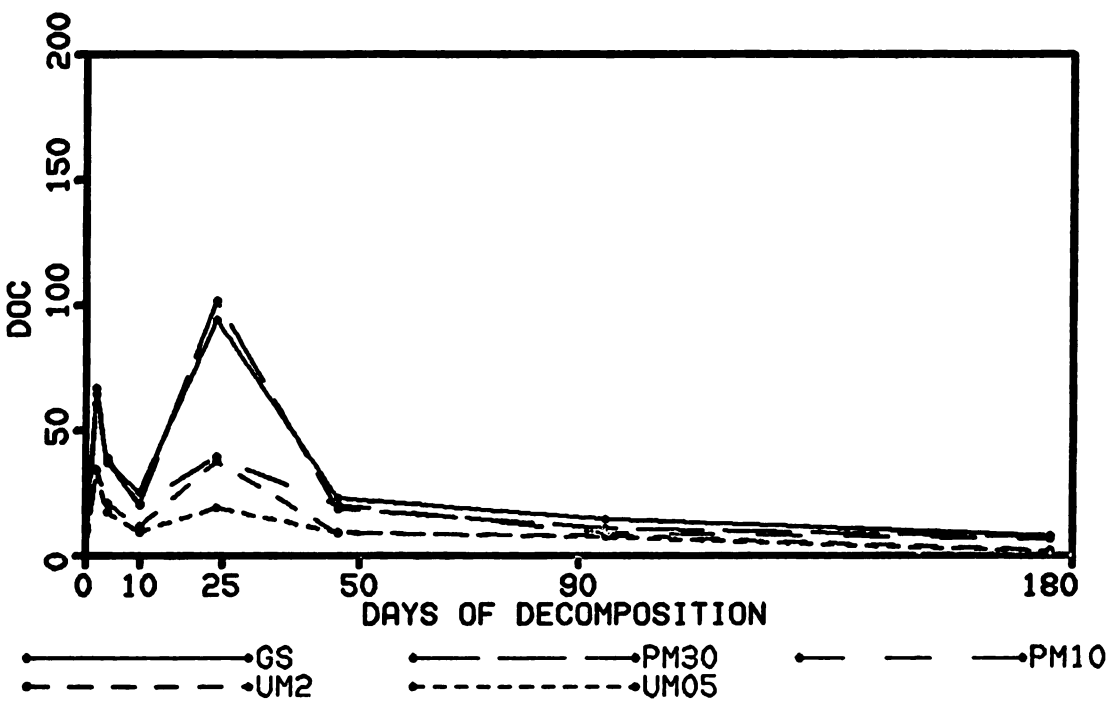
Appendix Figure 33. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



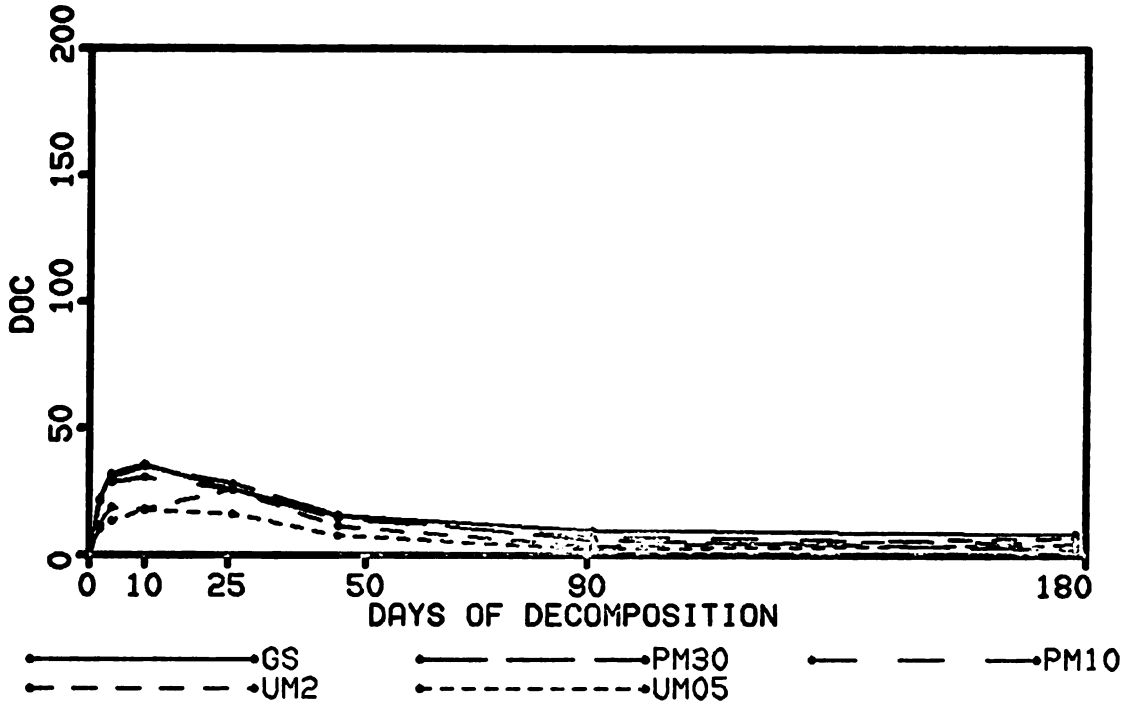
Appendix Figure 34. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



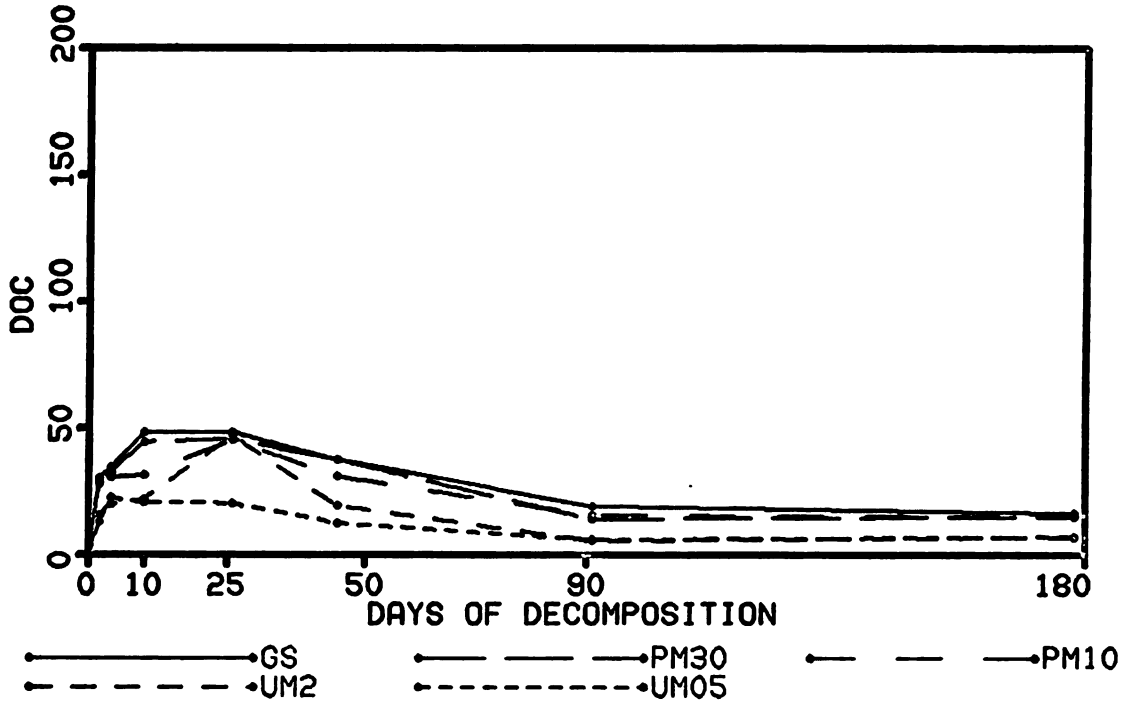
Appendix Figure 35. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



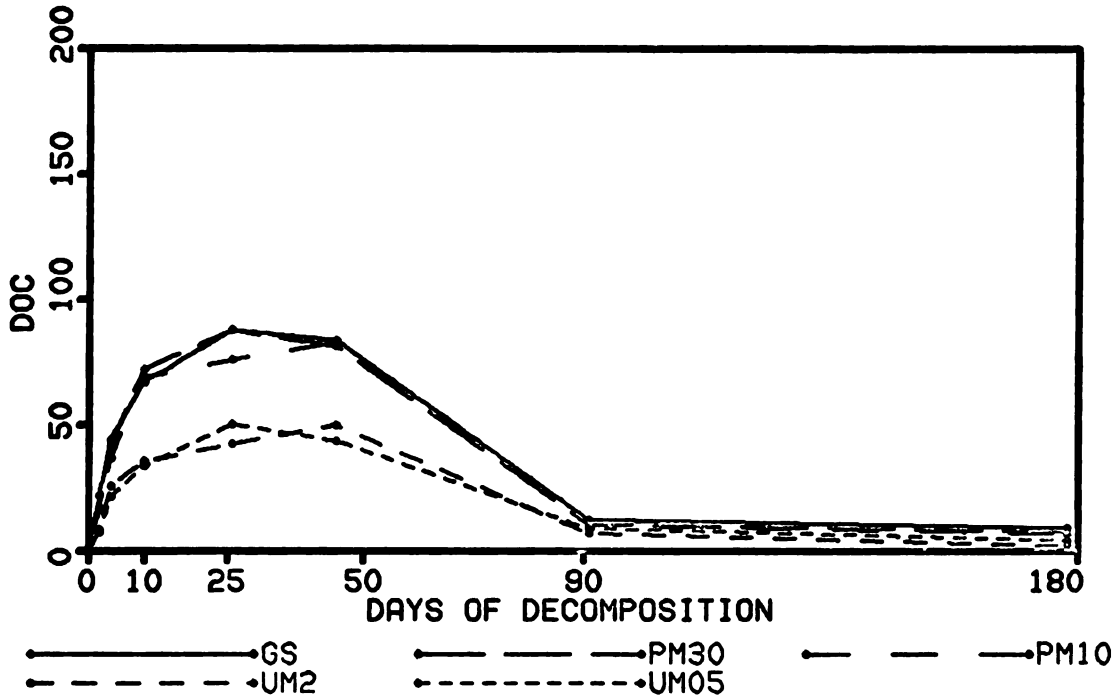
Appendix Figure 36. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



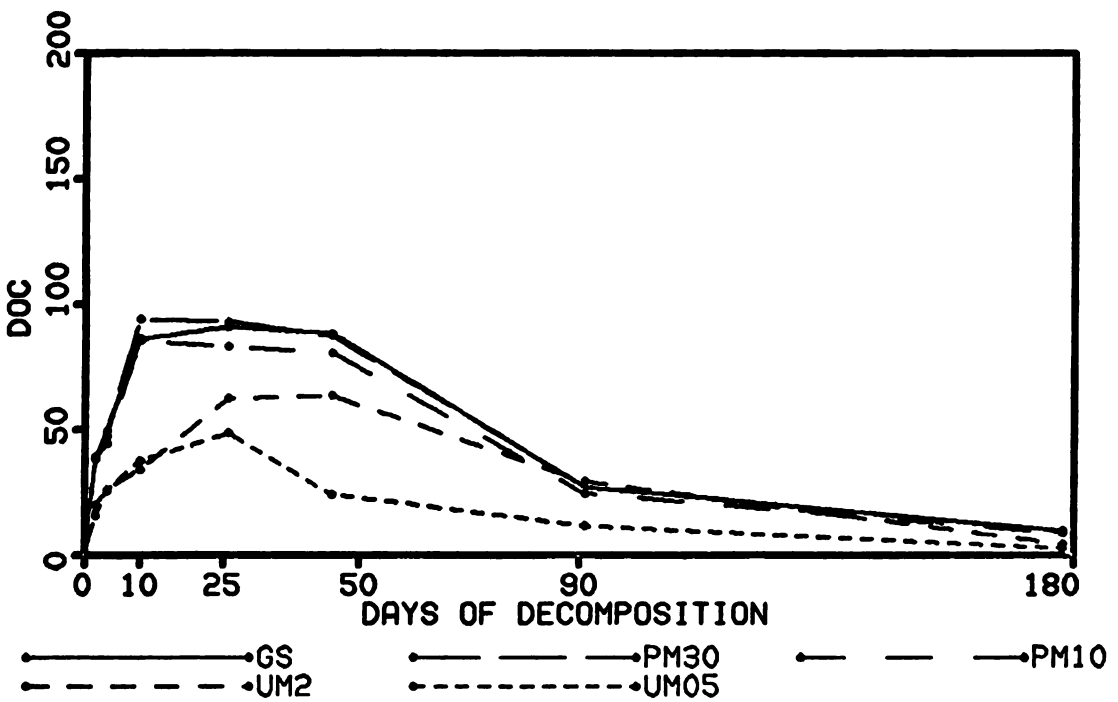
Appendix Figure 37. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



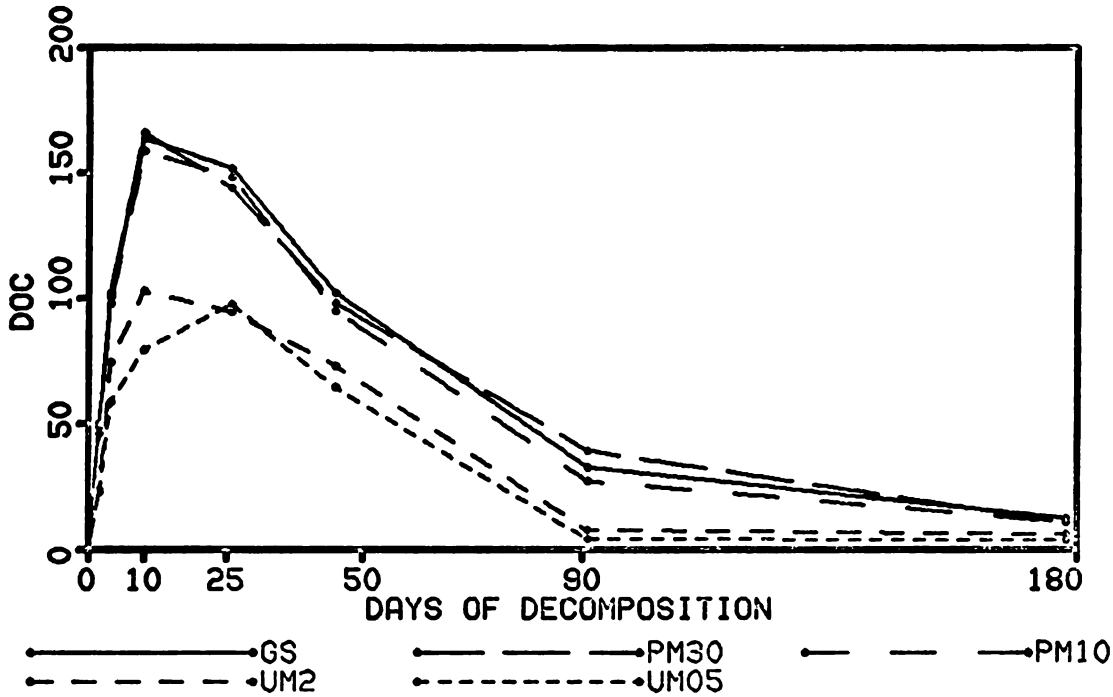
Appendix Figure 38. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



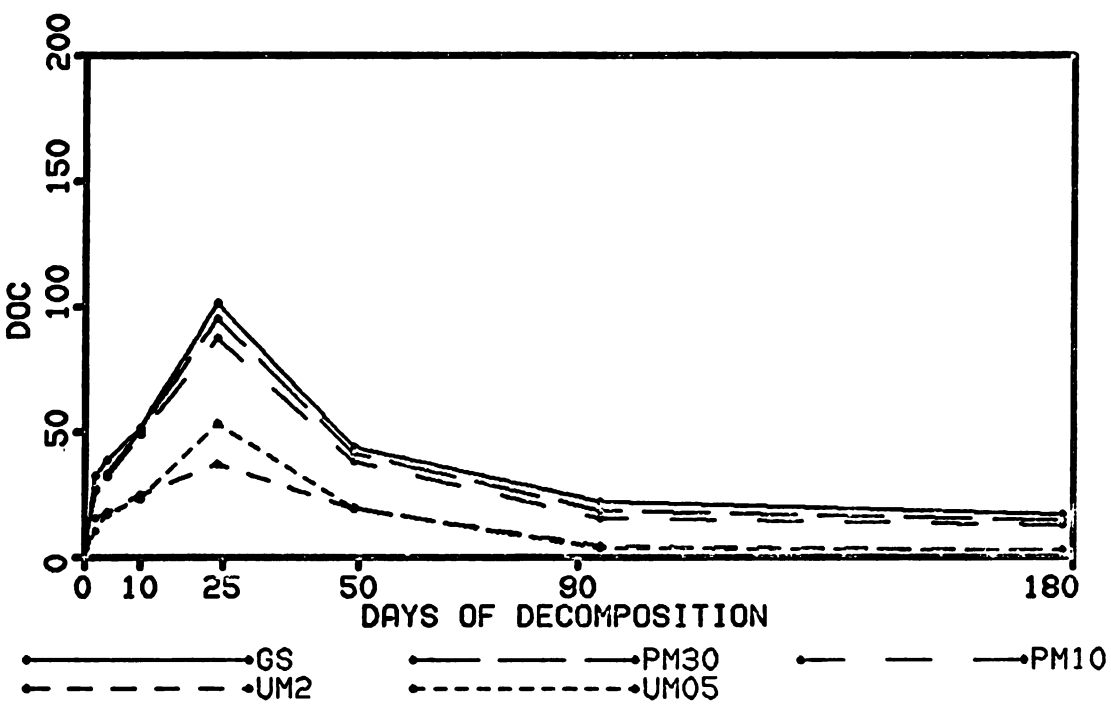
Appendix Figure 39. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



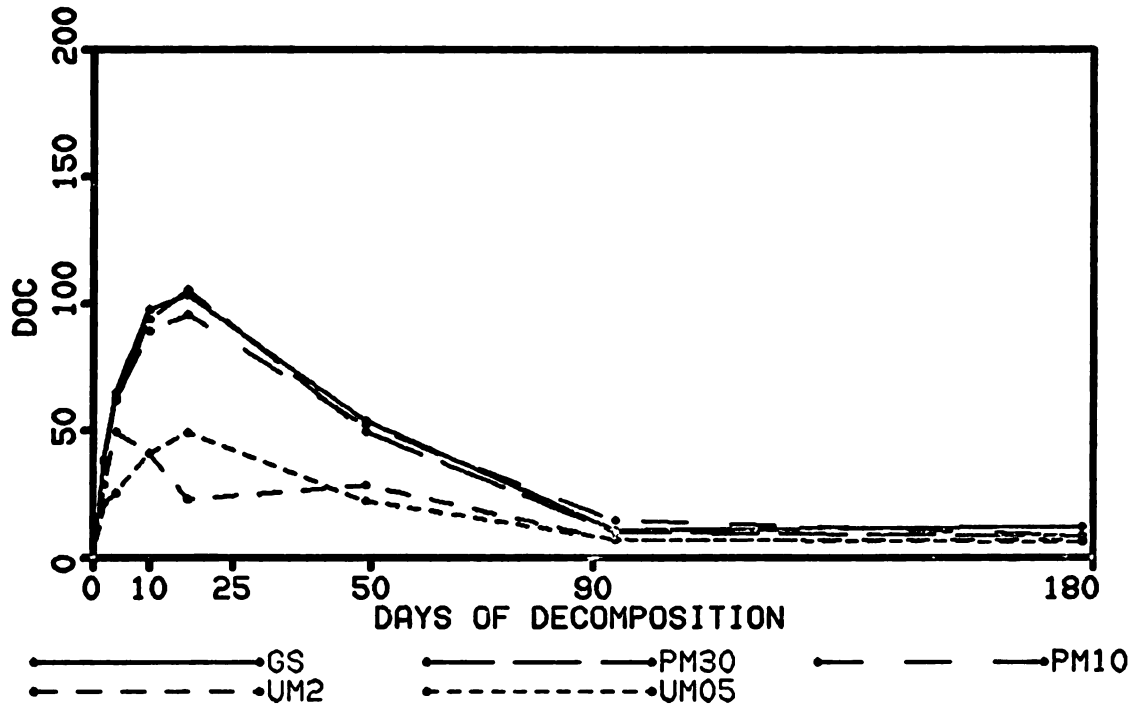
Appendix Figure 40. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



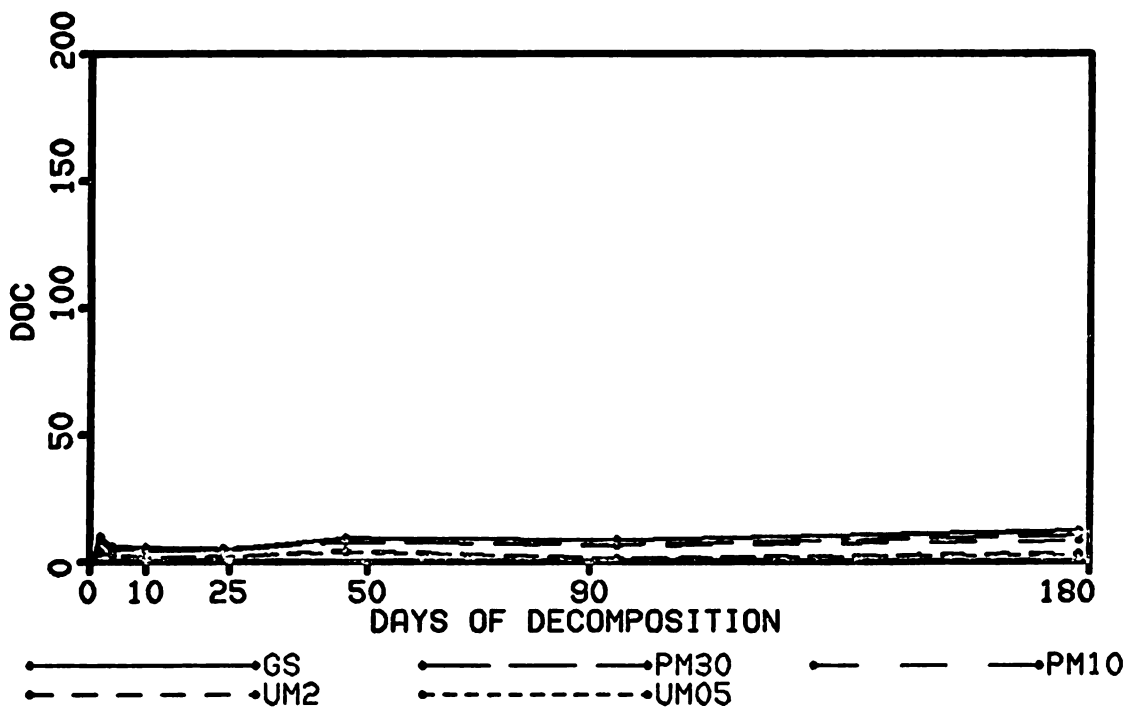
Appendix Figure 41. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



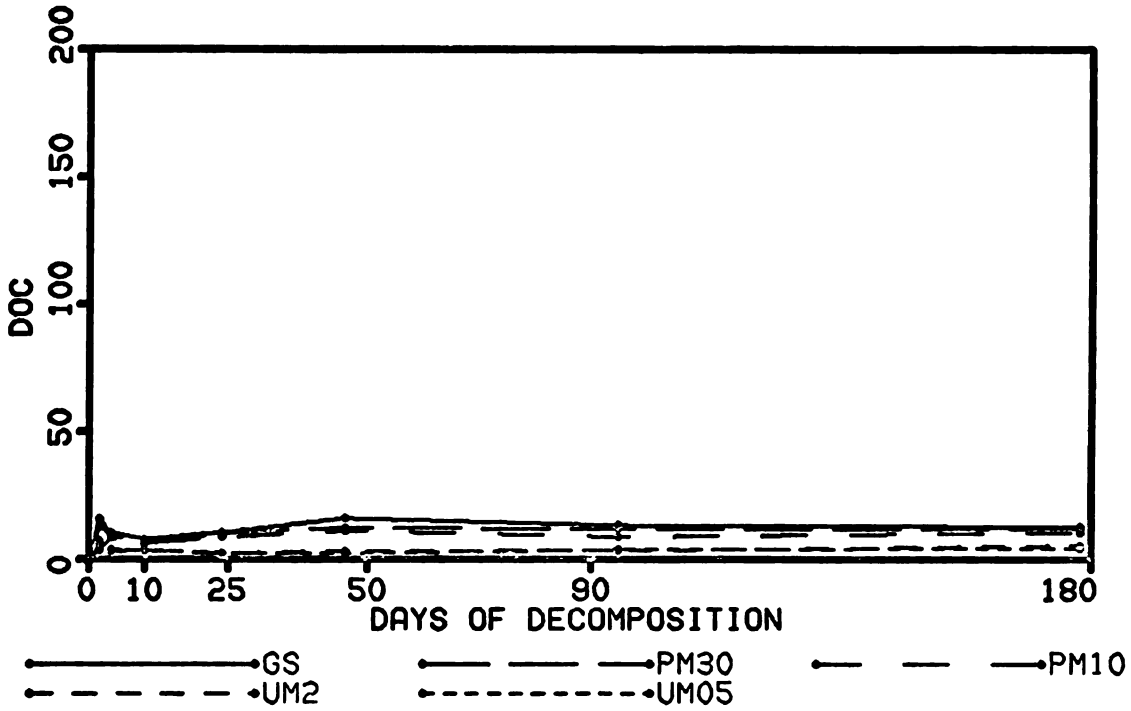
Appendix Figure 42. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



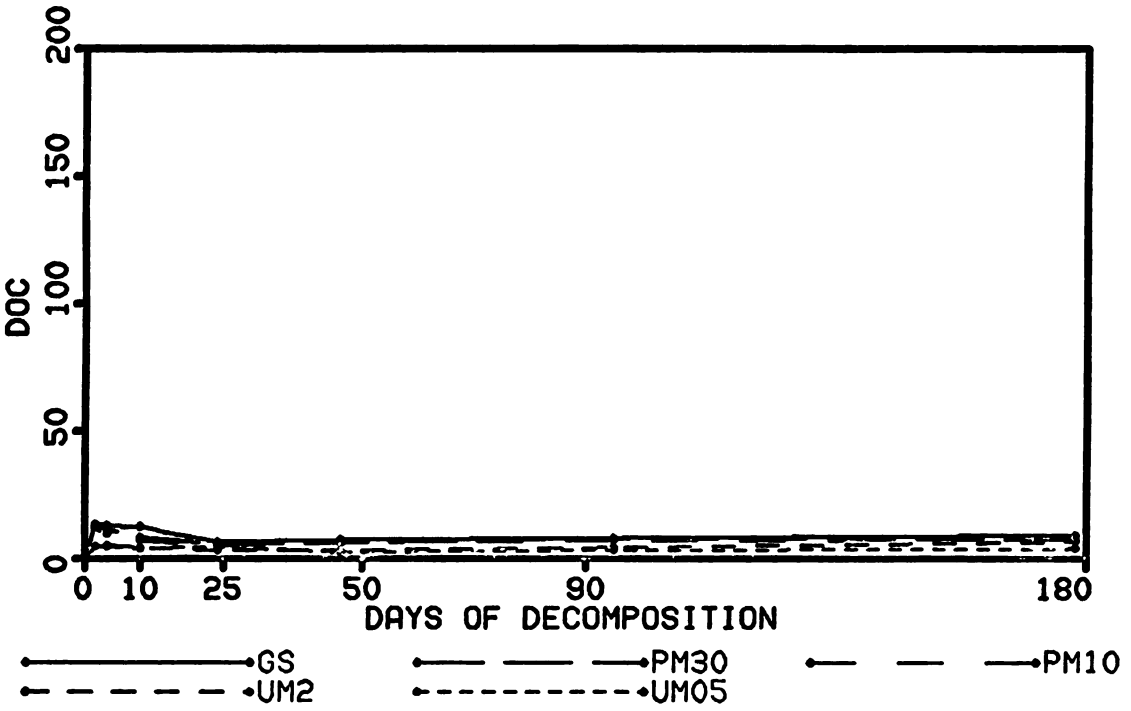
Appendix Figure 43. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



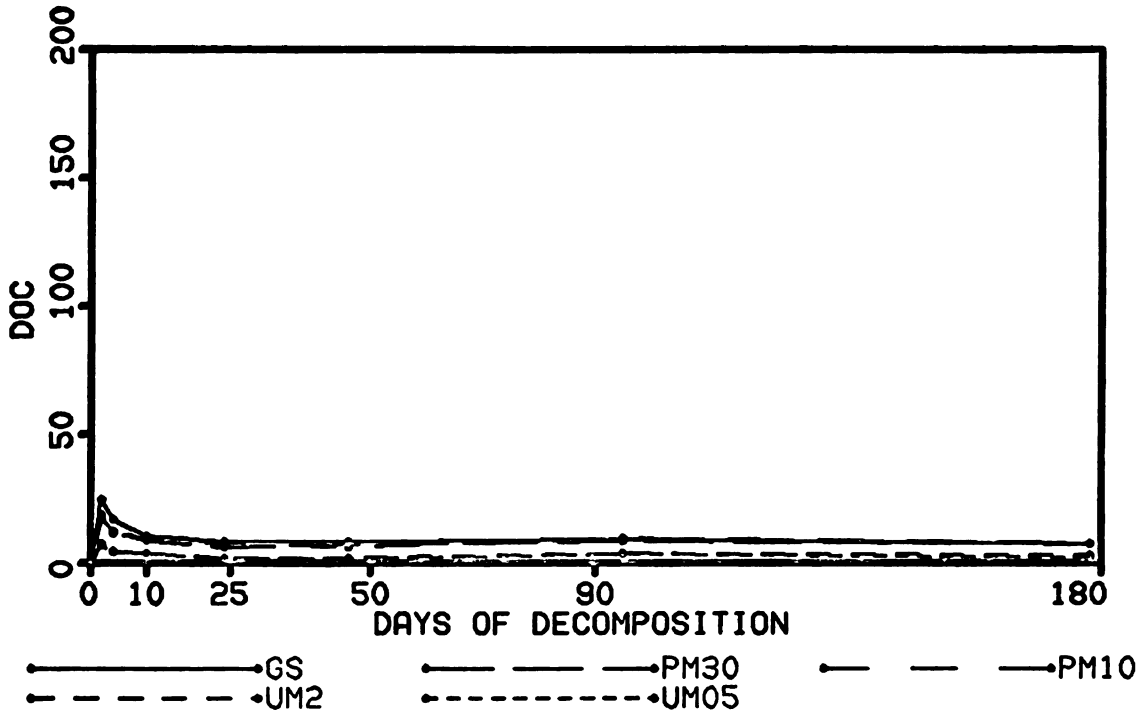
Appendix Figure 44. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



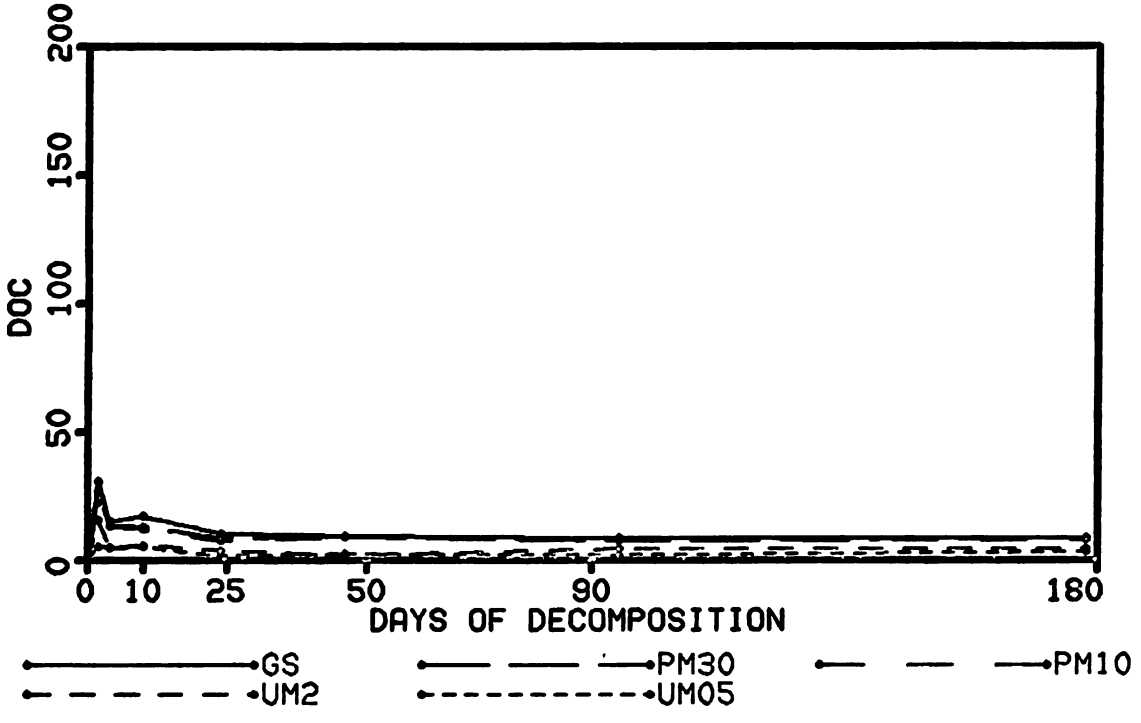
Appendix Figure 45. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



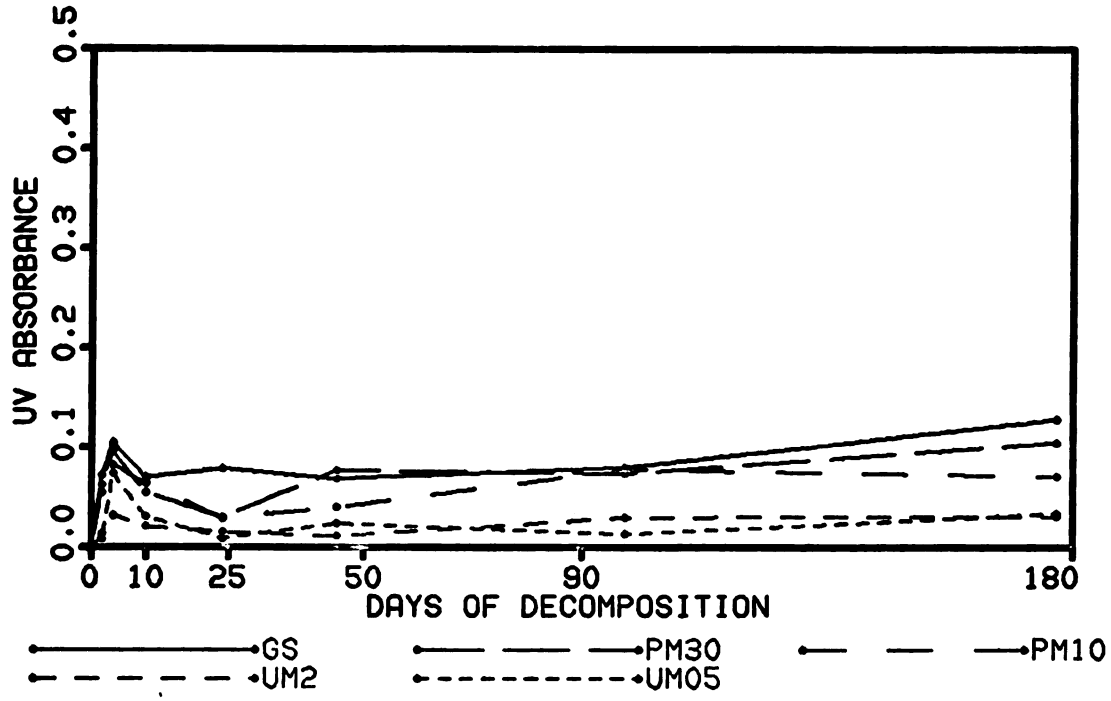
Appendix Figure 46. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



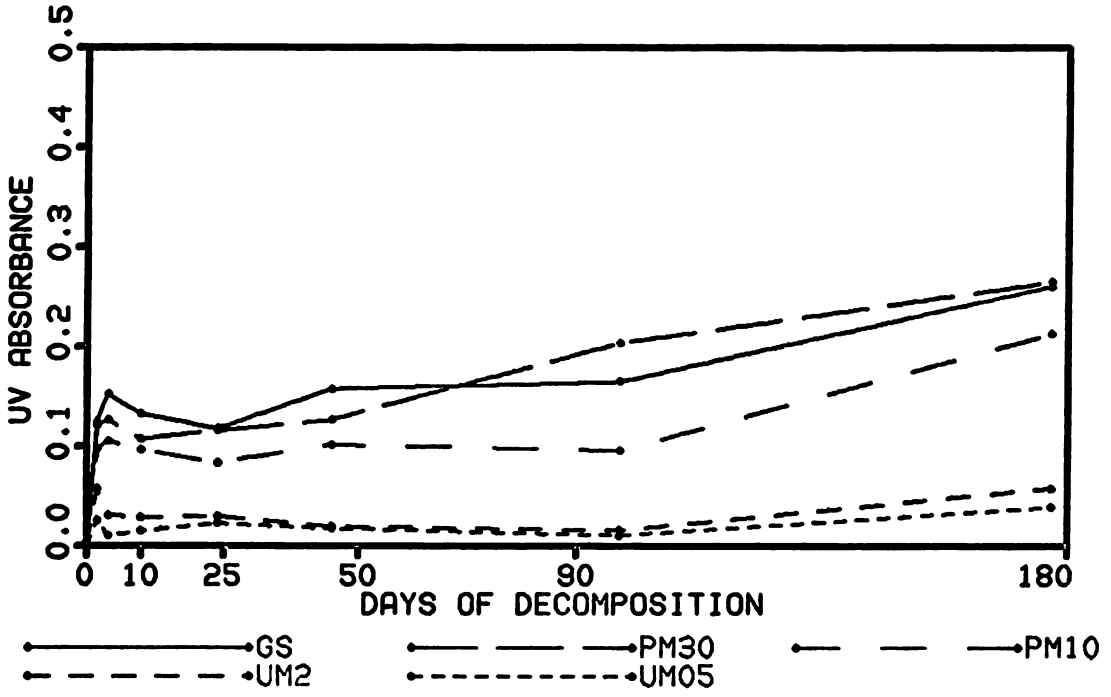
Appendix Figure 47. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



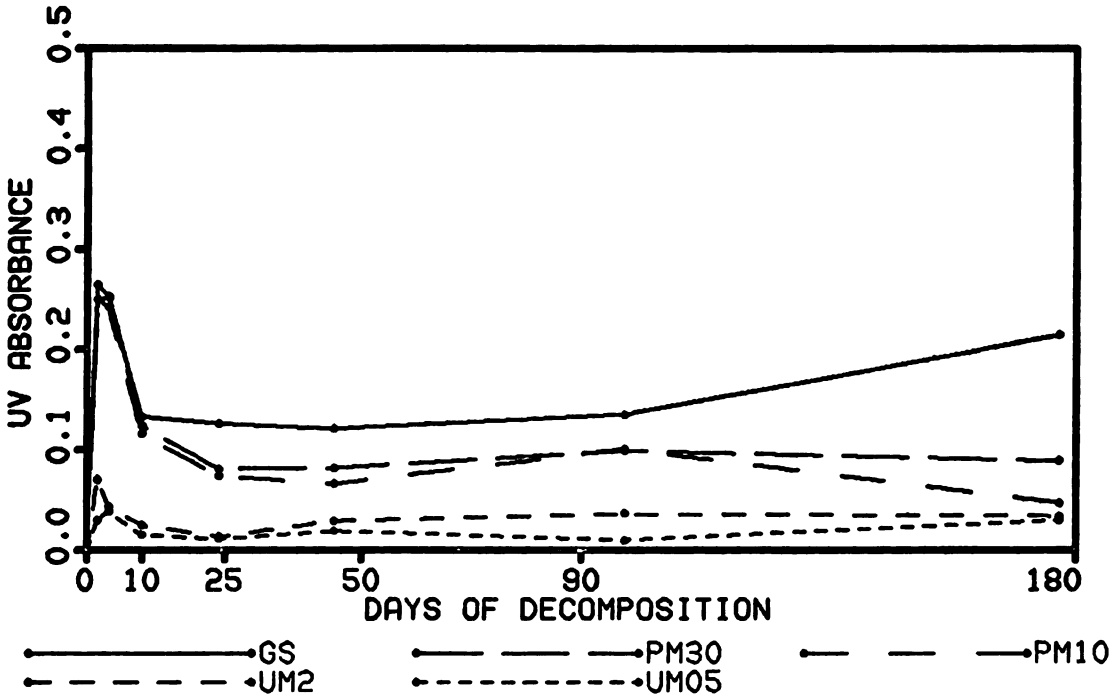
Appendix Figure 48. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. Dissolved organic carbon (mg/l/g initial AFDW) in various molecular weight fractions of DOM.



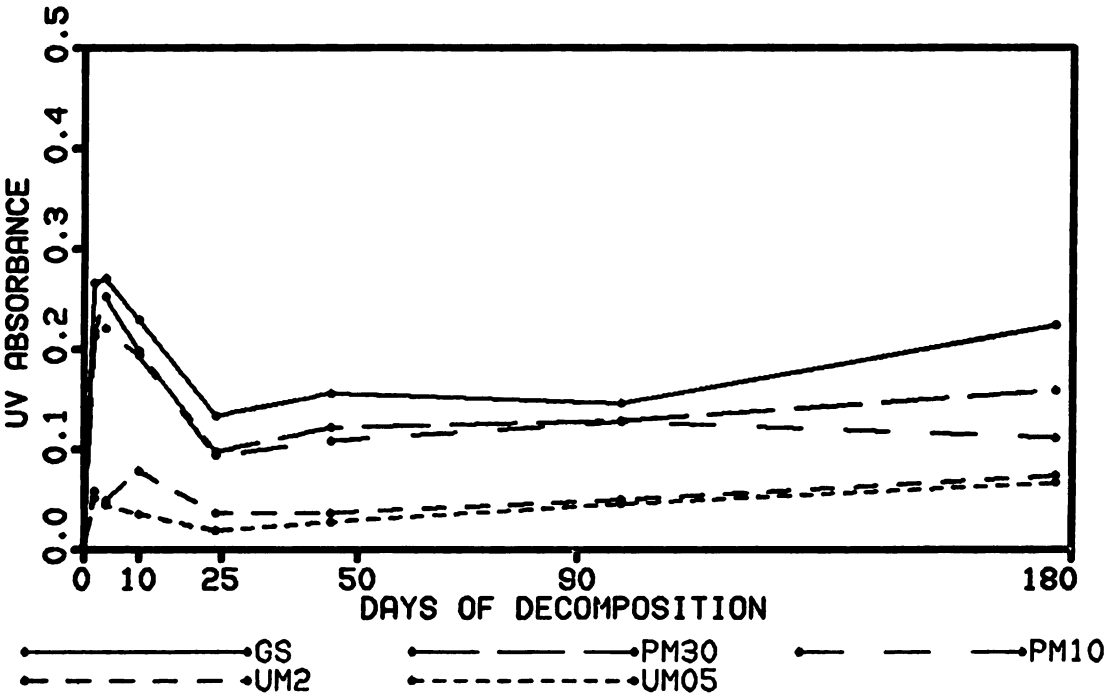
Appendix Figure 49. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



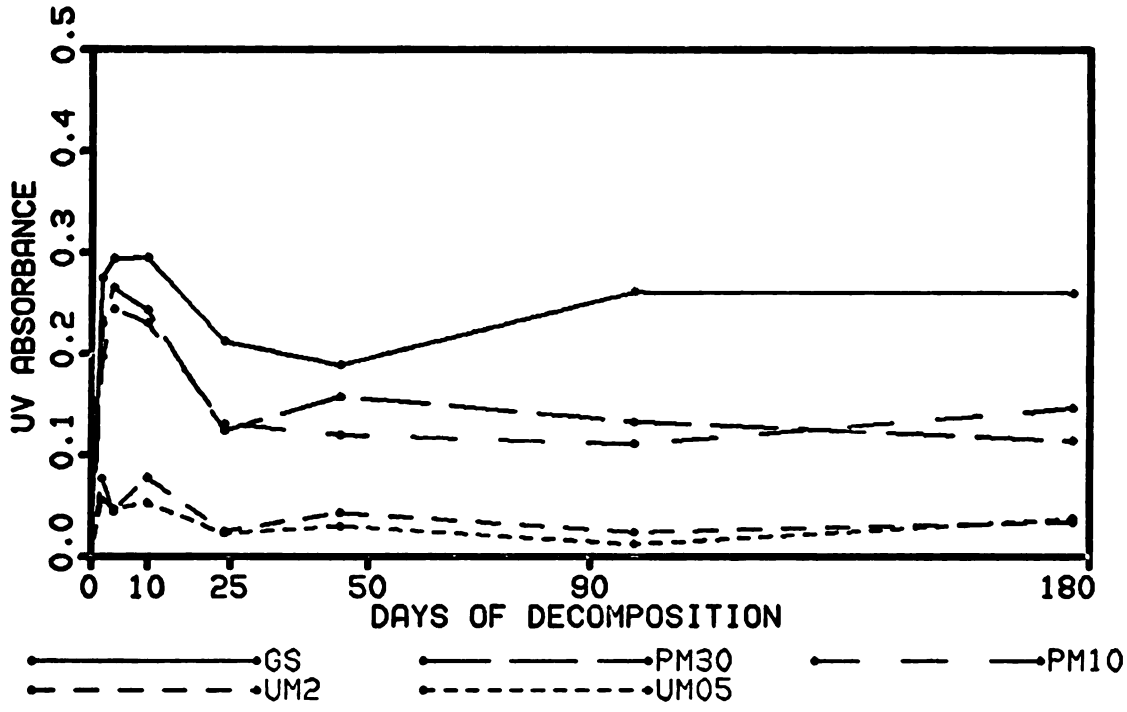
Appendix Figure 50. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



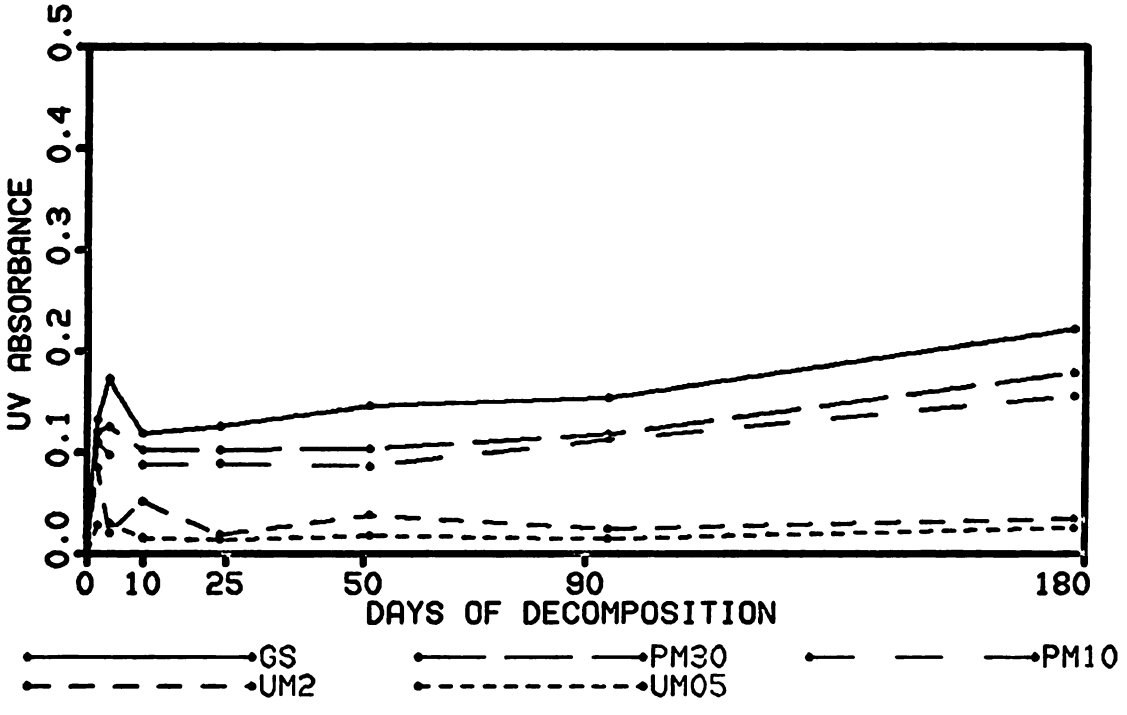
Appendix Figure 51. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



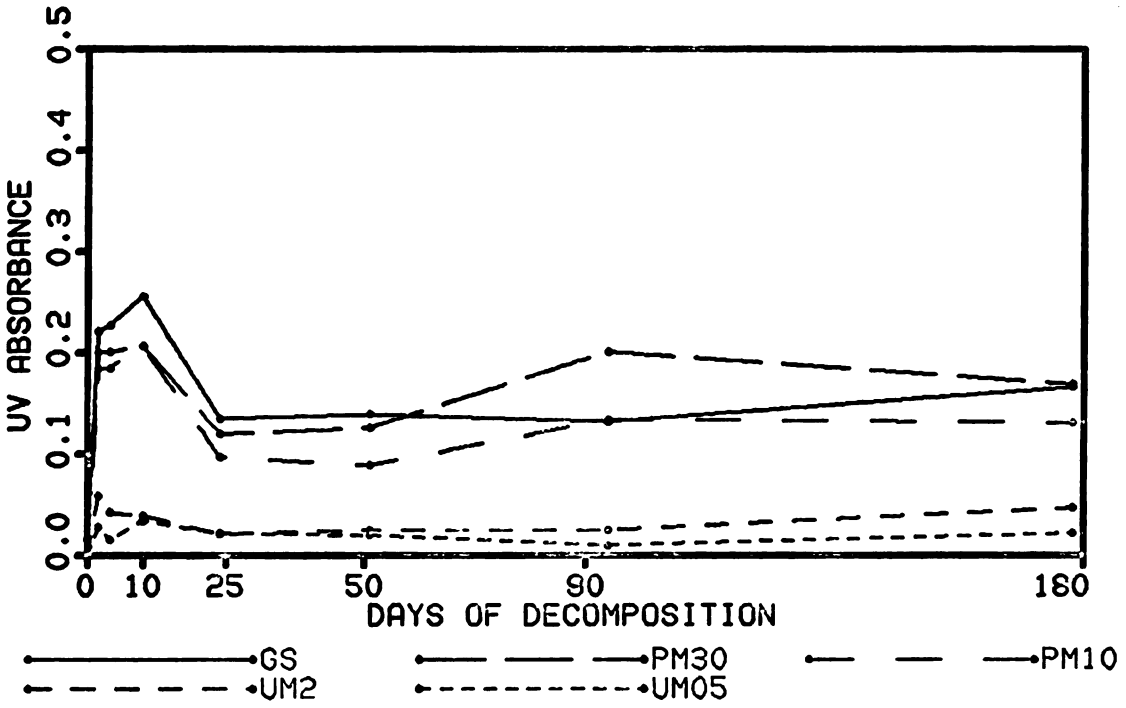
Appendix Figure 52. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



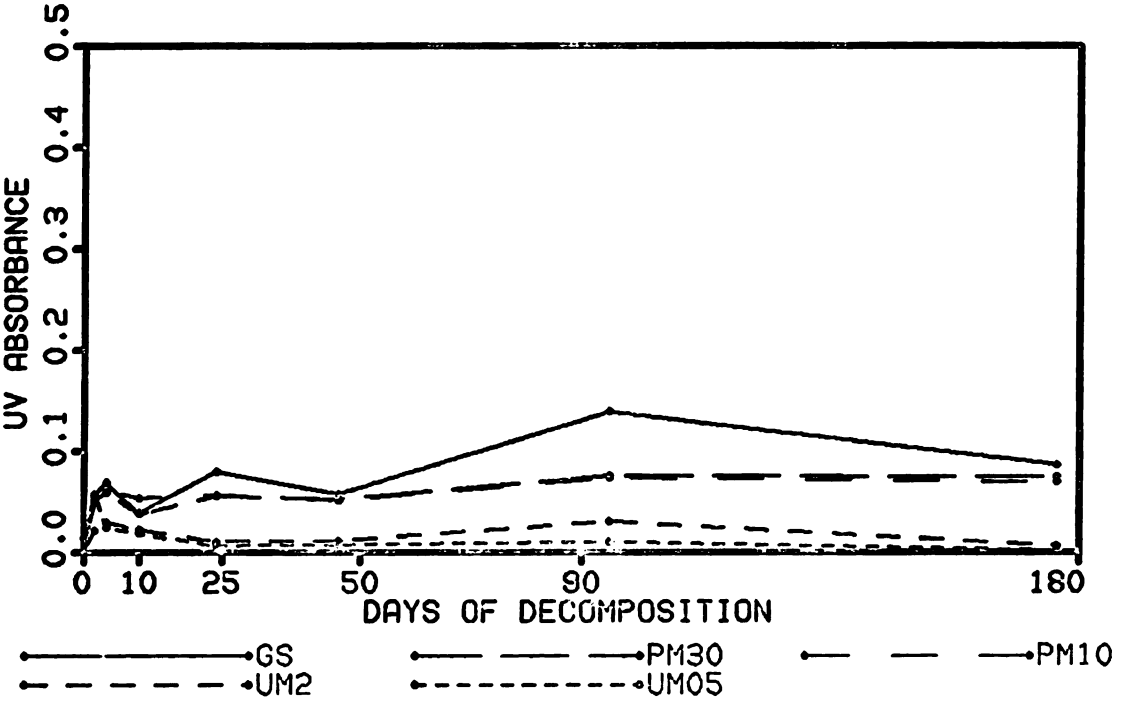
Appendix Figure 53. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



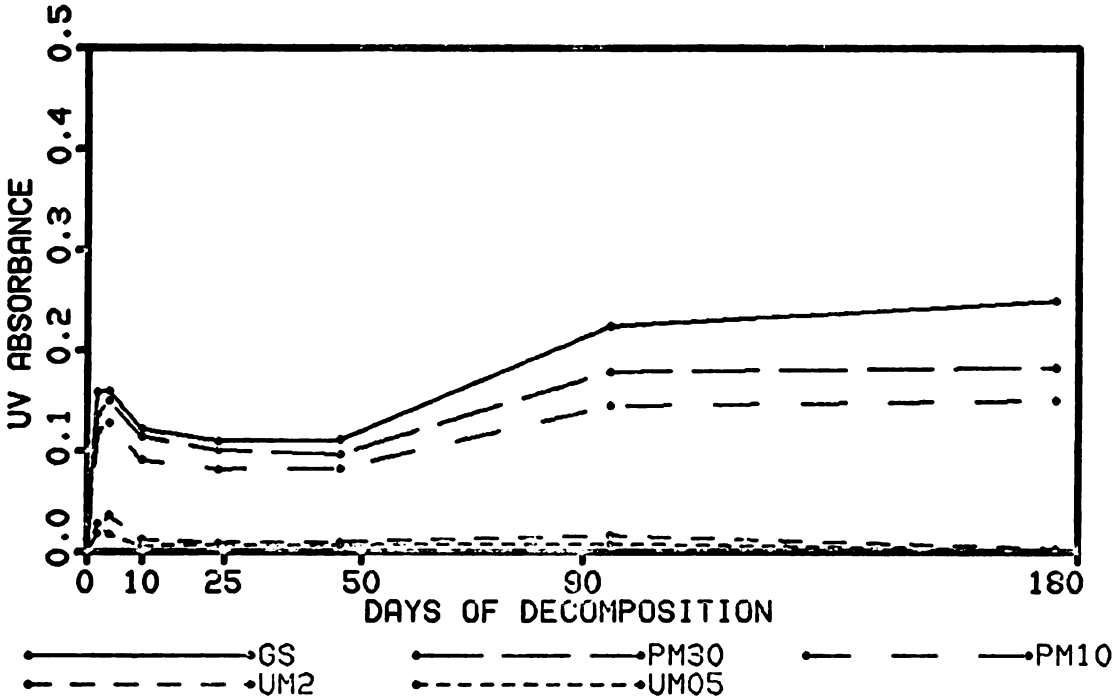
Appendix Figure 54. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



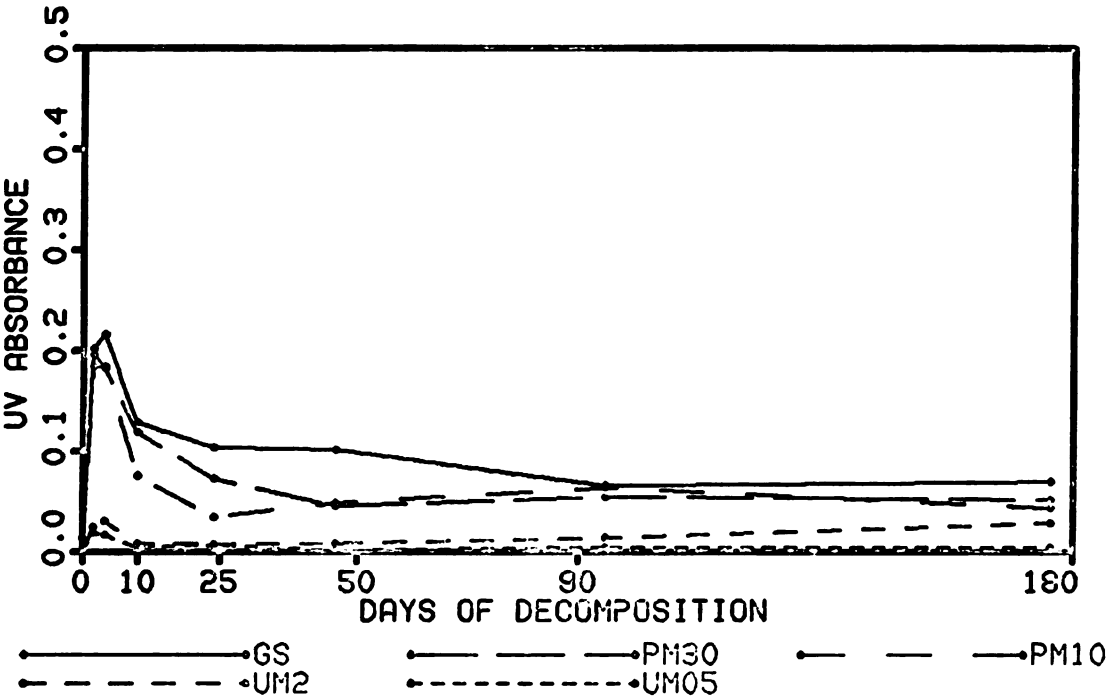
Appendix Figure 55. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



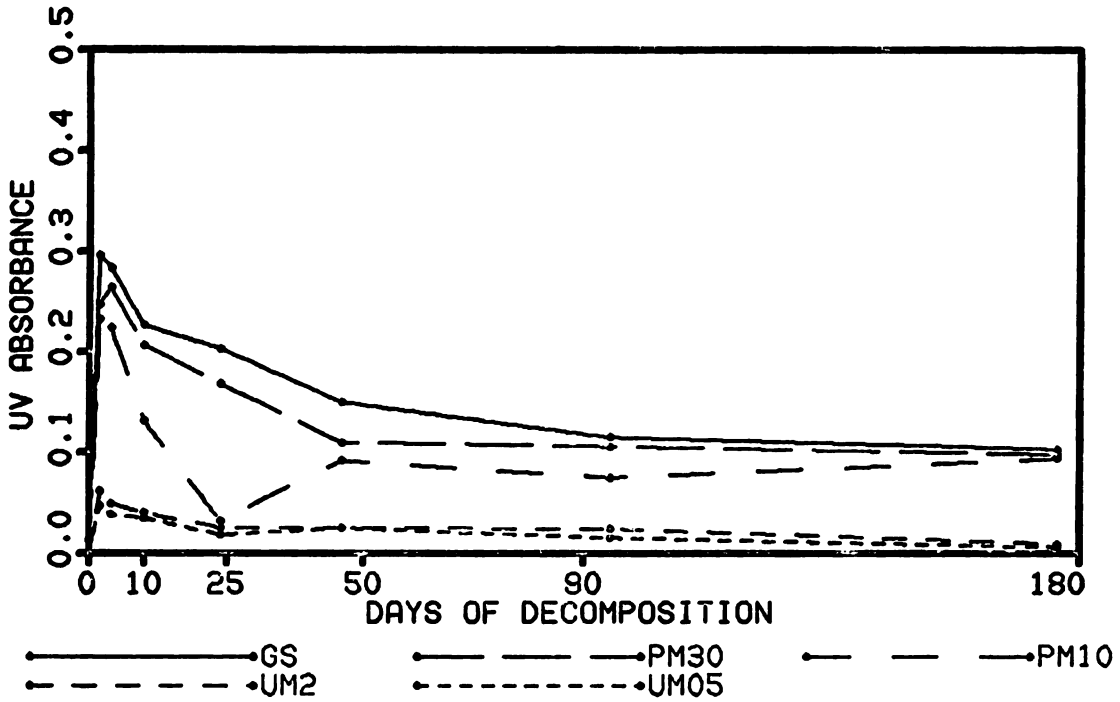
Appendix Figure 56. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



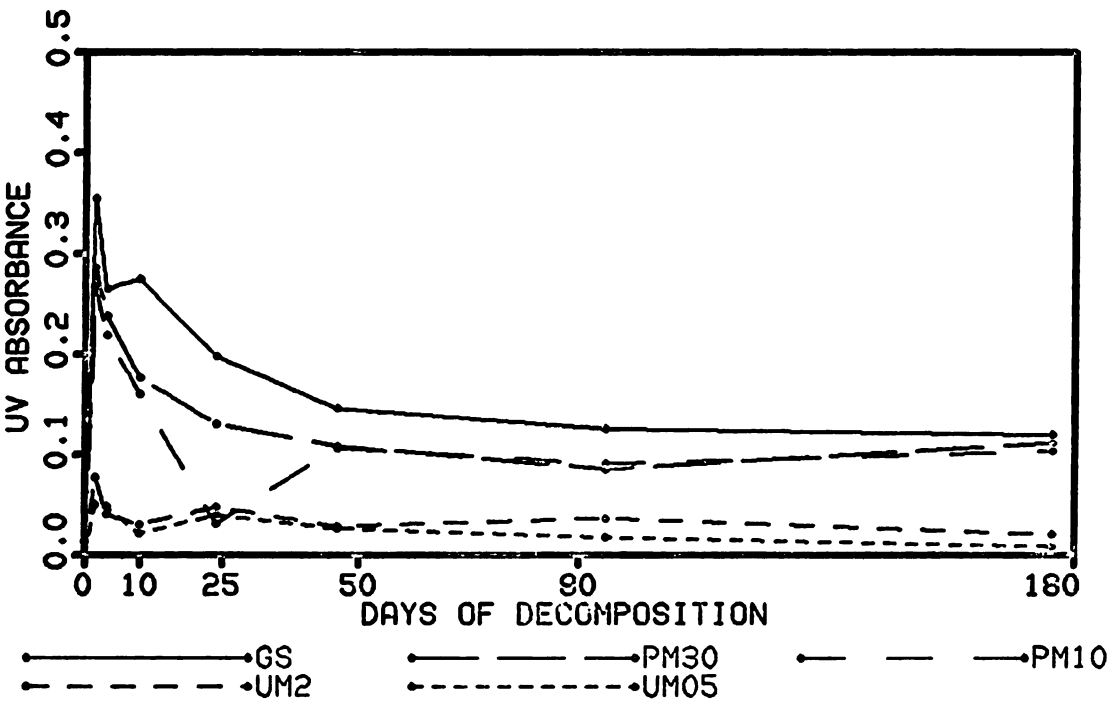
Appendix Figure 57. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



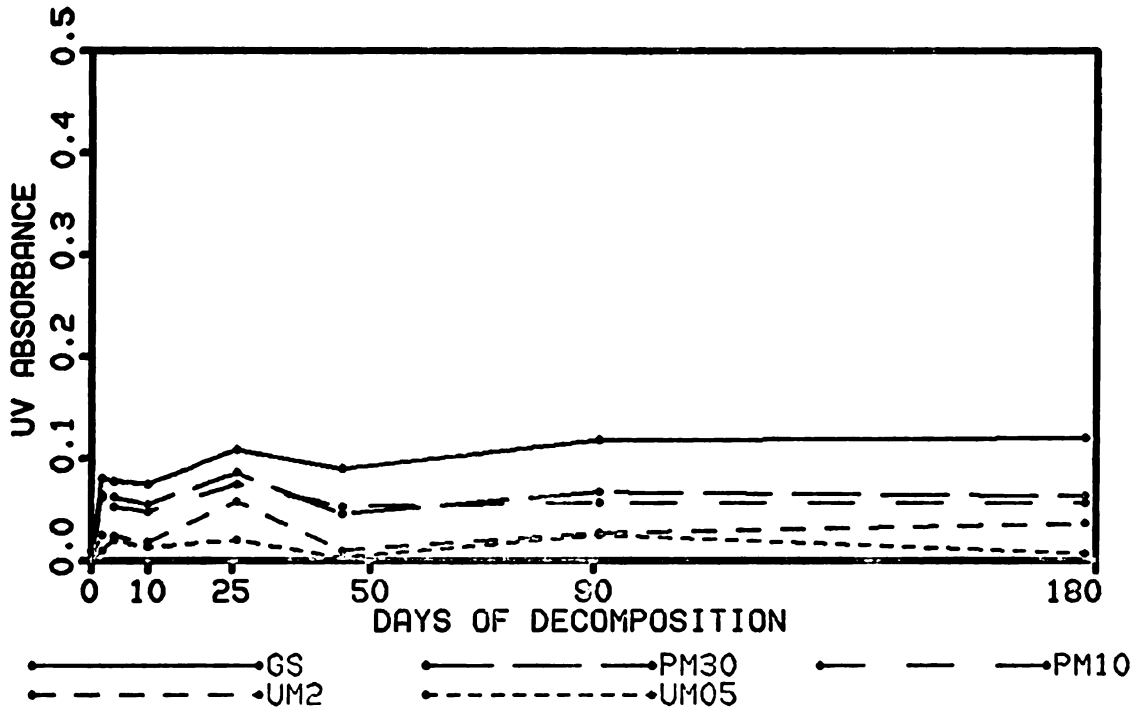
Appendix Figure 58. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



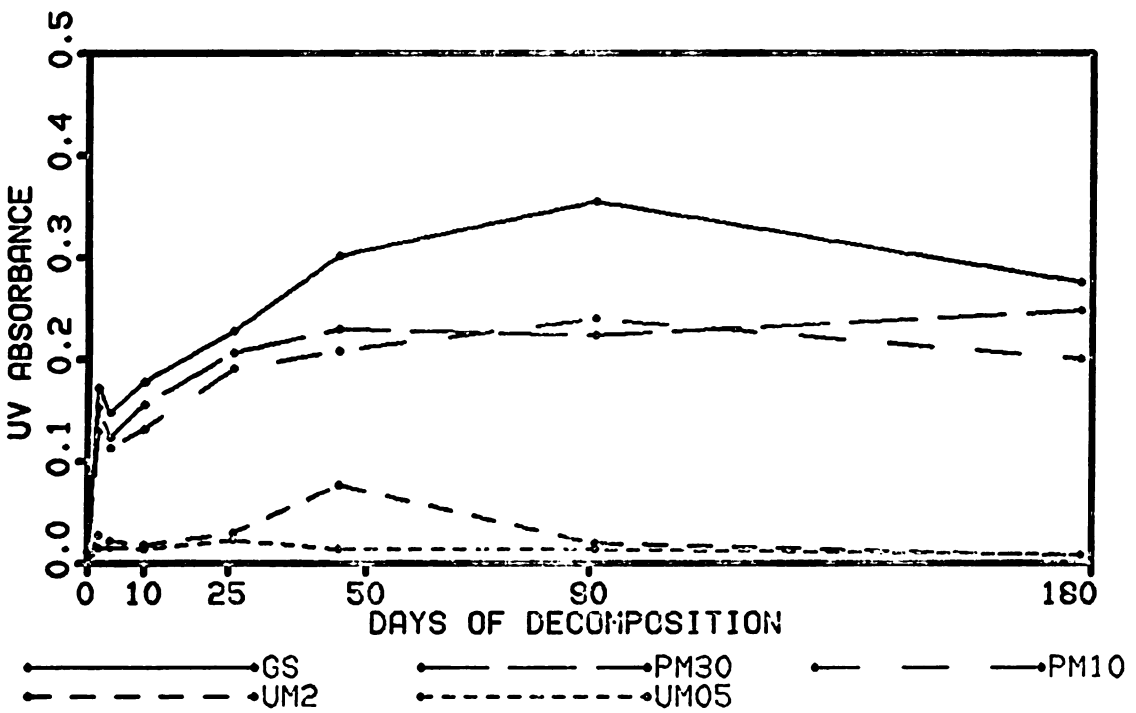
Appendix Figure 59. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



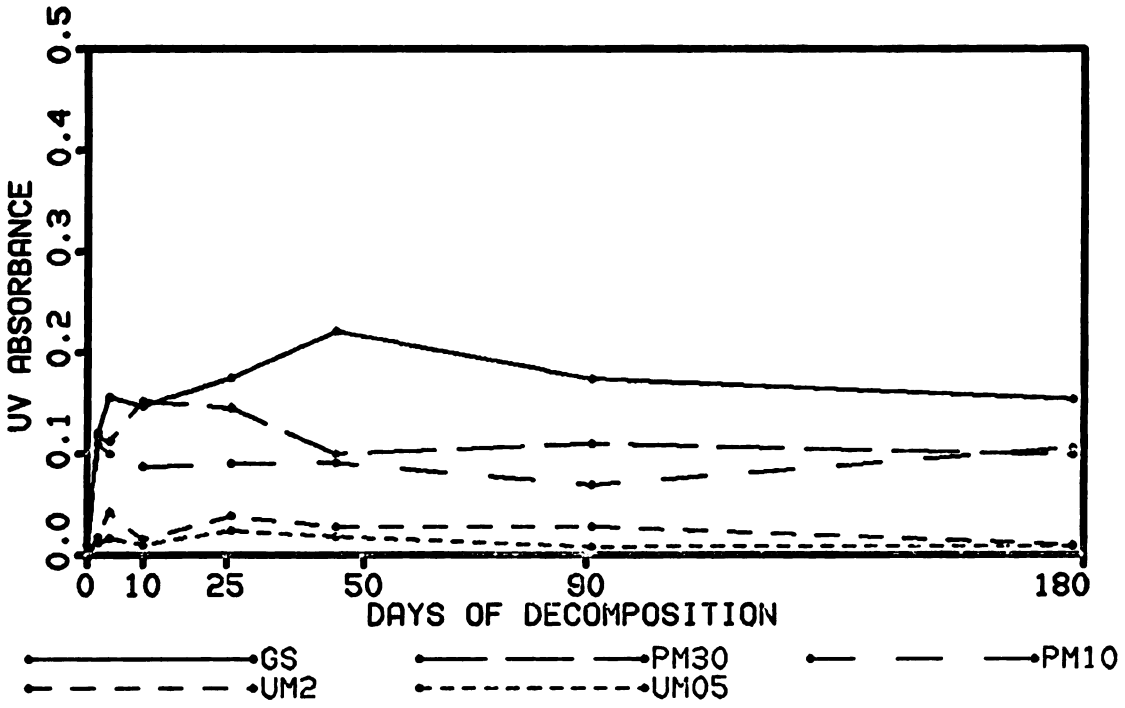
Appendix Figure 60. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



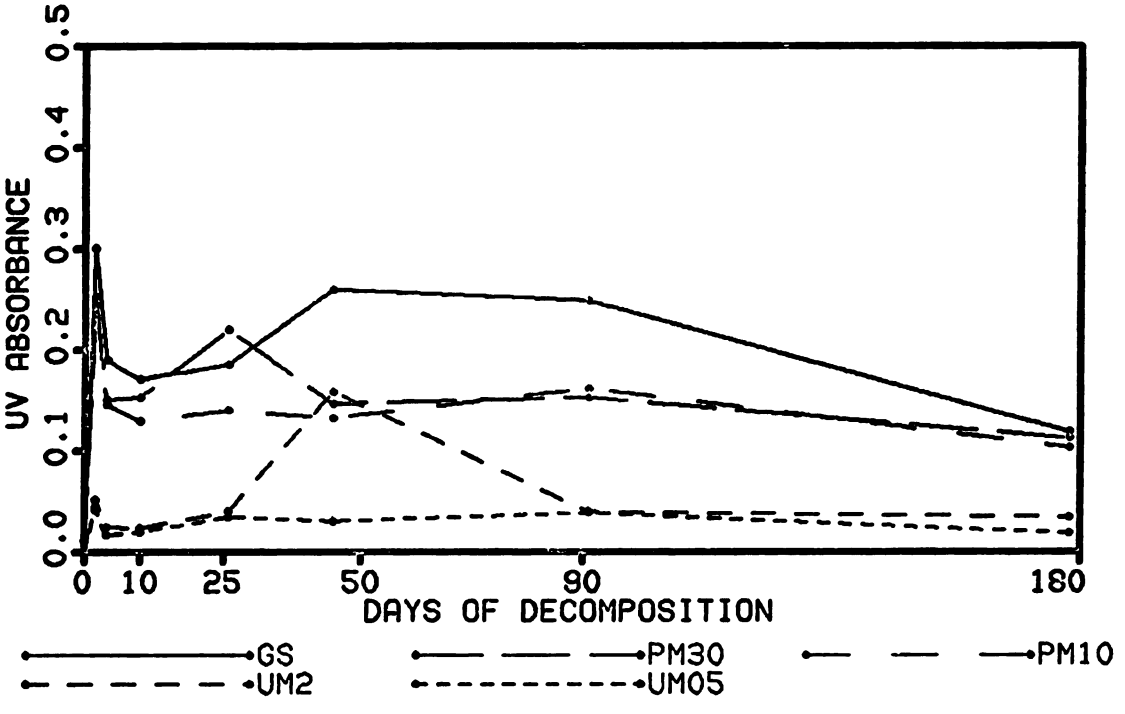
Appendix Figure 61. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



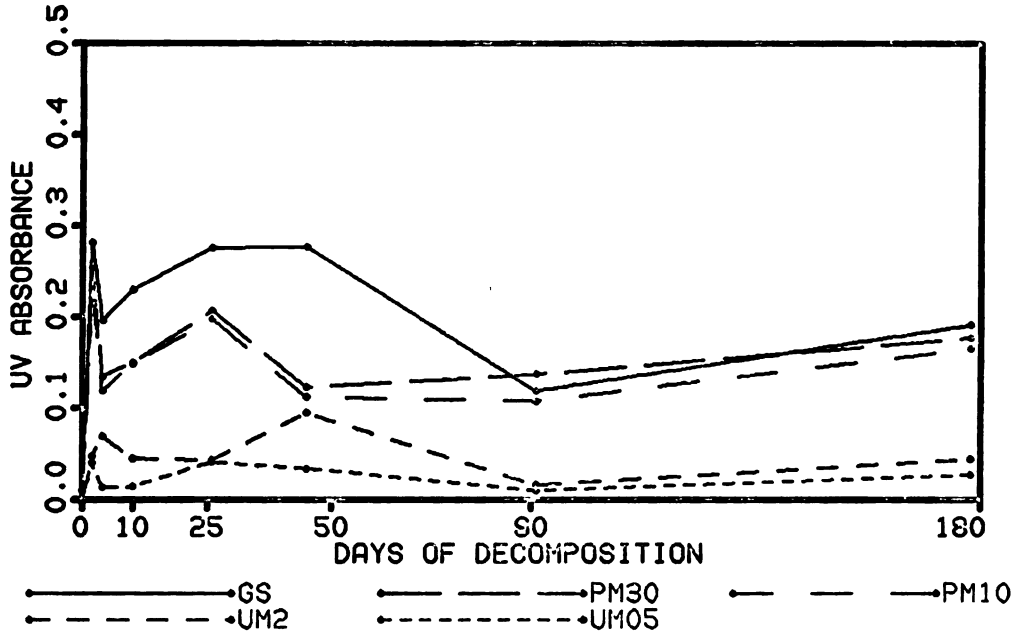
Appendix Figure 62. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



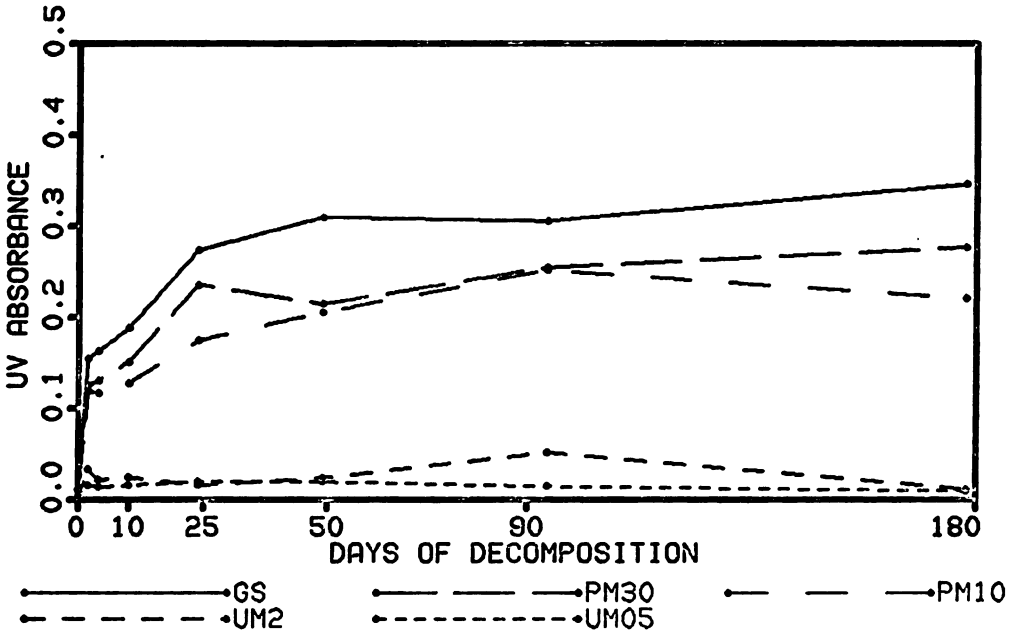
Appendix Figure 63. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



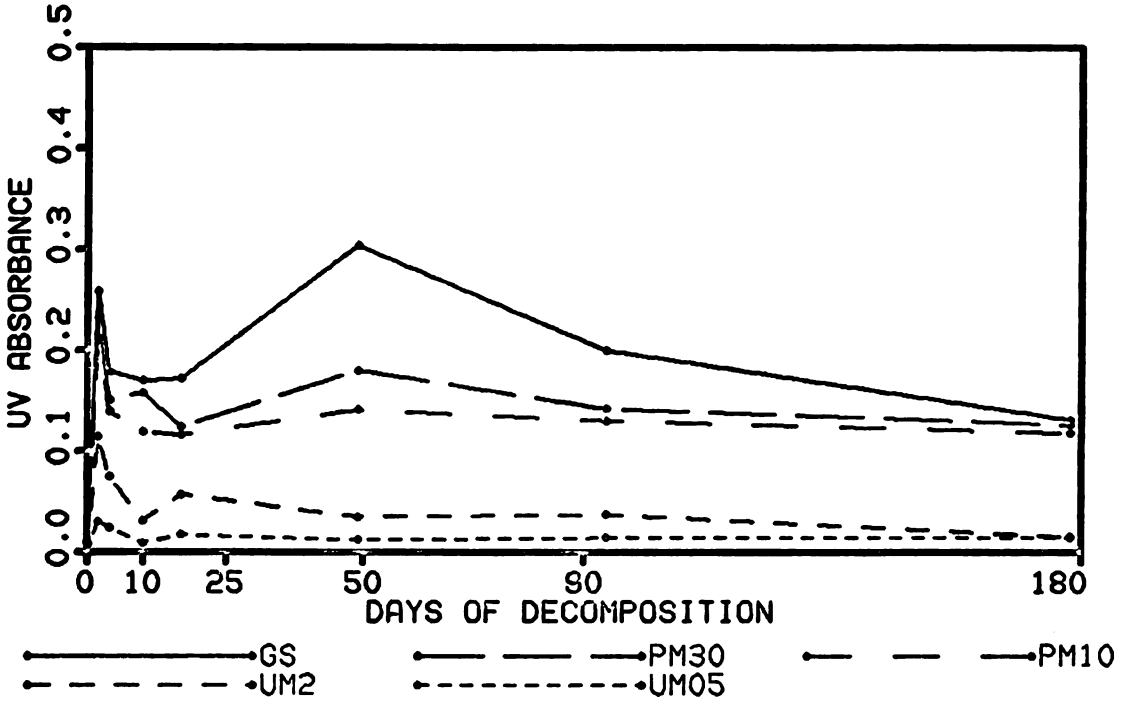
Appendix Figure 64. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



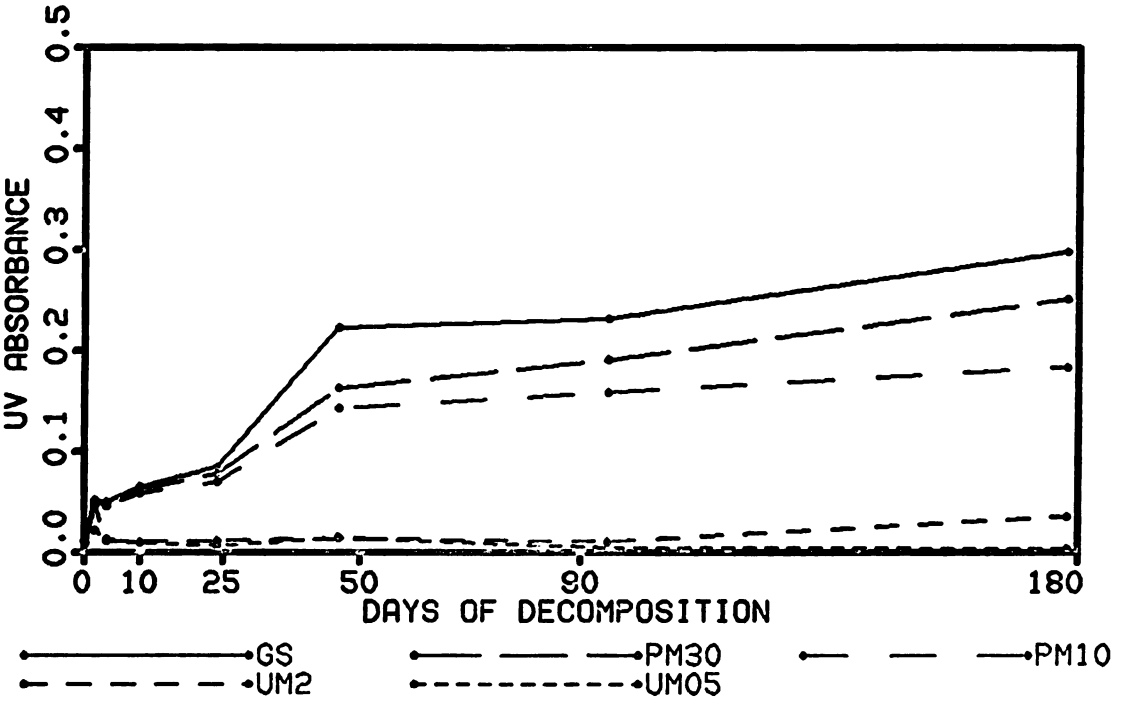
Appendix Figure 65. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



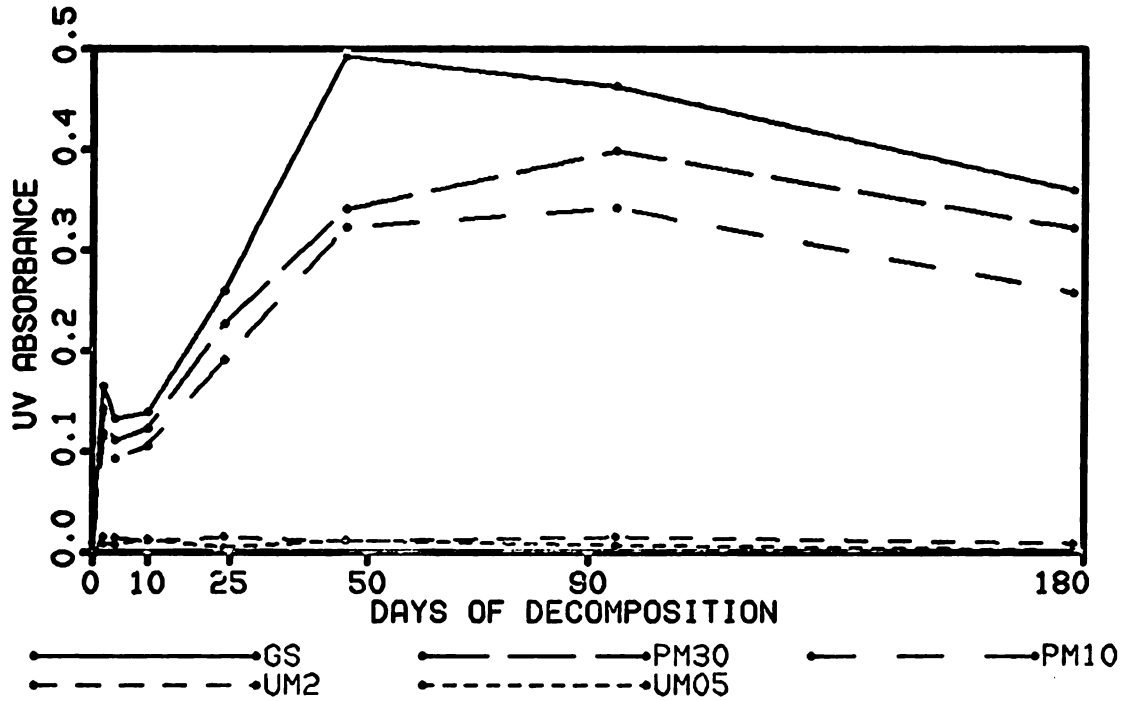
Appendix Figure 66. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



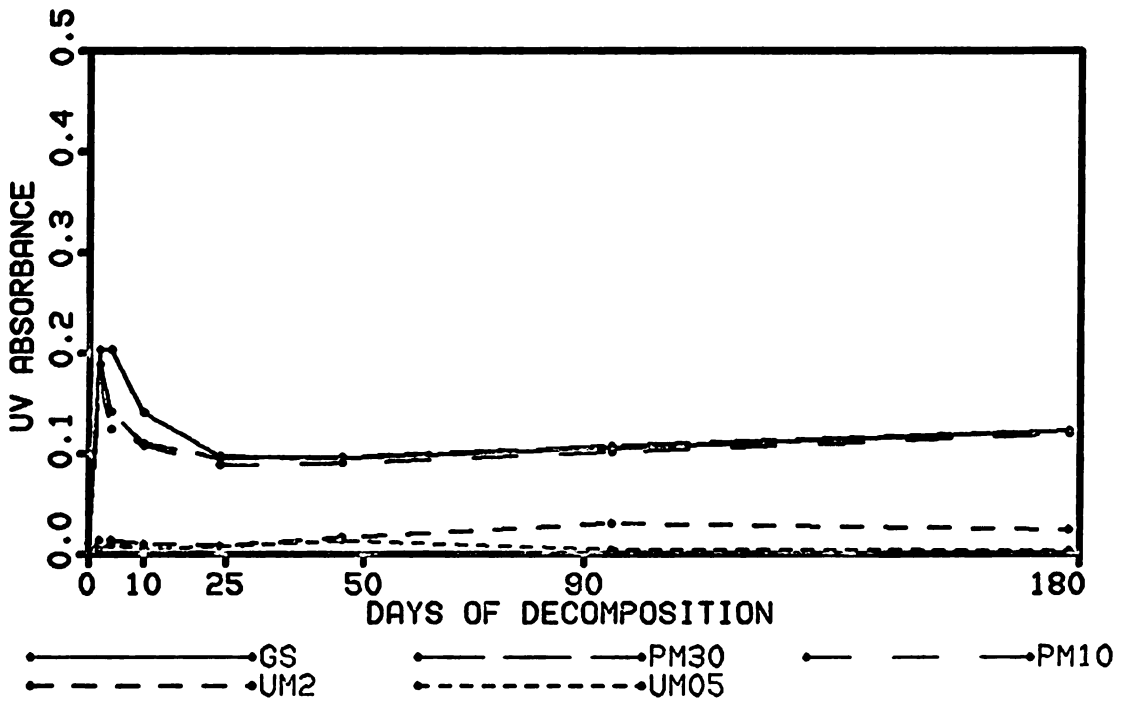
Appendix Figure 67. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



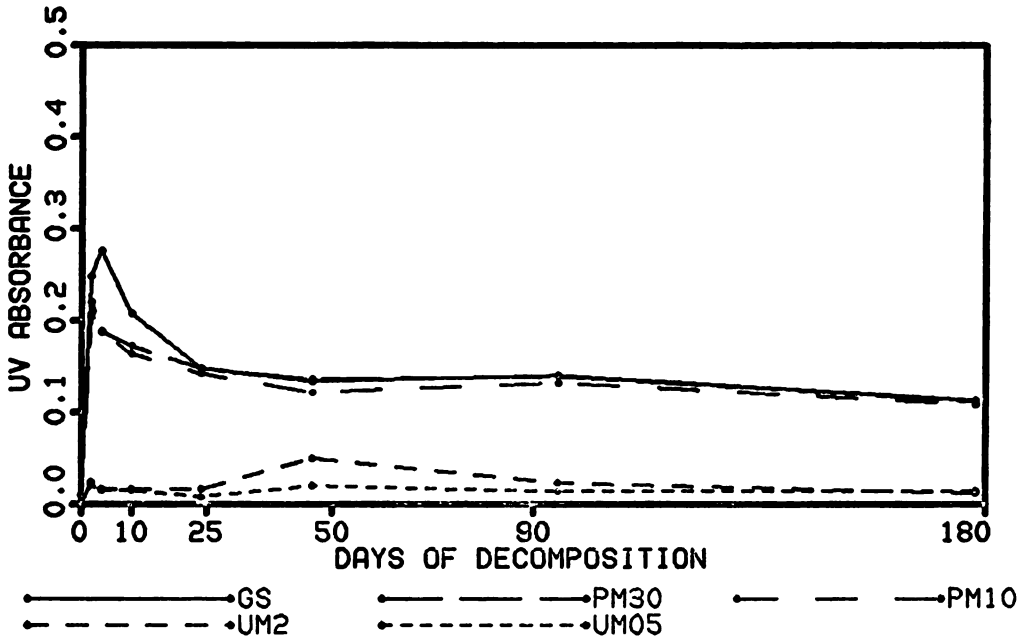
Appendix Figure 68. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



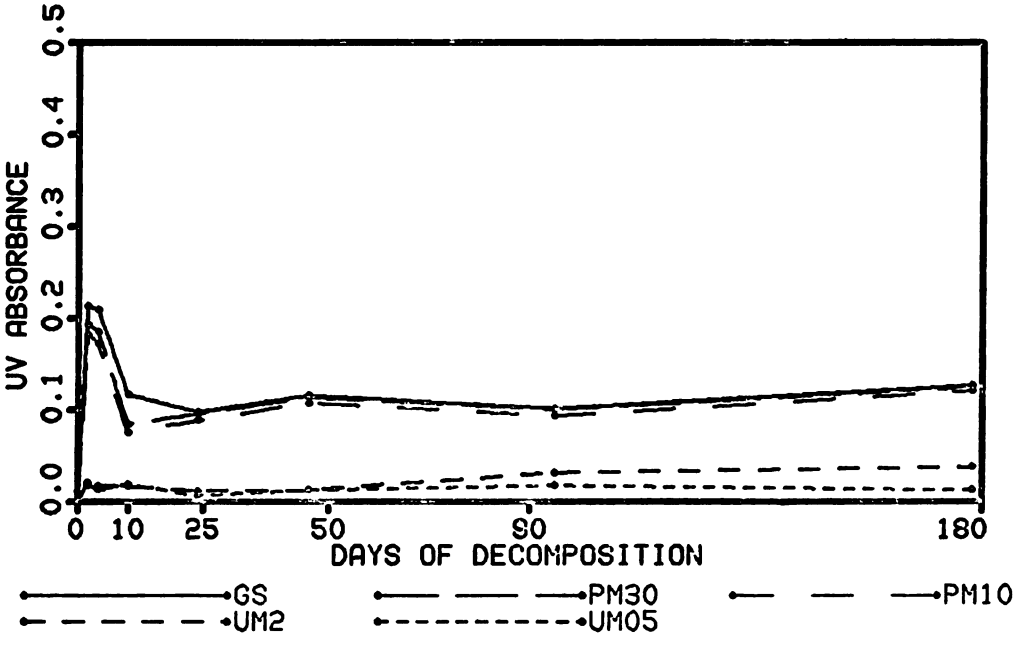
Appendix Figure 69. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



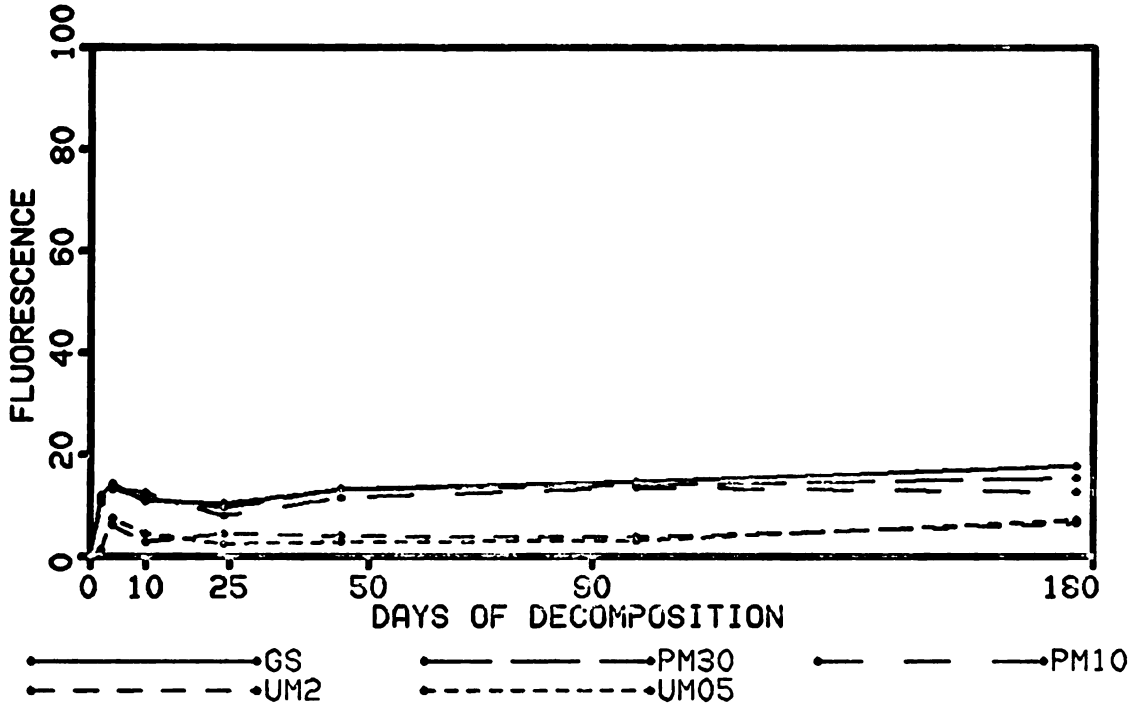
Appendix Figure 70. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



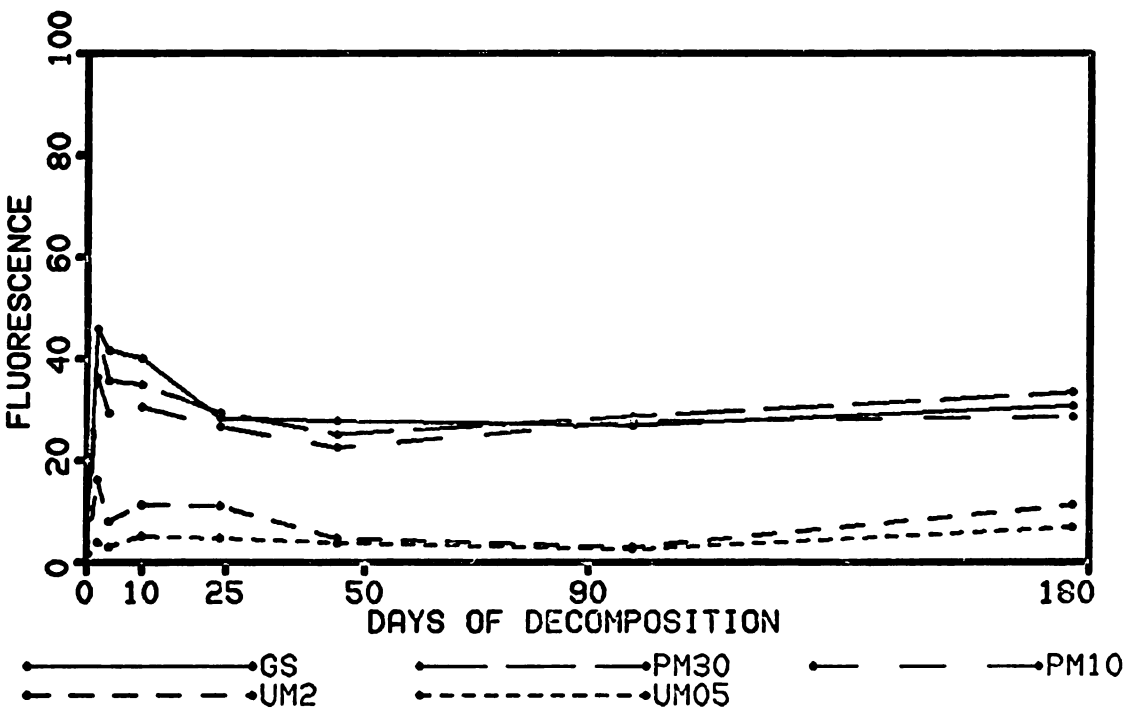
Appendix Figure 71. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



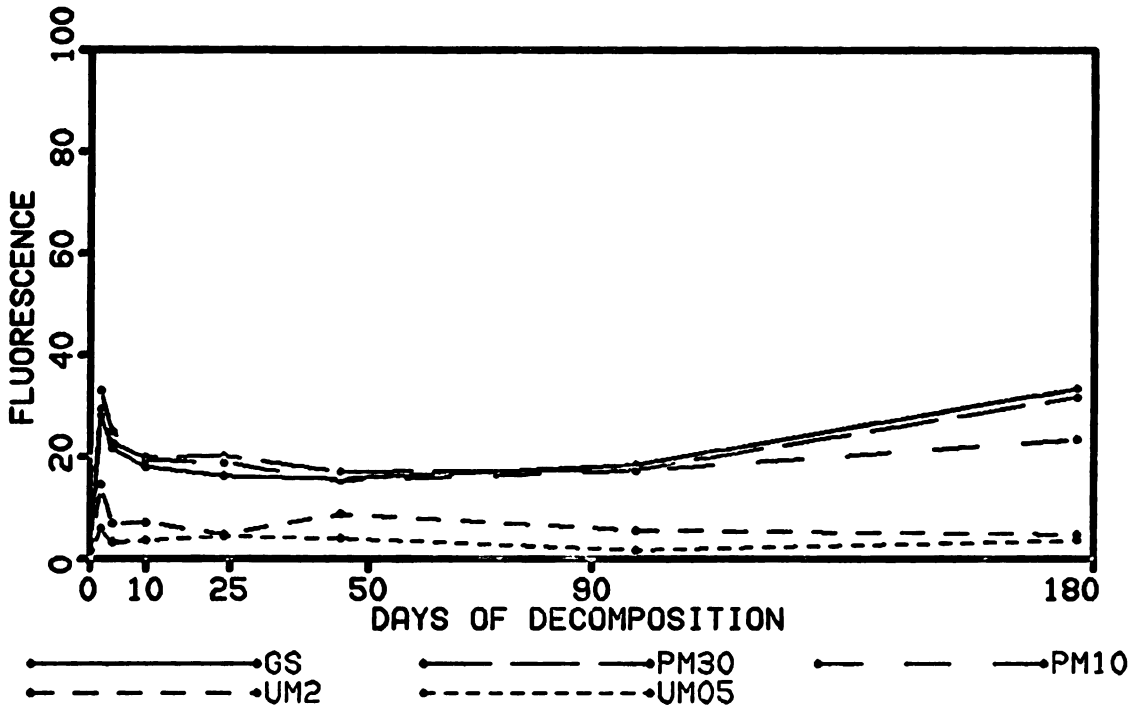
Appendix Figure 72. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. Absorbance of UV light (250 nm) by various molecular weight fractions of DOM, per g initial AFDW.



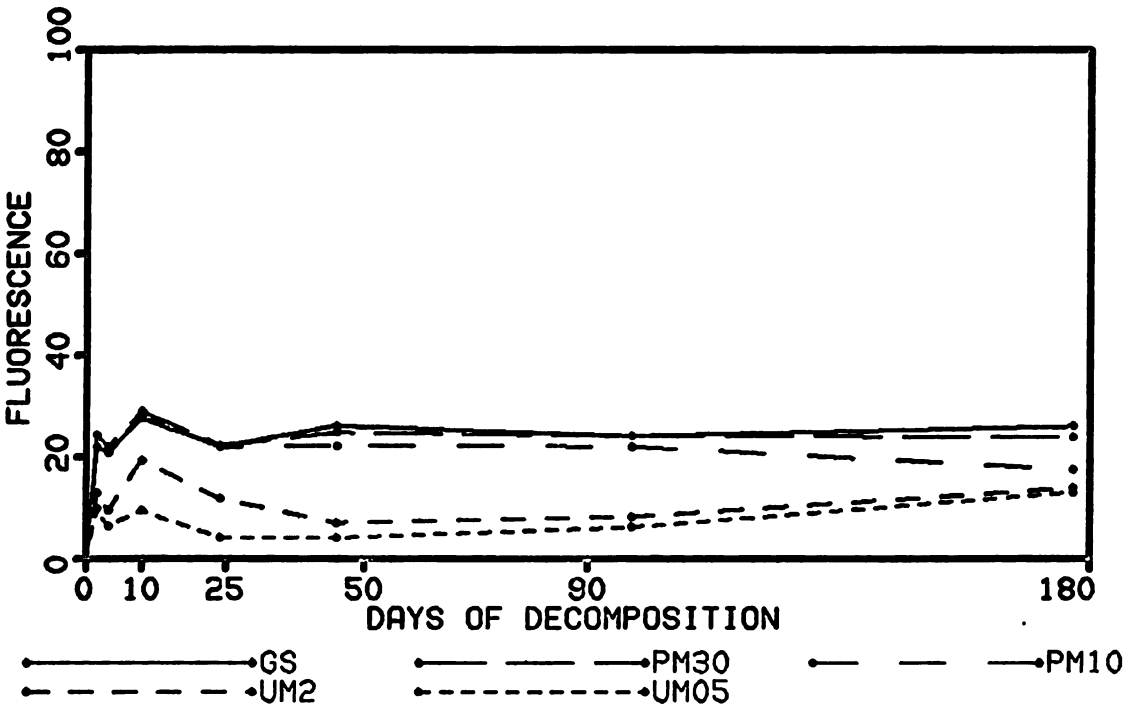
Appendix Figure 73. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



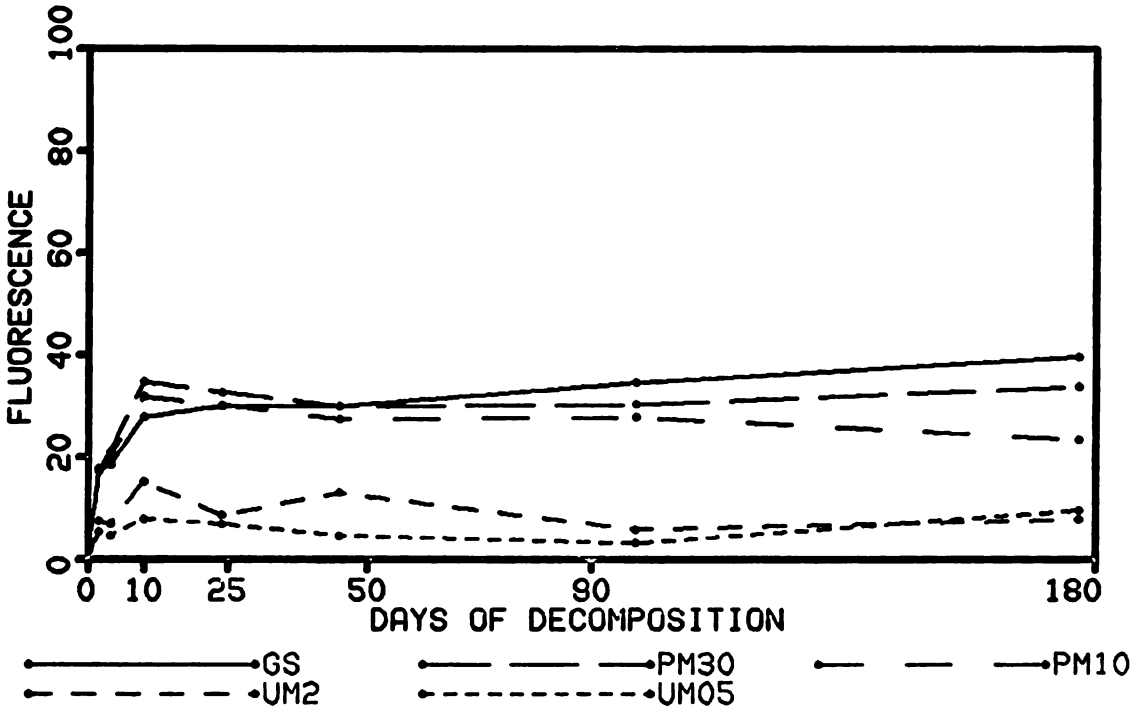
Appendix Figure 74. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



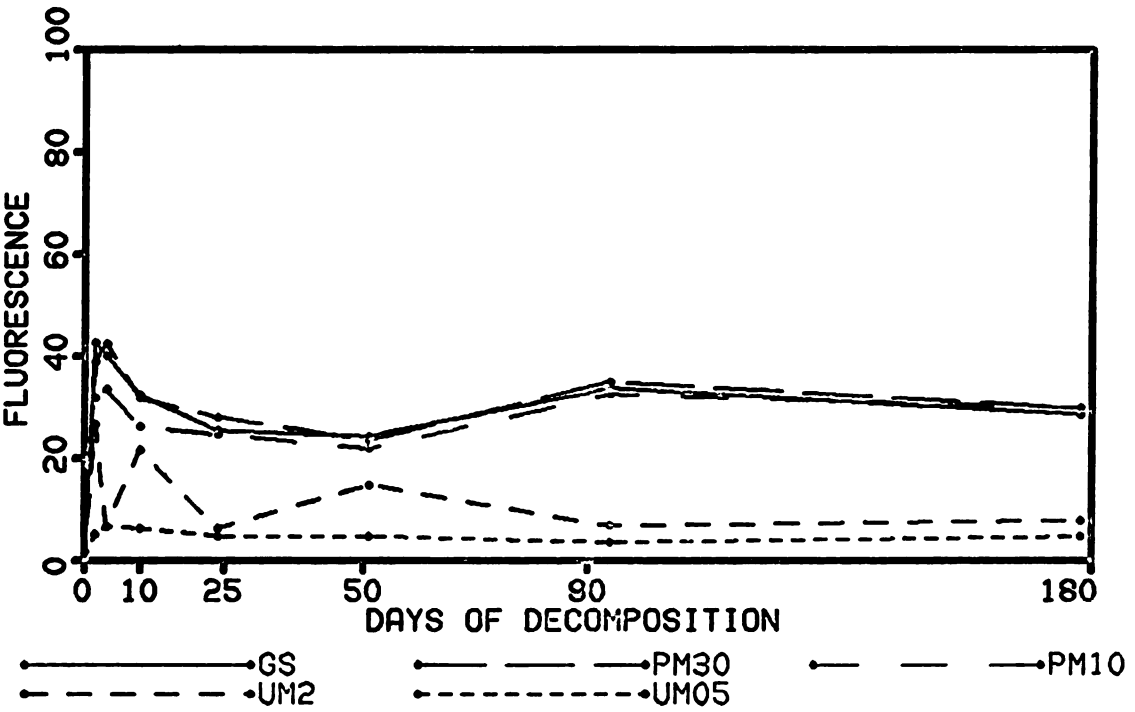
Appendix Figure 75. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



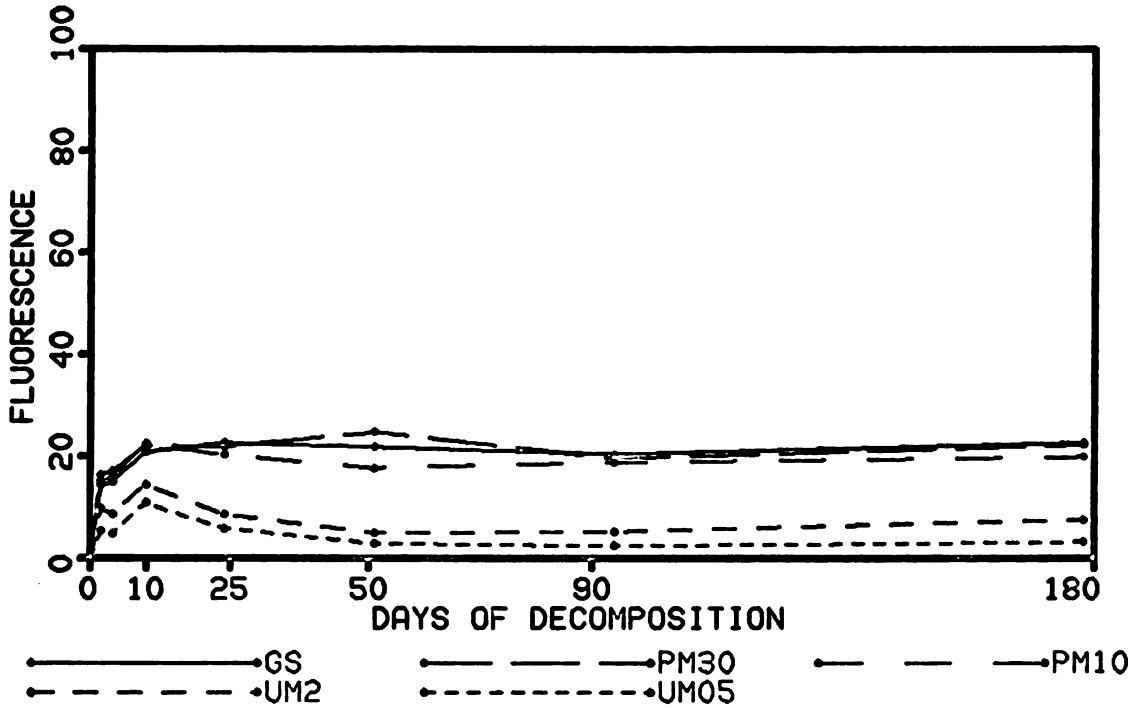
Appendix Figure 76. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



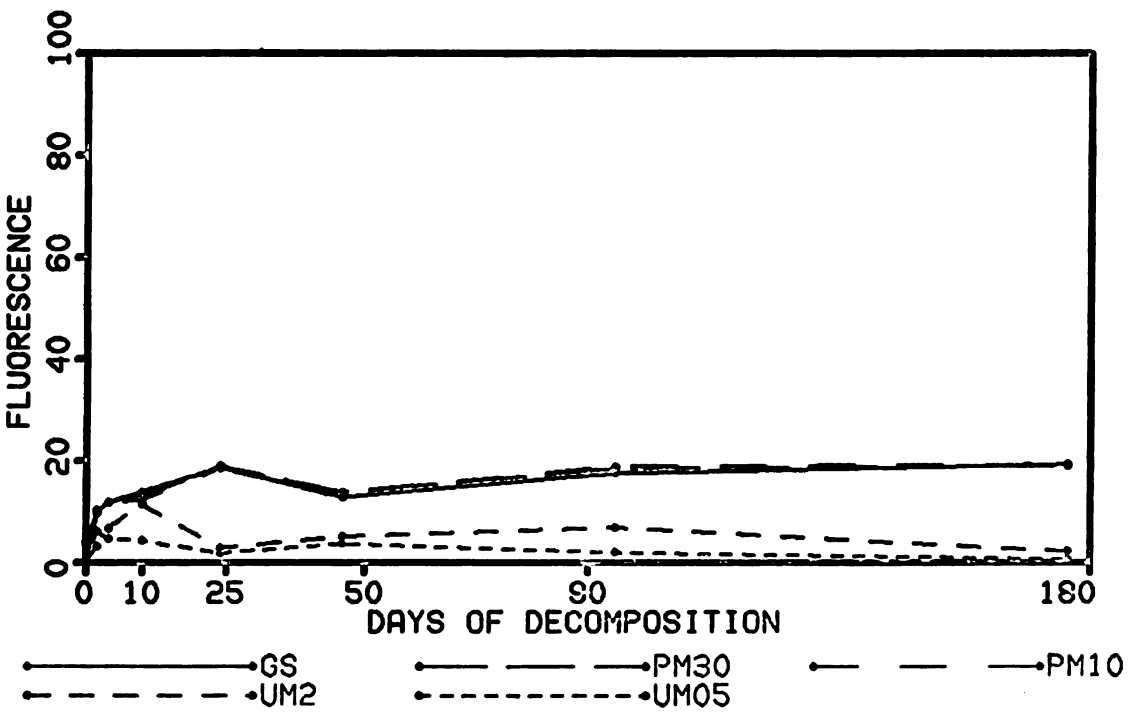
Appendix Figure 77. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



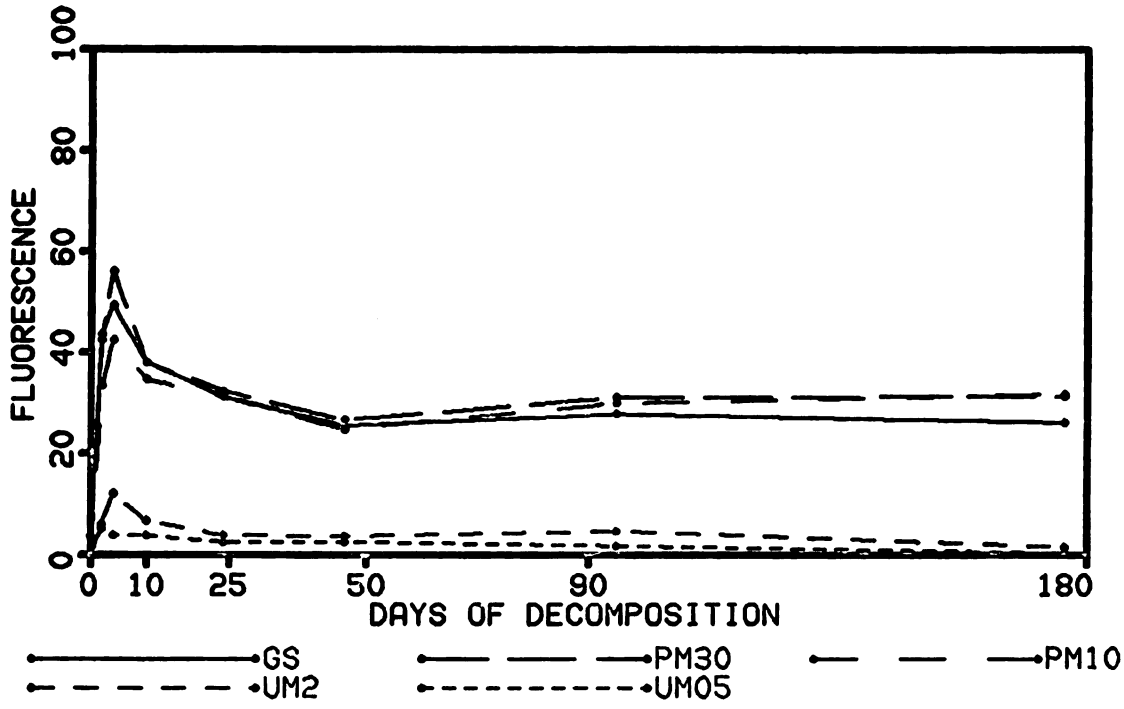
Appendix Figure 78. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



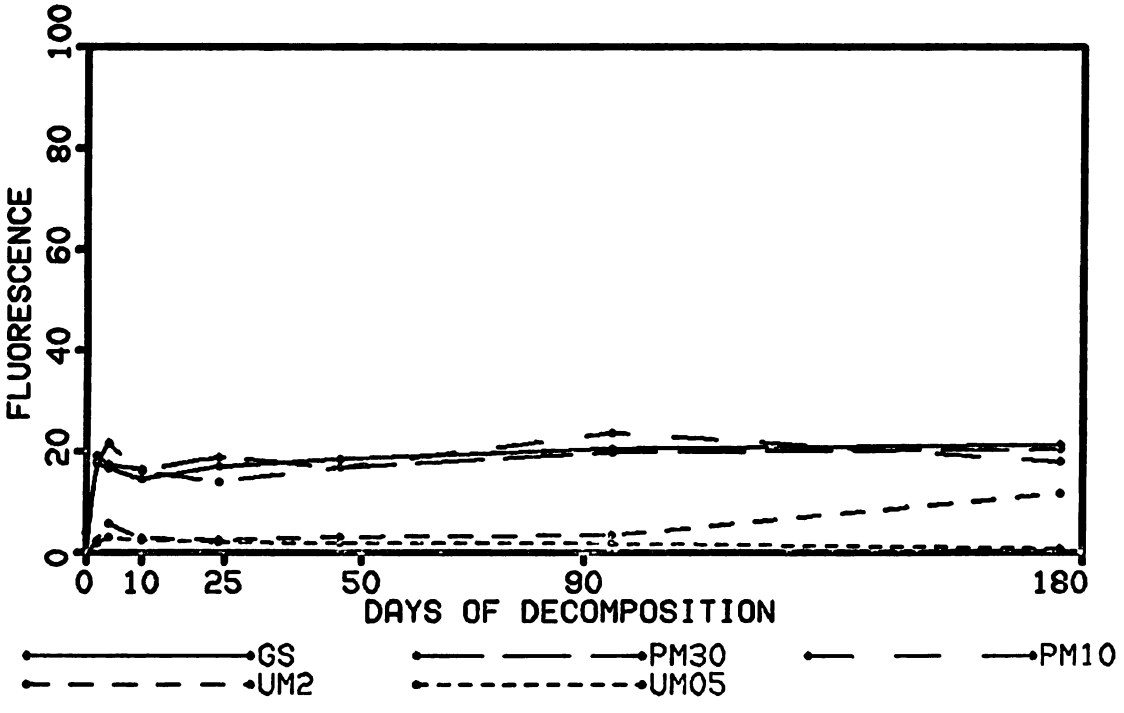
Appendix Figure 79. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



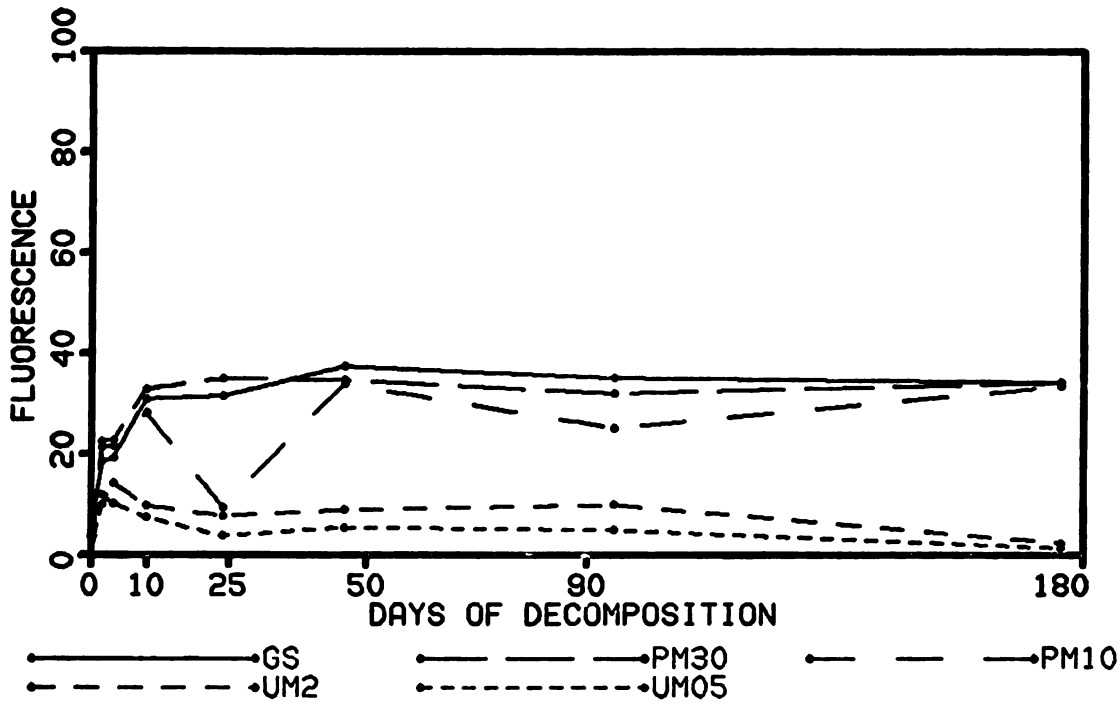
Appendix Figure 80. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



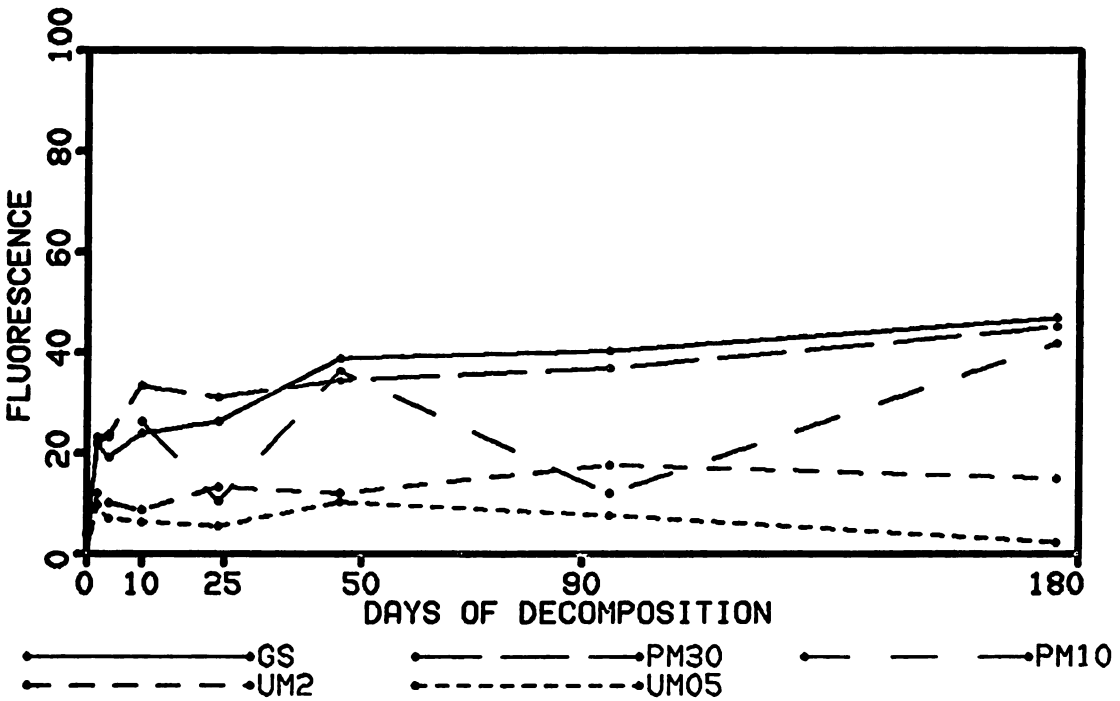
Appendix Figure 81. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



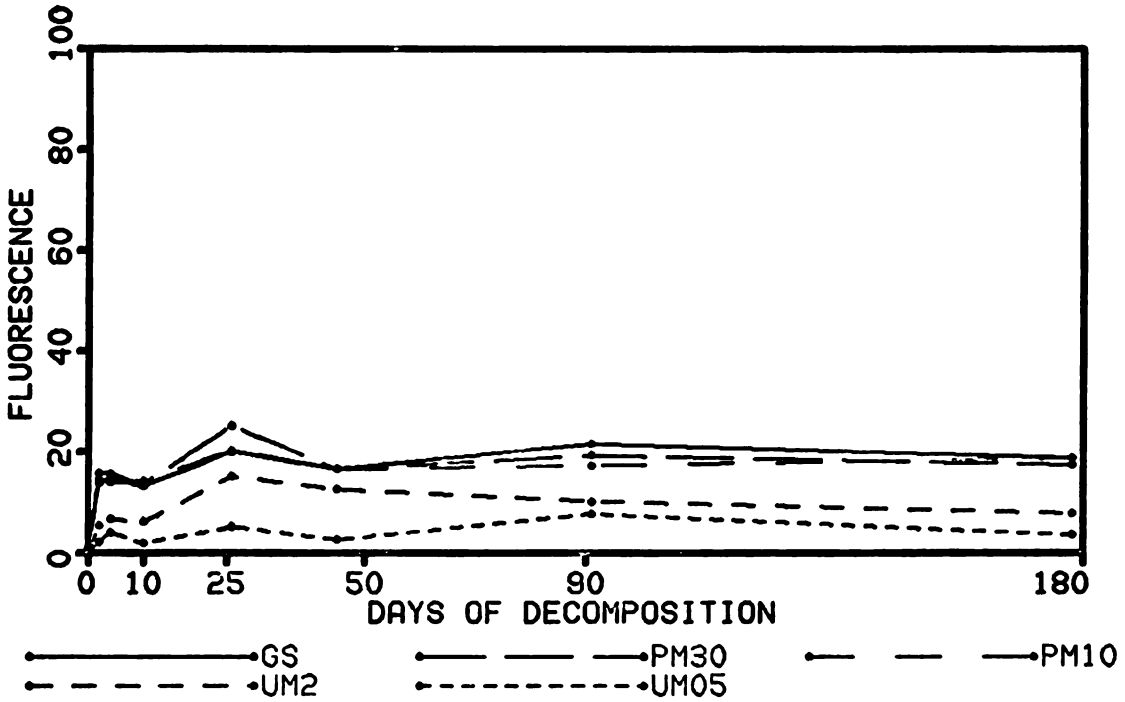
Appendix Figure 82. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



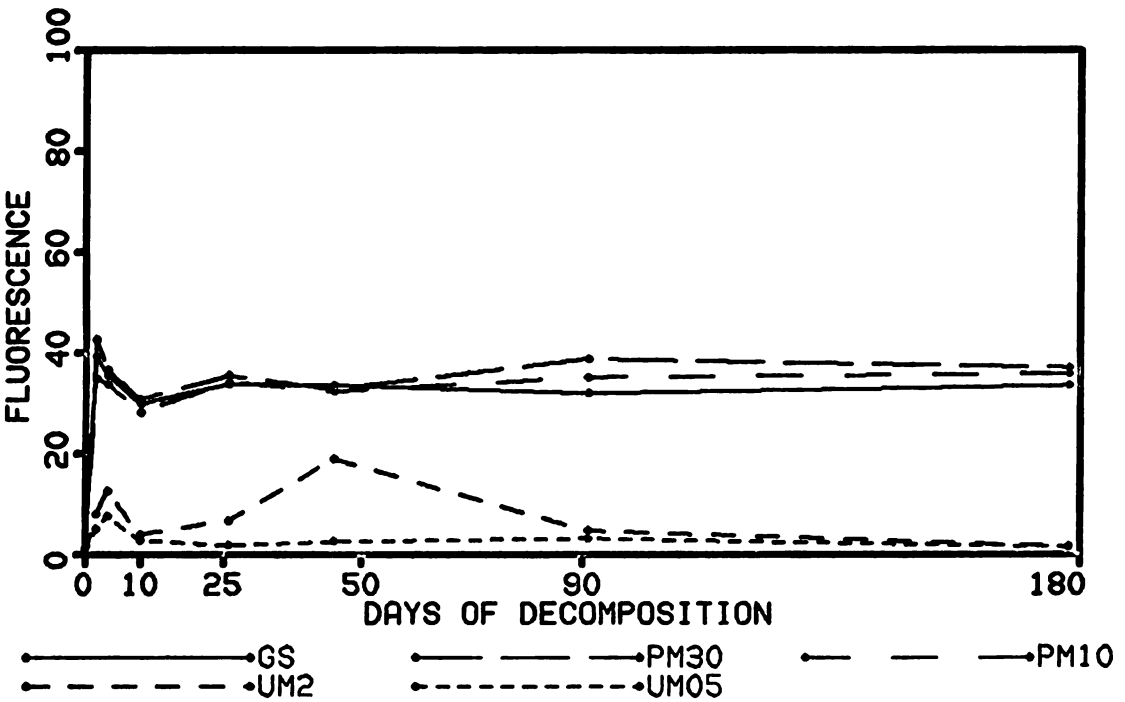
Appendix Figure 83. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



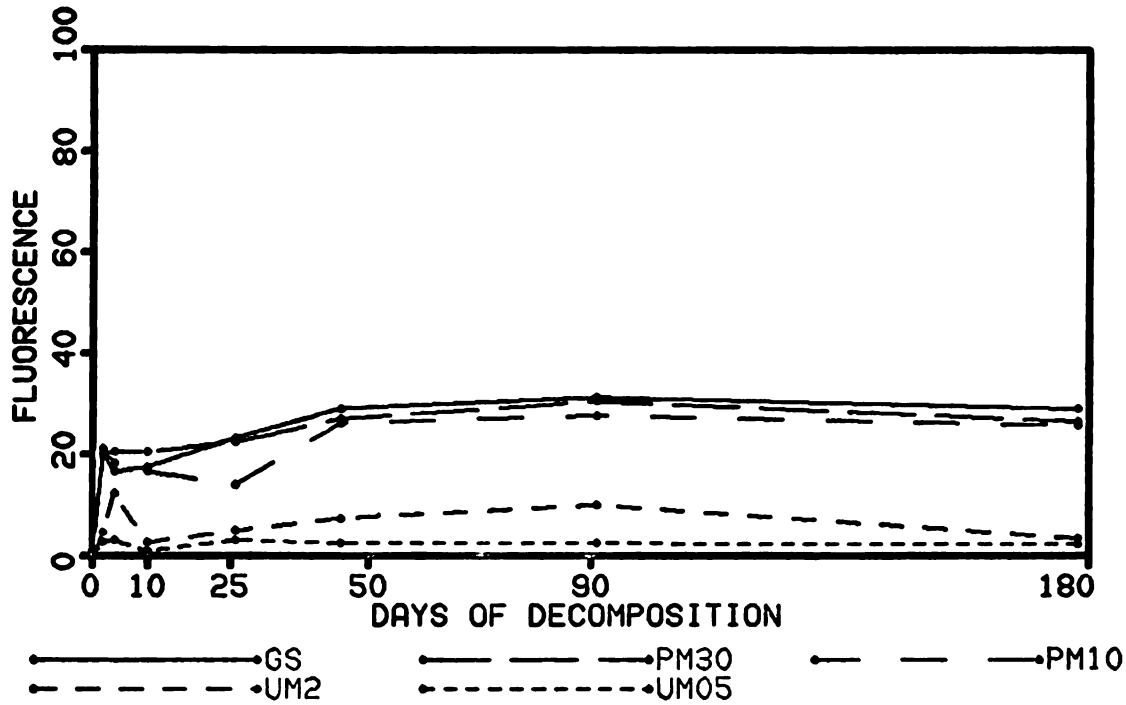
Appendix Figure 84. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



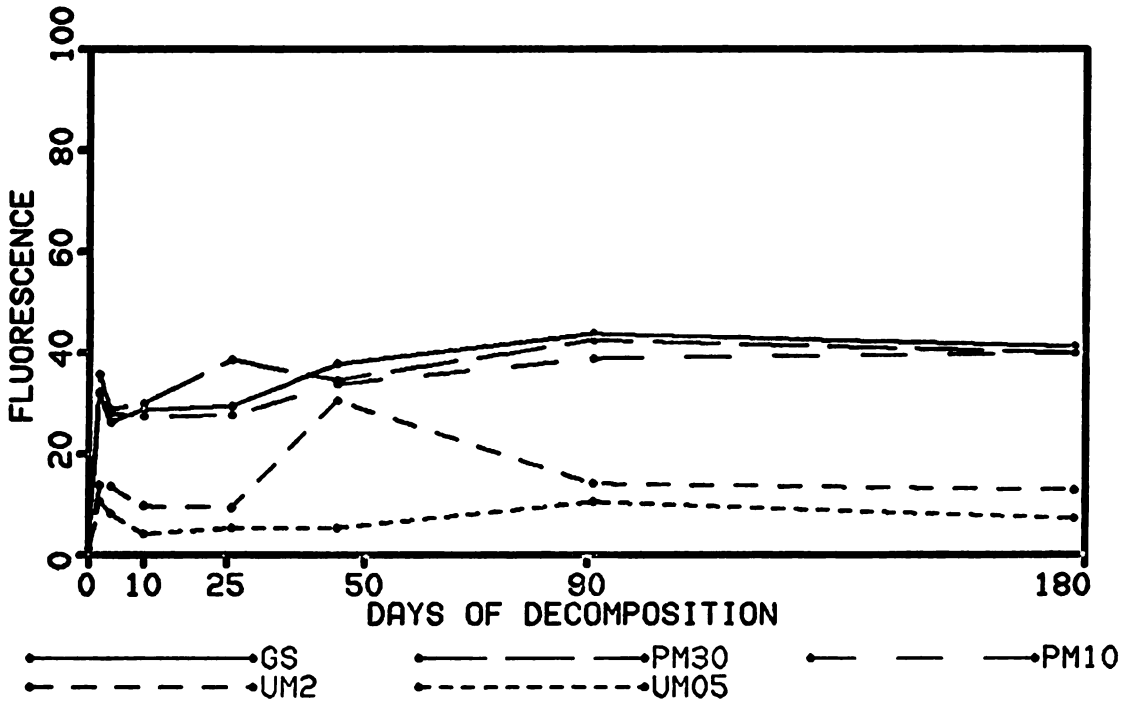
Appendix Figure 85. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



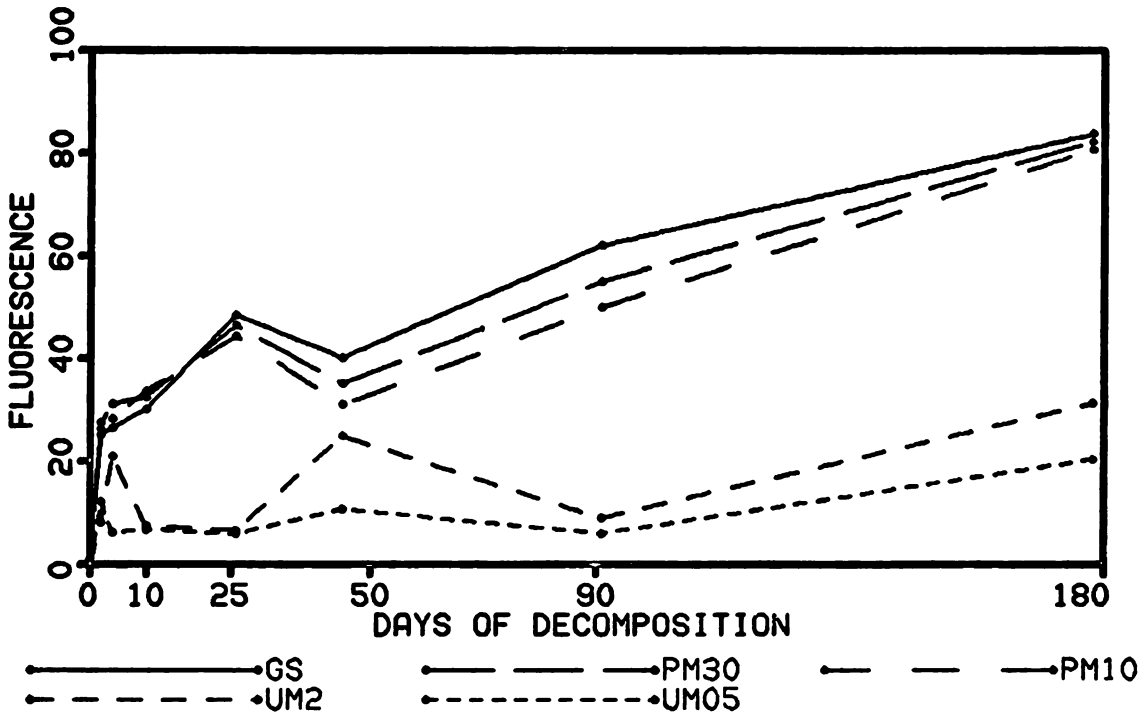
Appendix Figure 86. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



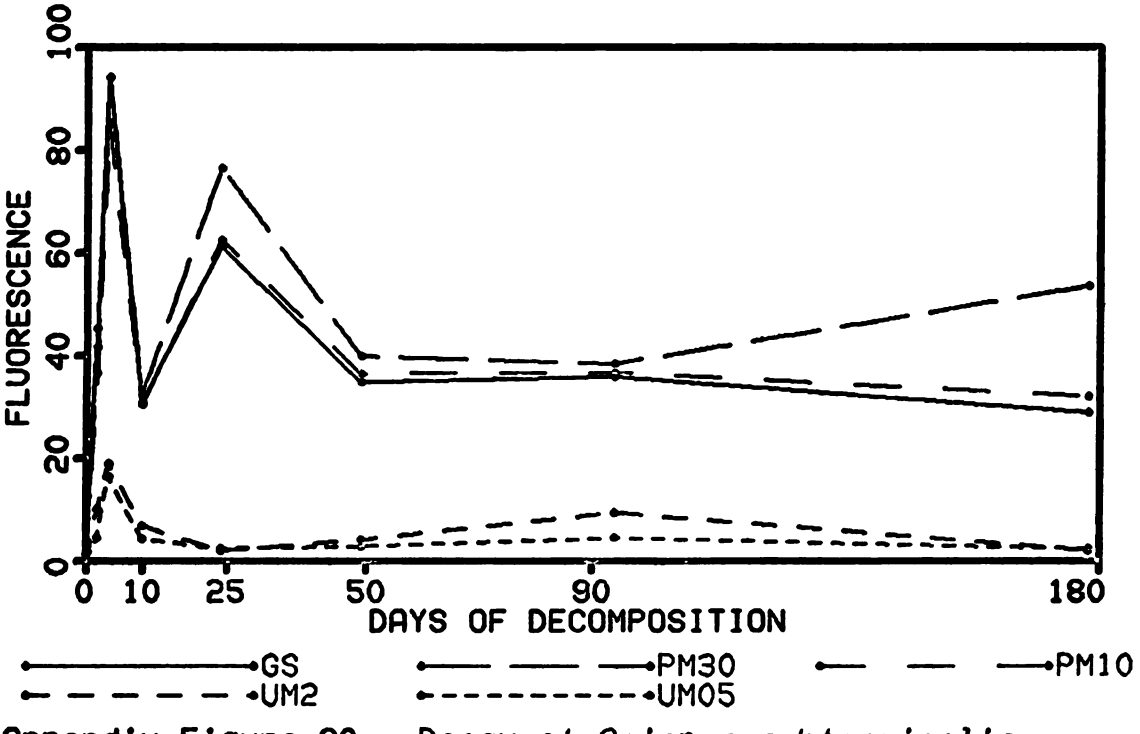
Appendix Figure 87. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



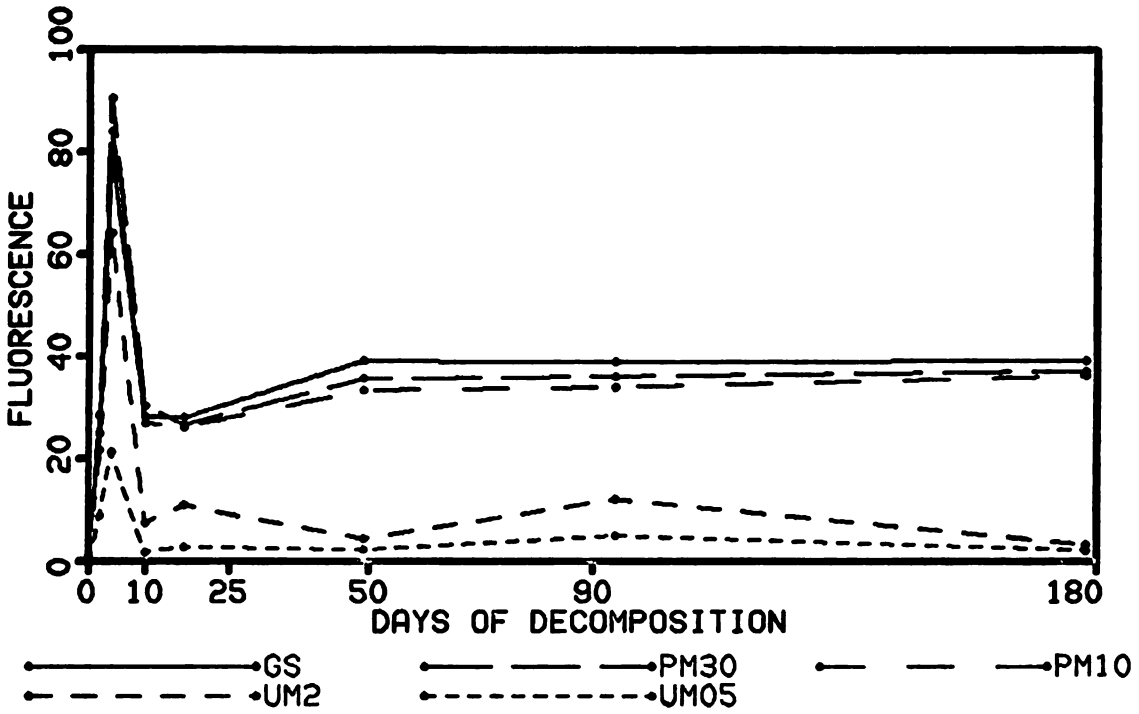
Appendix Figure 88. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



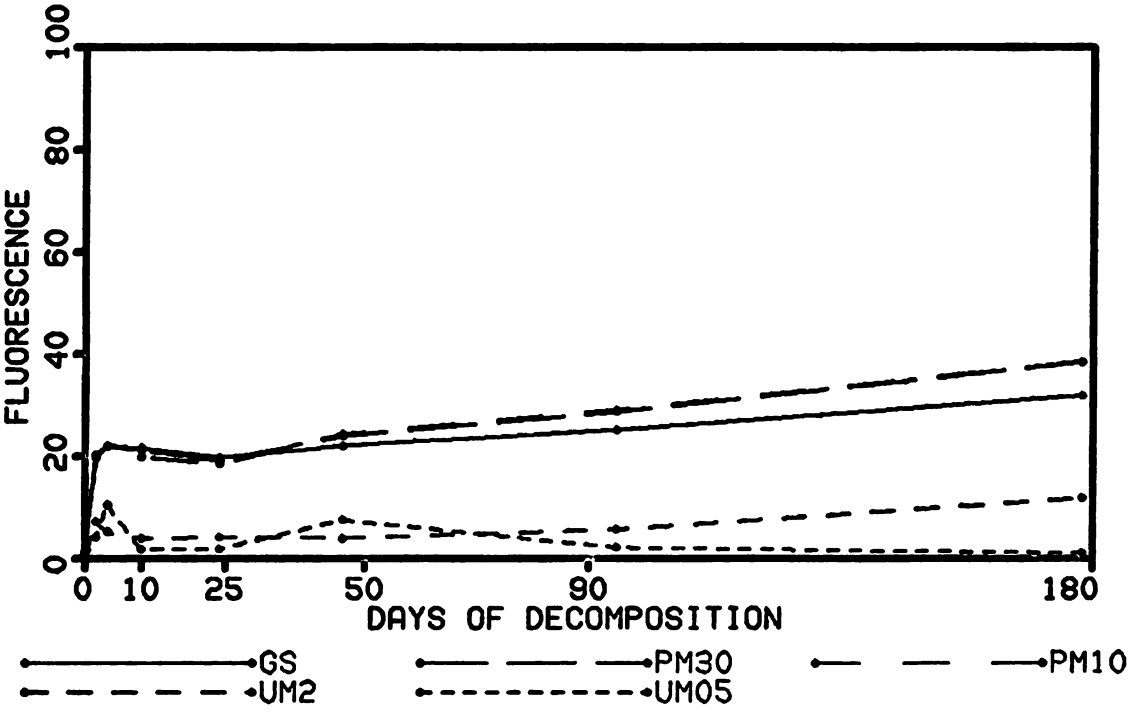
Appendix Figure 89. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



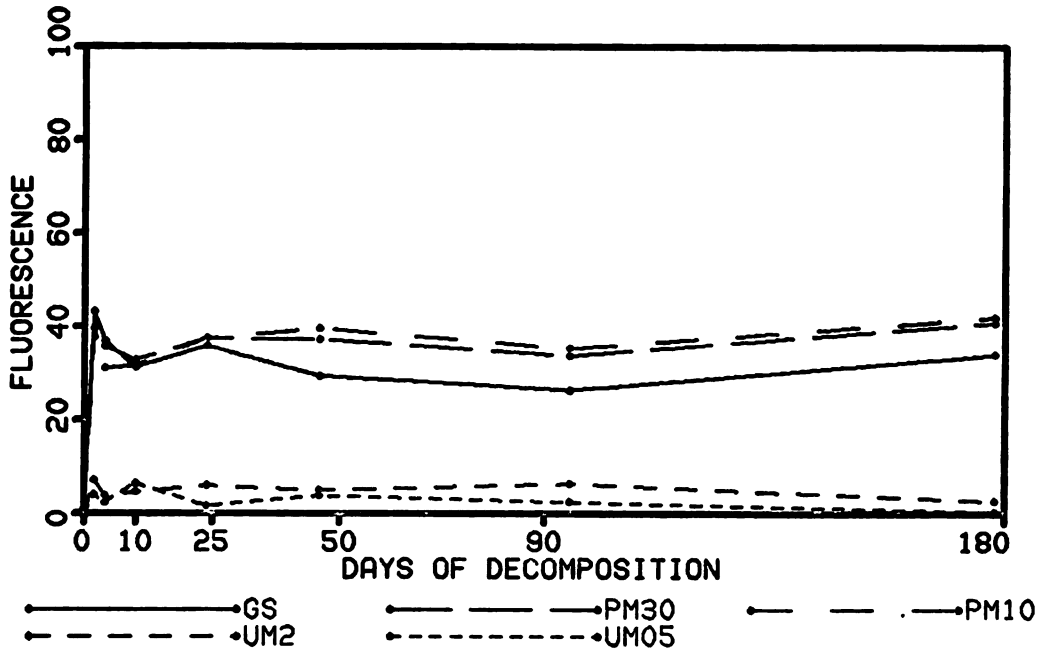
Appendix Figure 90. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



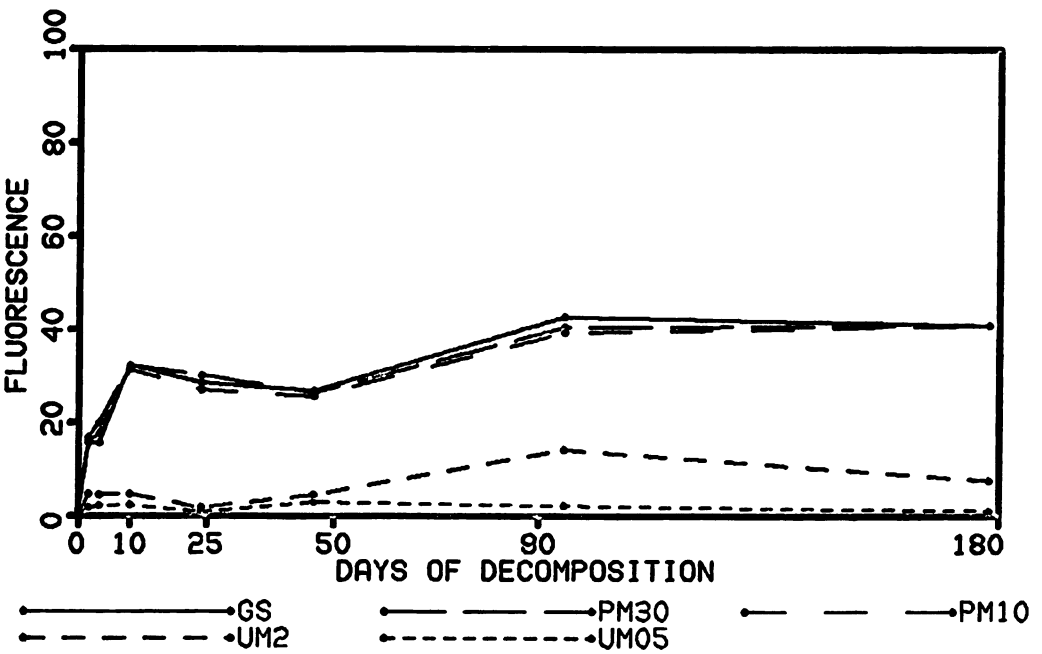
Appendix Figure 91. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



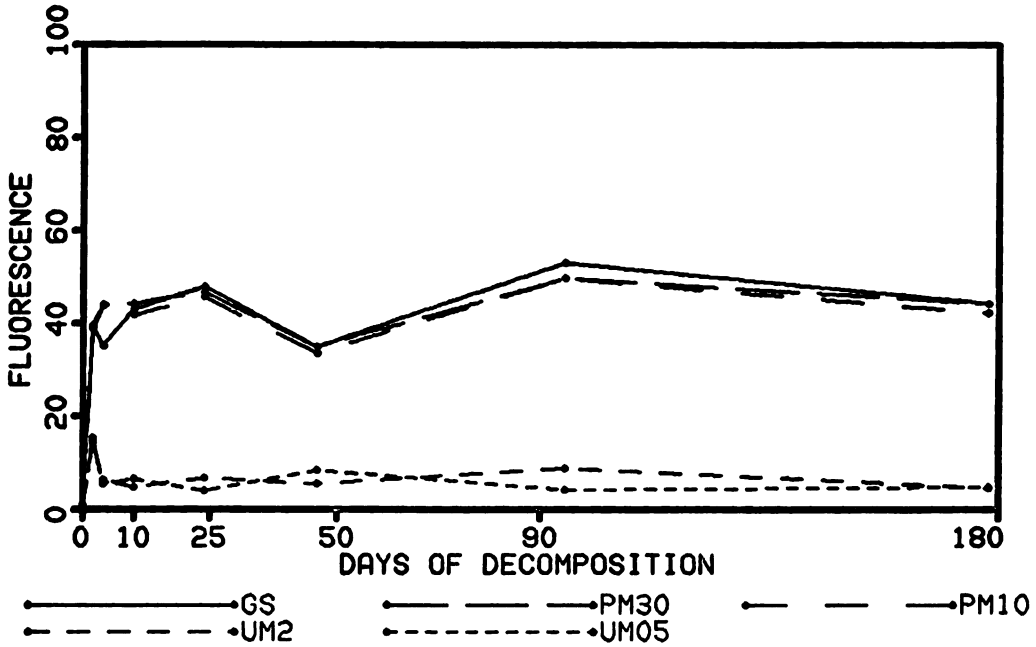
Appendix Figure 92. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



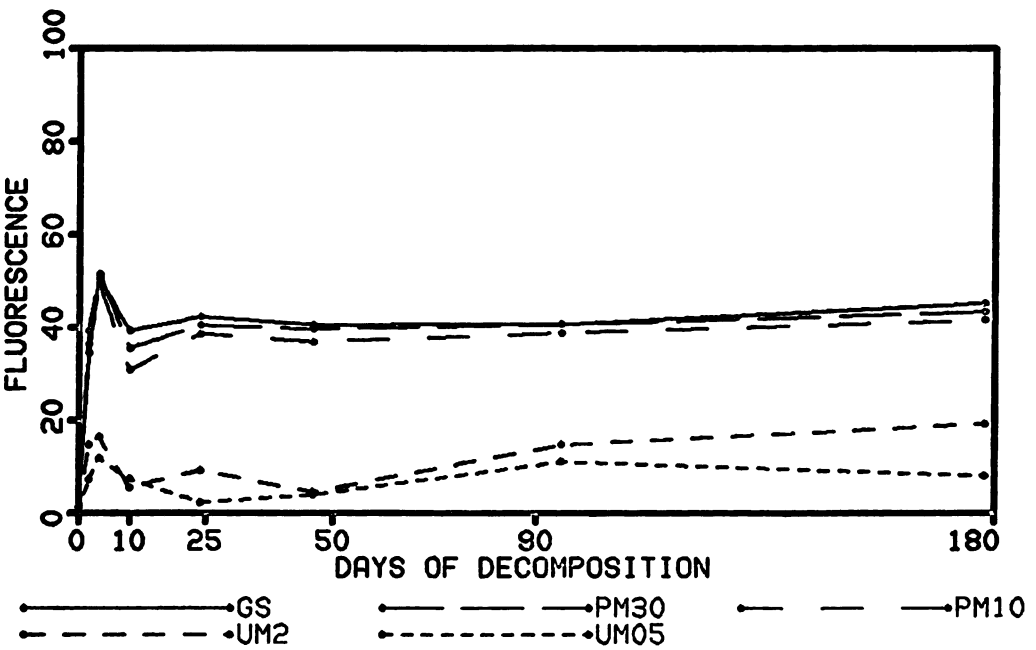
Appendix Figure 93. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



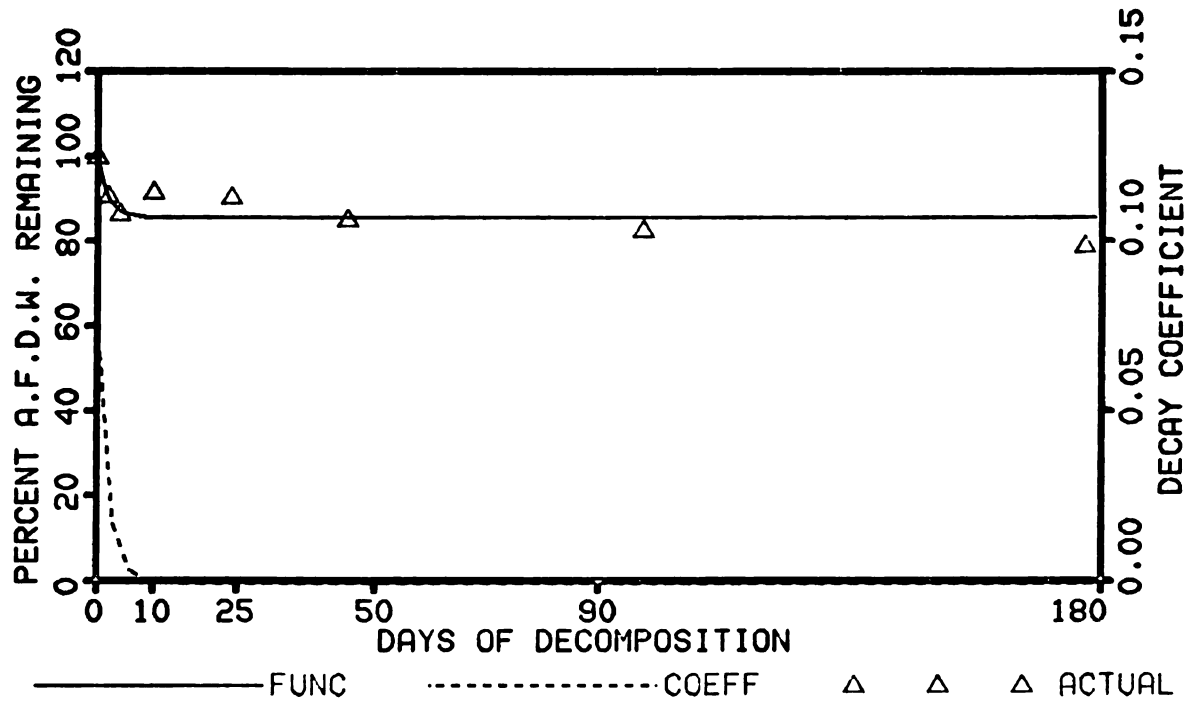
Appendix Figure 94. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



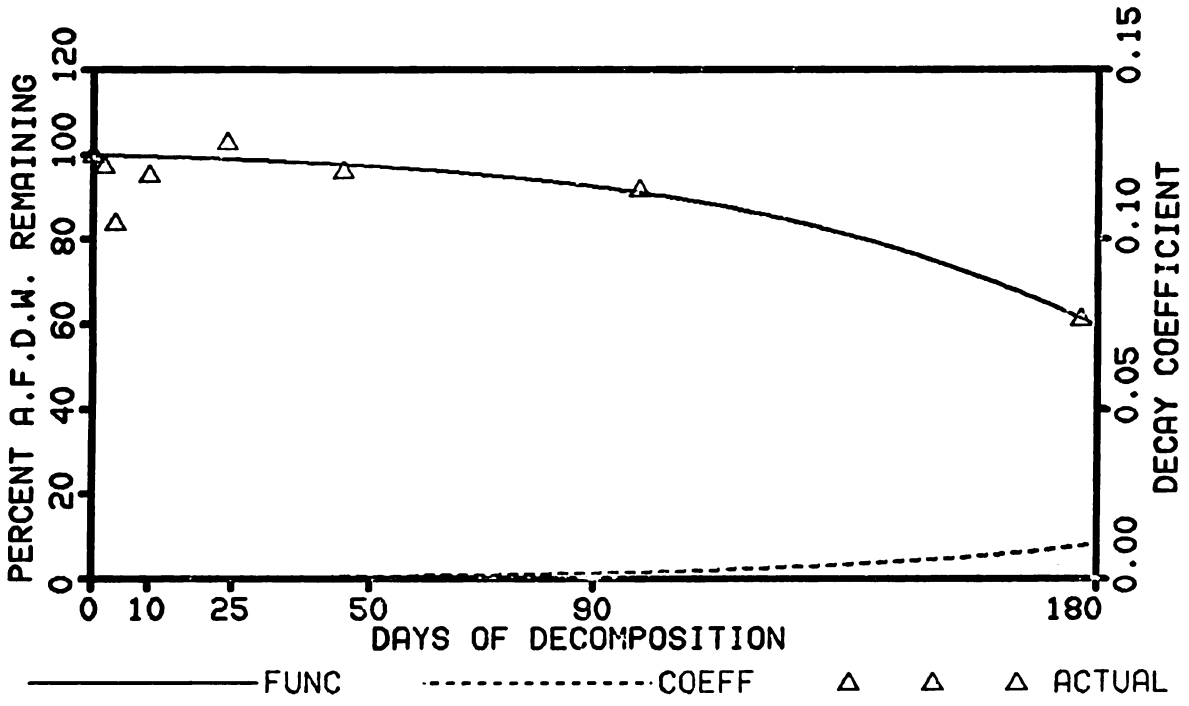
Appendix Figure 95. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



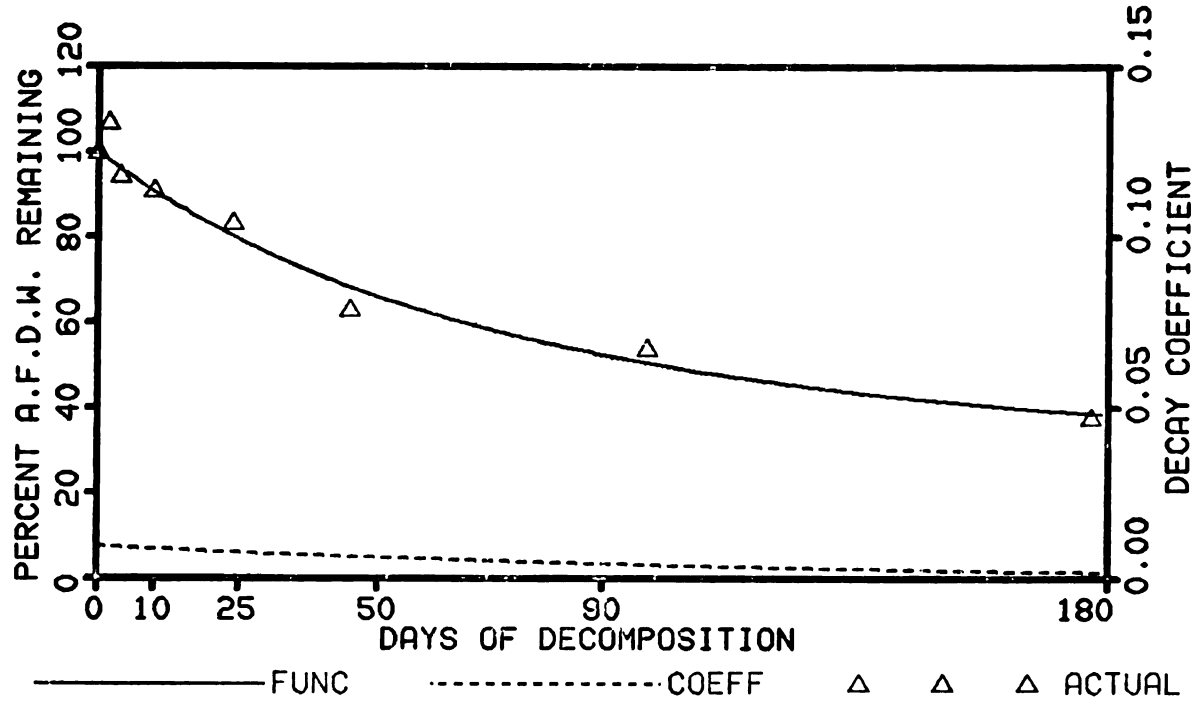
Appendix Figure 96. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. Fluorescence activity (activation 365 nm, emmission 545 nm), in relative fluorometer units, of various molecular weight fractions of DOM, per g initial AFDW.



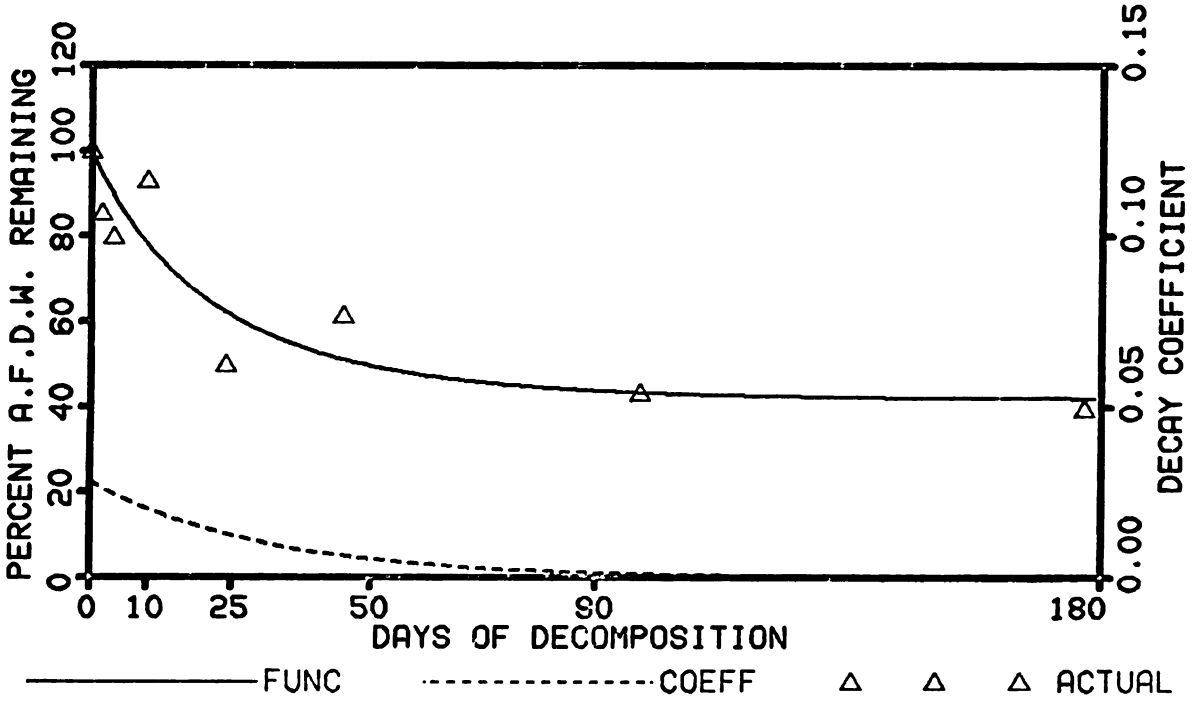
Appendix Figure 97. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



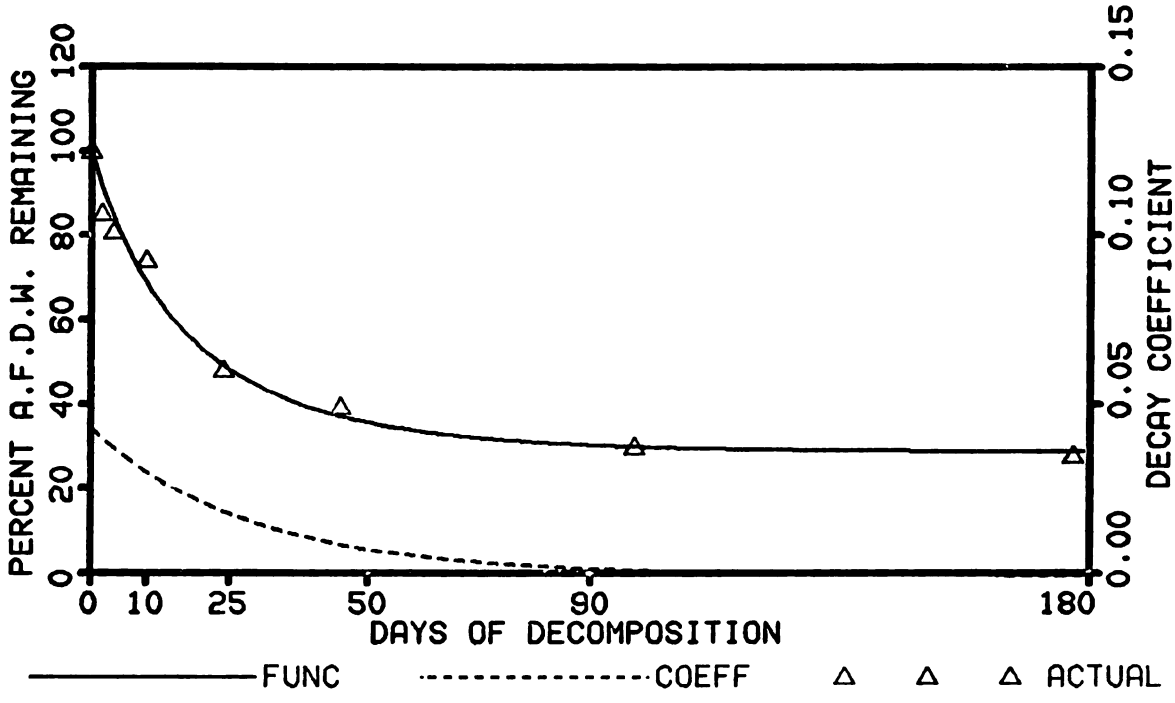
Appendix Figure 98. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



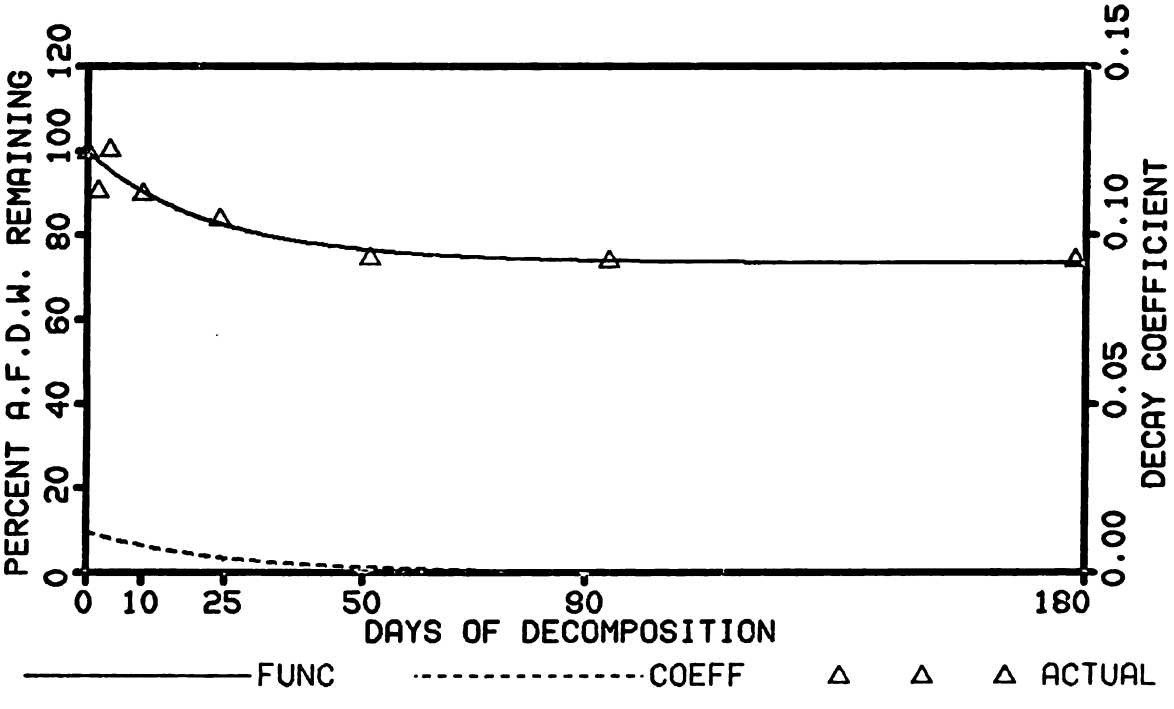
Appendix Figure 99. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



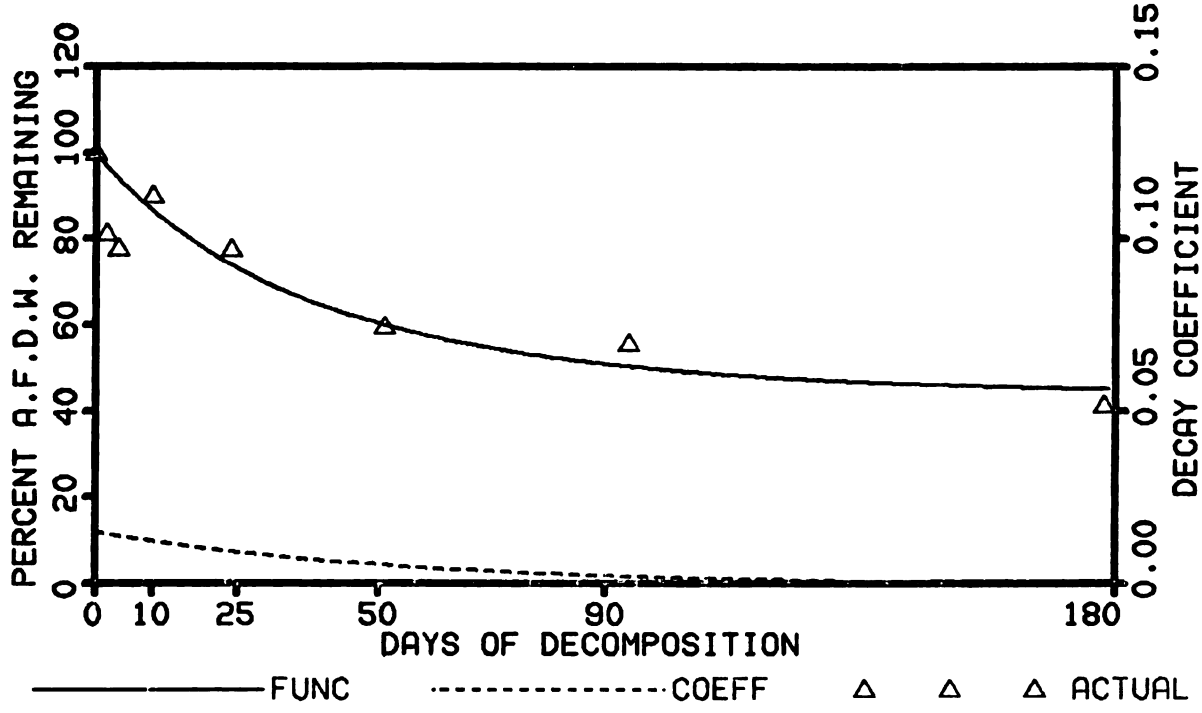
Appendix Figure 100. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



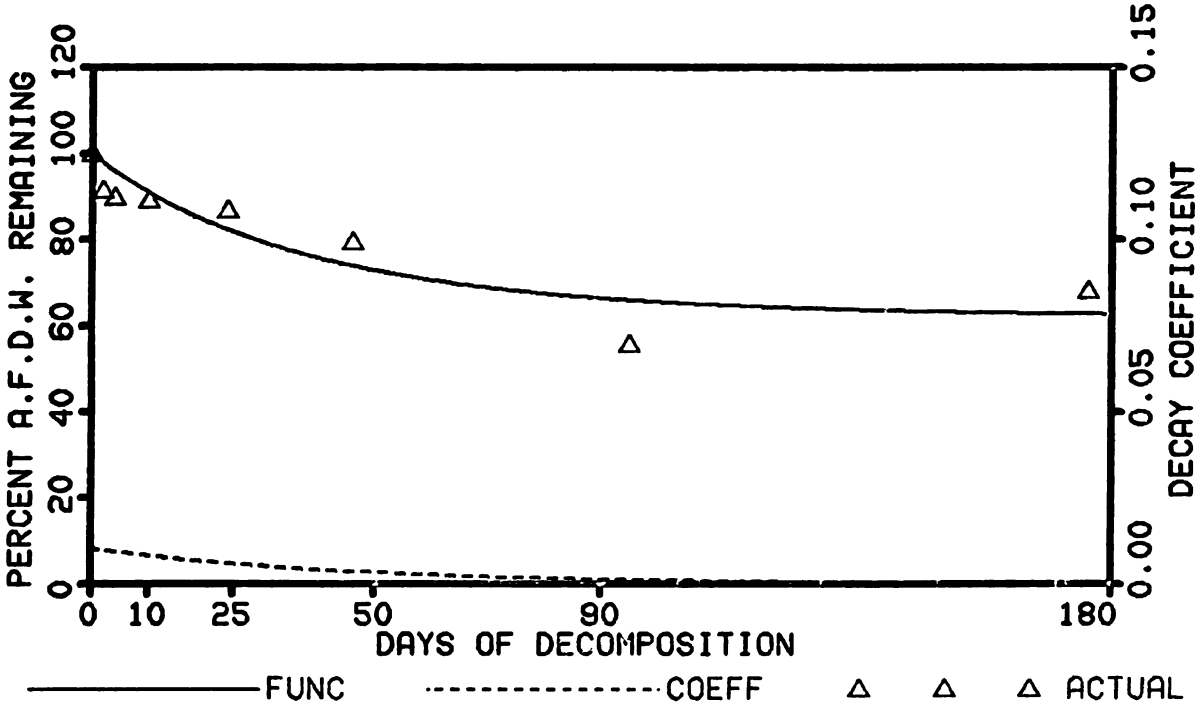
Appendix Figure 101. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



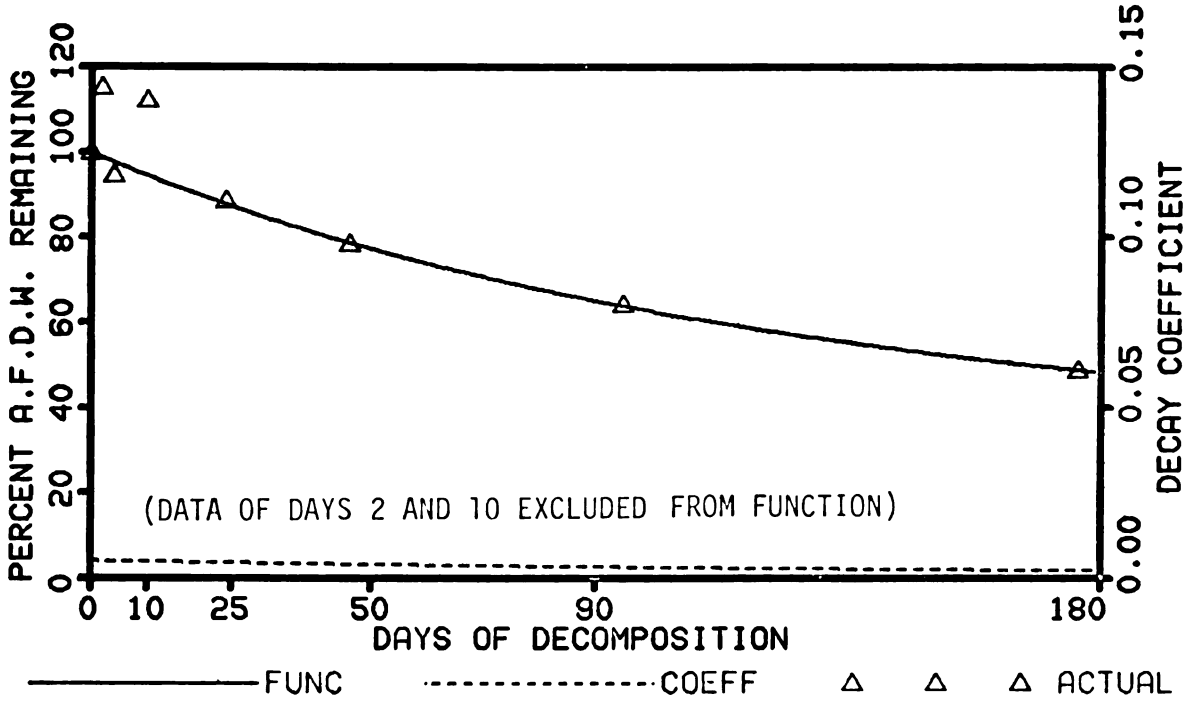
Appendix Figure 102. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



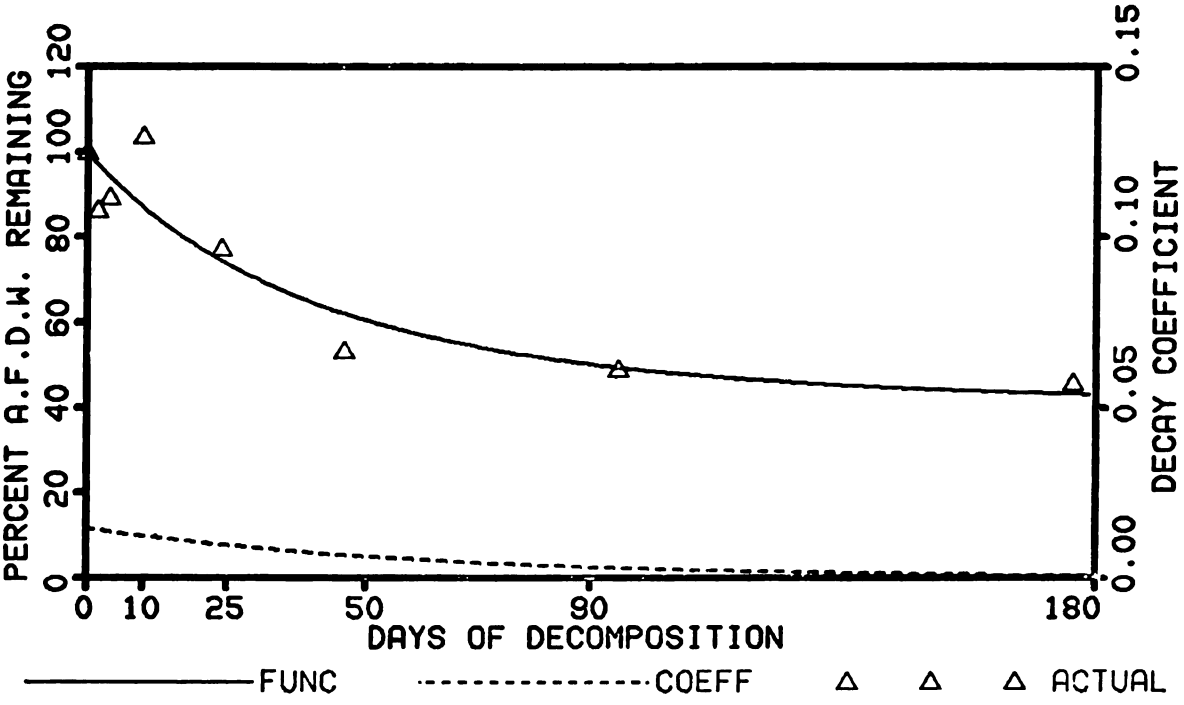
Appendix Figure 103. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



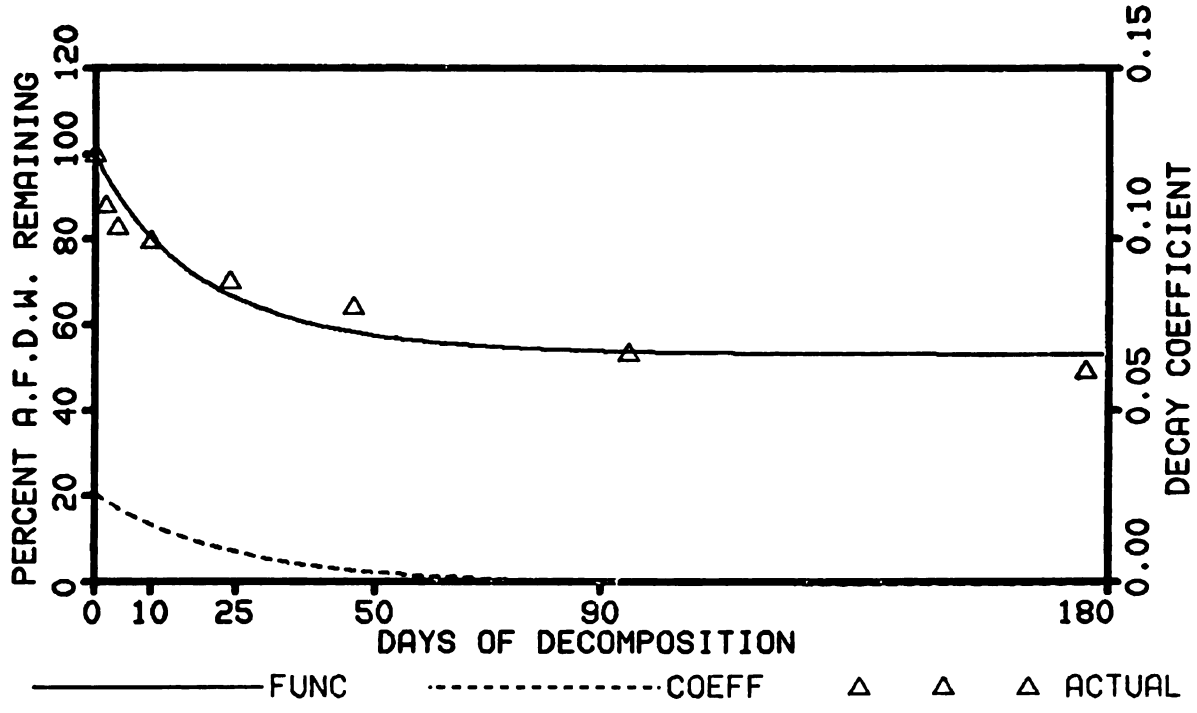
Appendix Figure 104. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



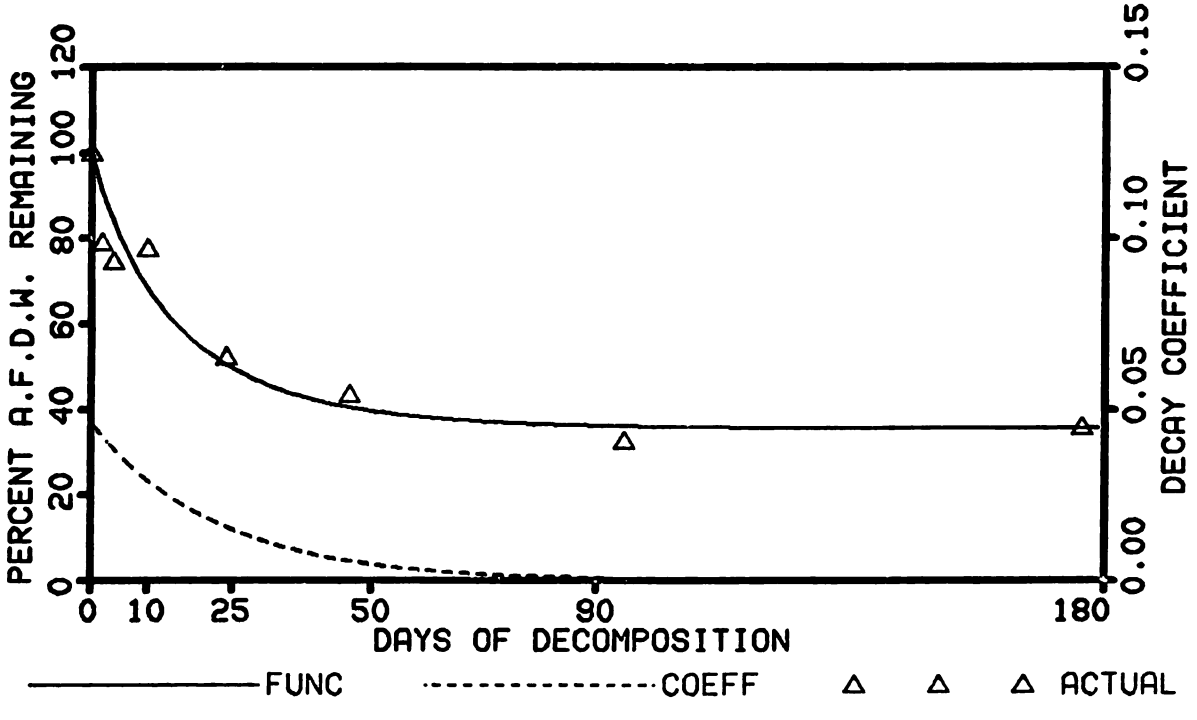
Appendix Figure 105. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



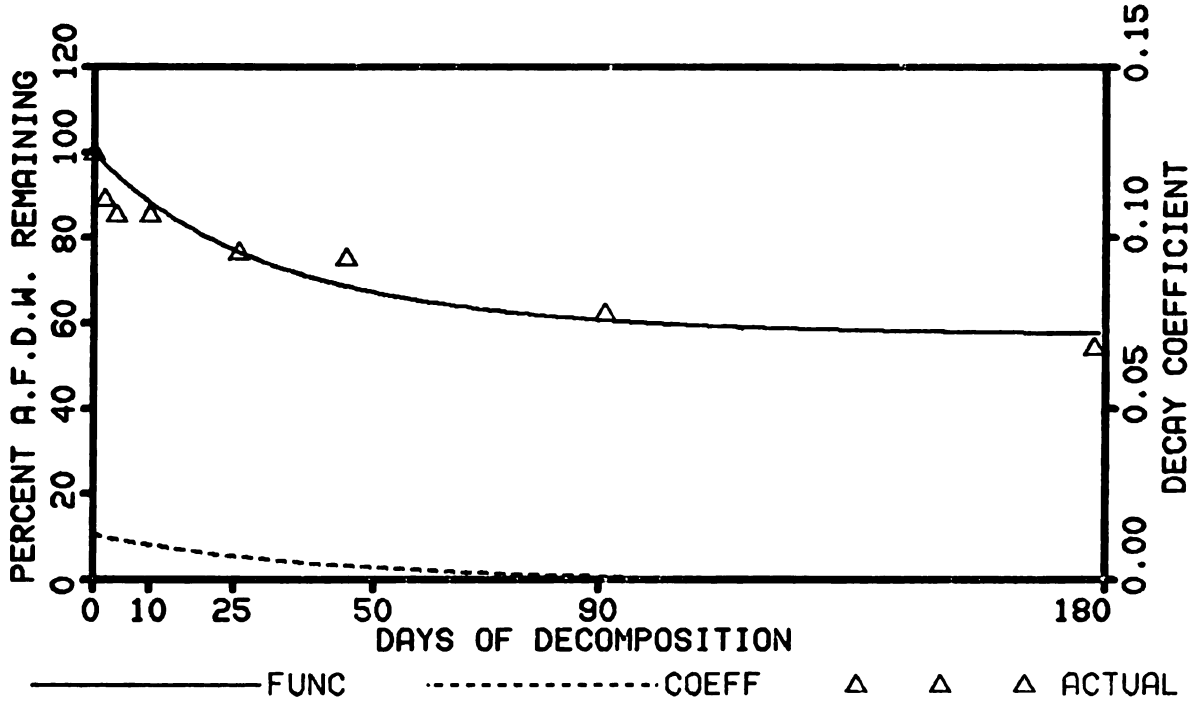
Appendix Figure 106. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



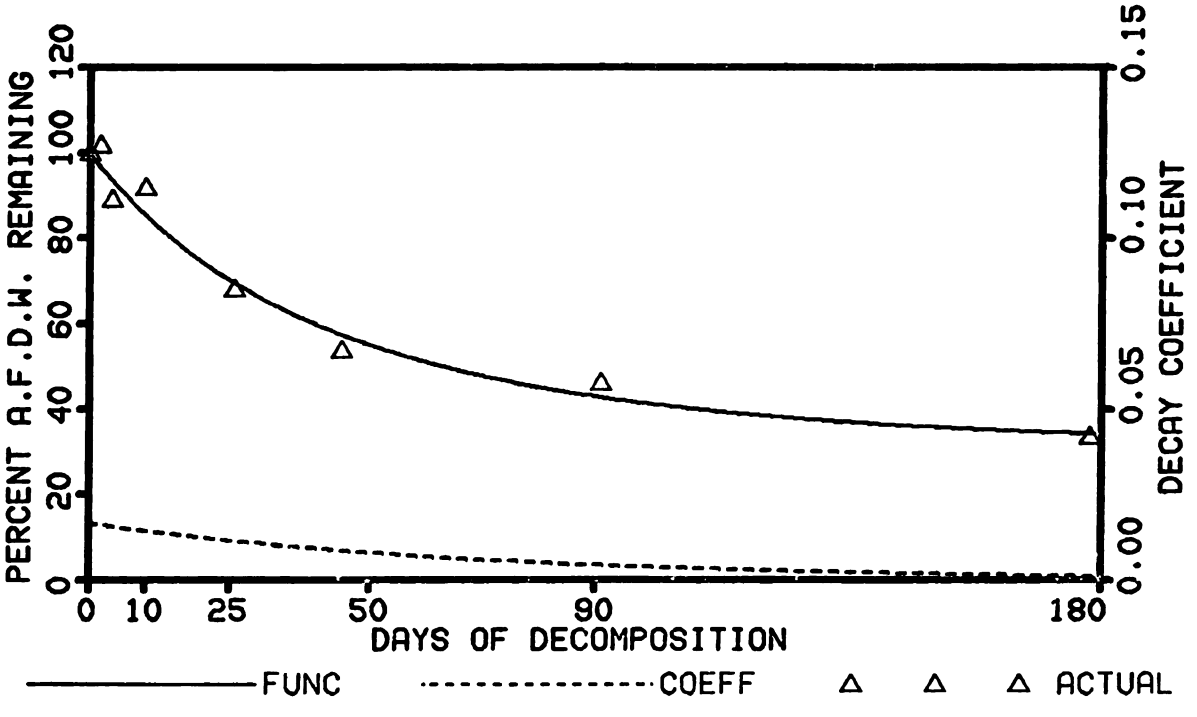
Appendix Figure 107. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



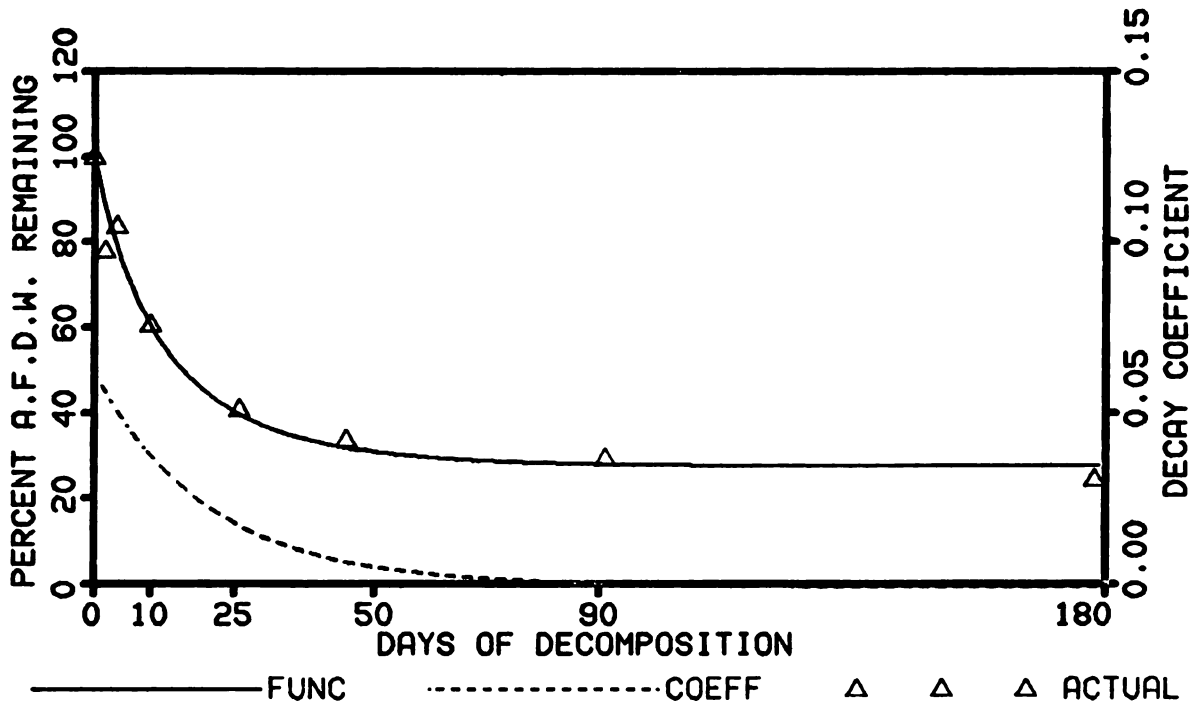
Appendix Figure 108. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



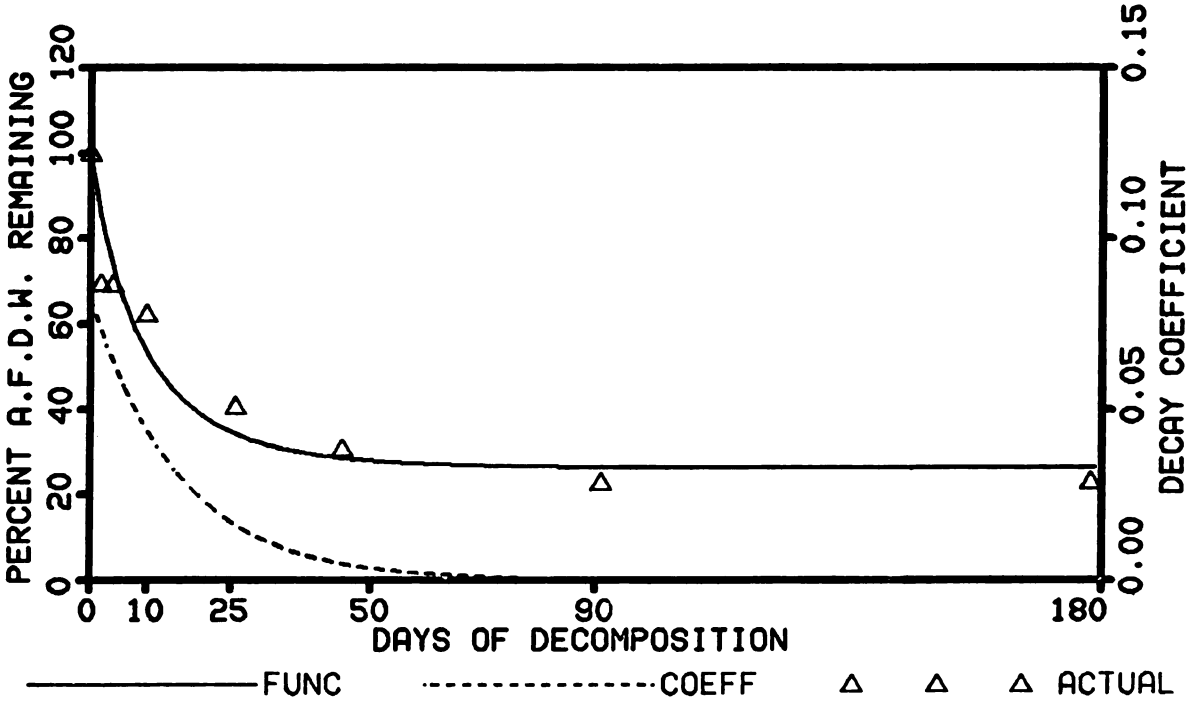
Appendix Figure 109. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



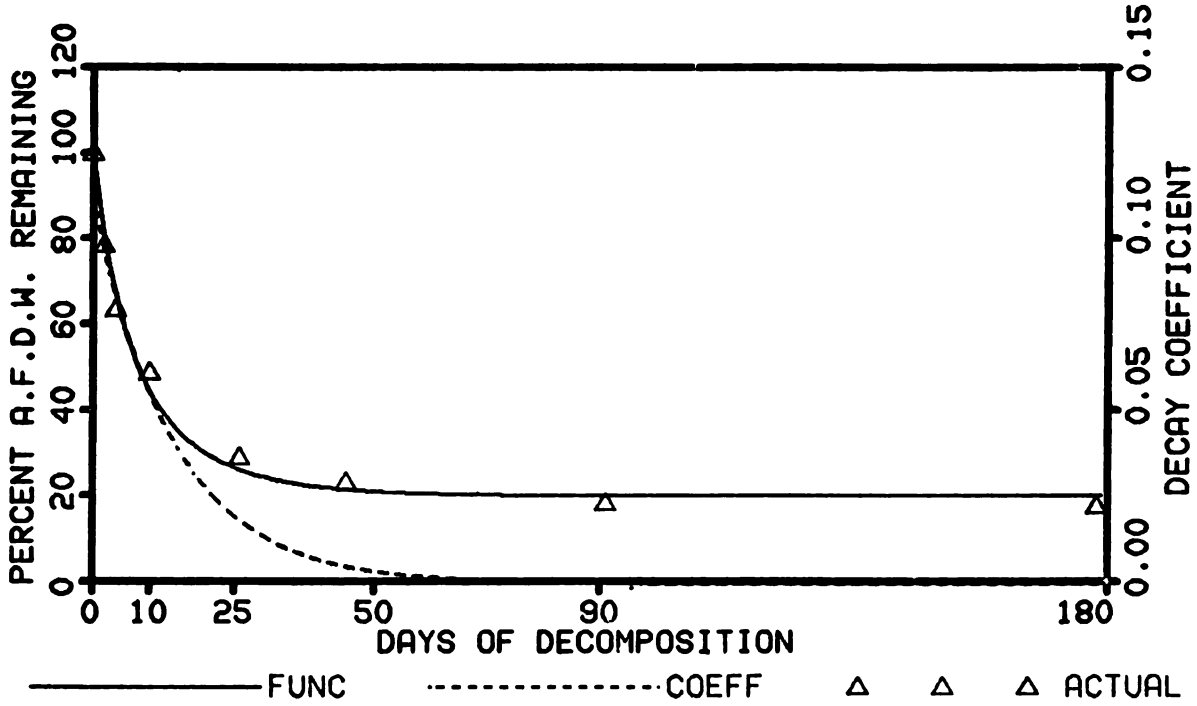
Appendix Figure 110. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



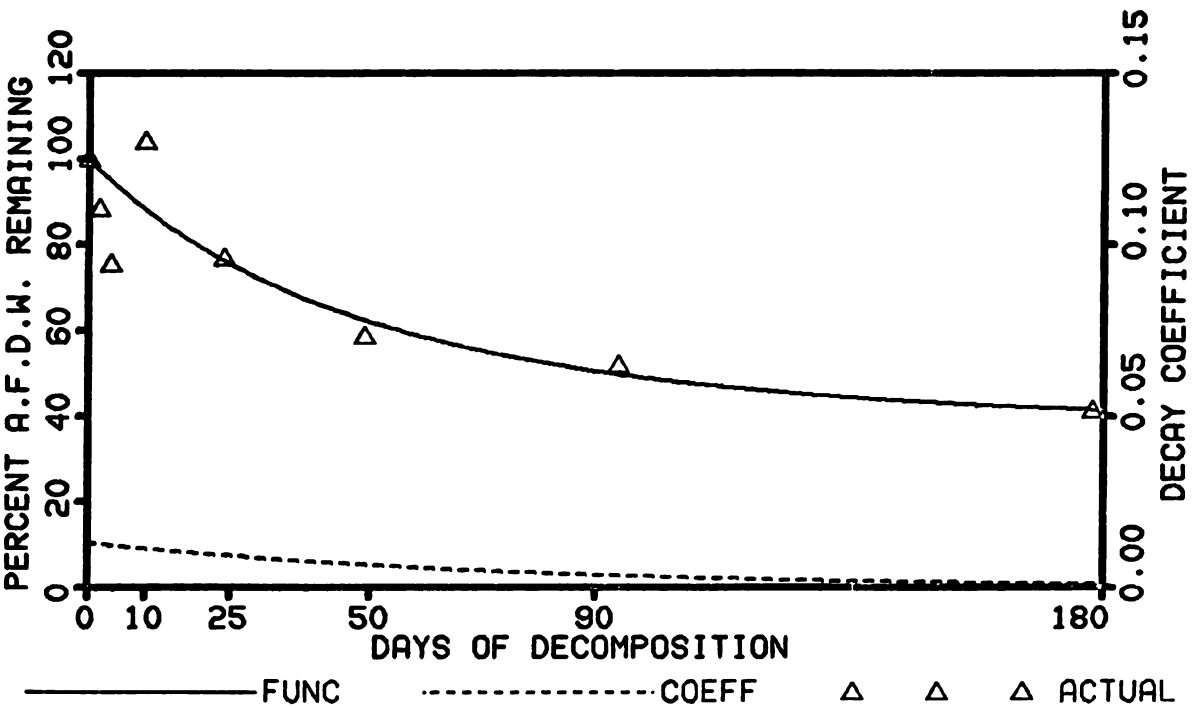
Appendix Figure 111. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



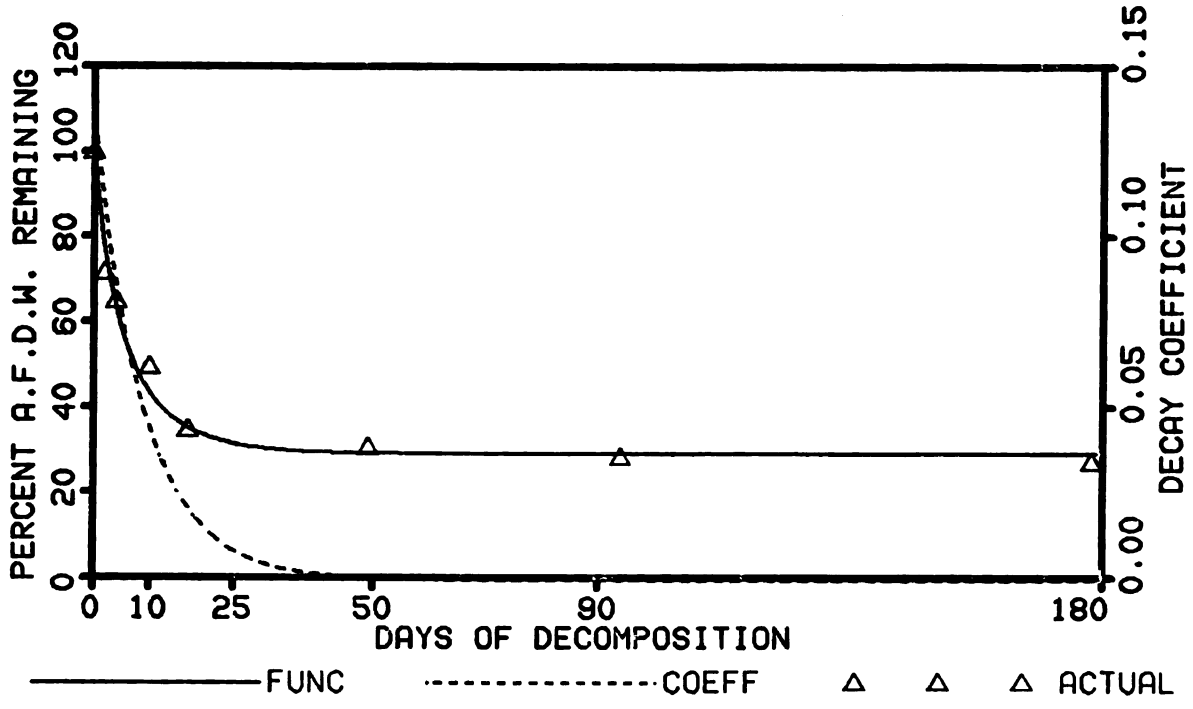
Appendix Figure 112. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



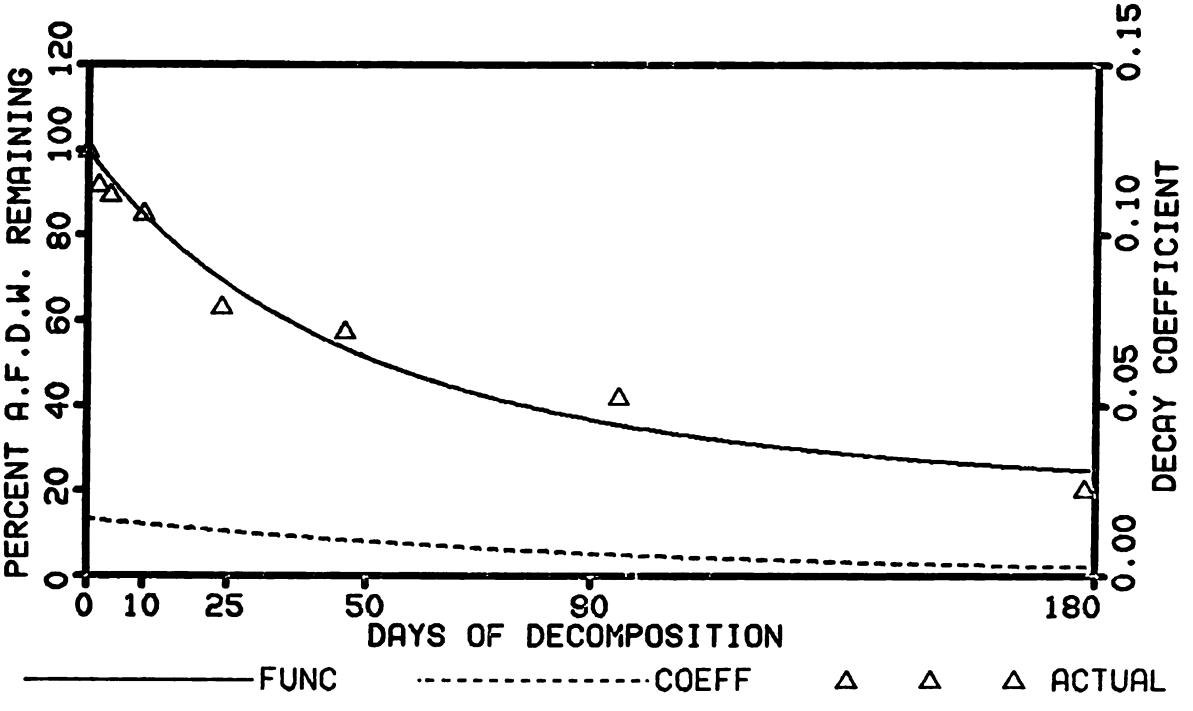
Appendix Figure 113. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



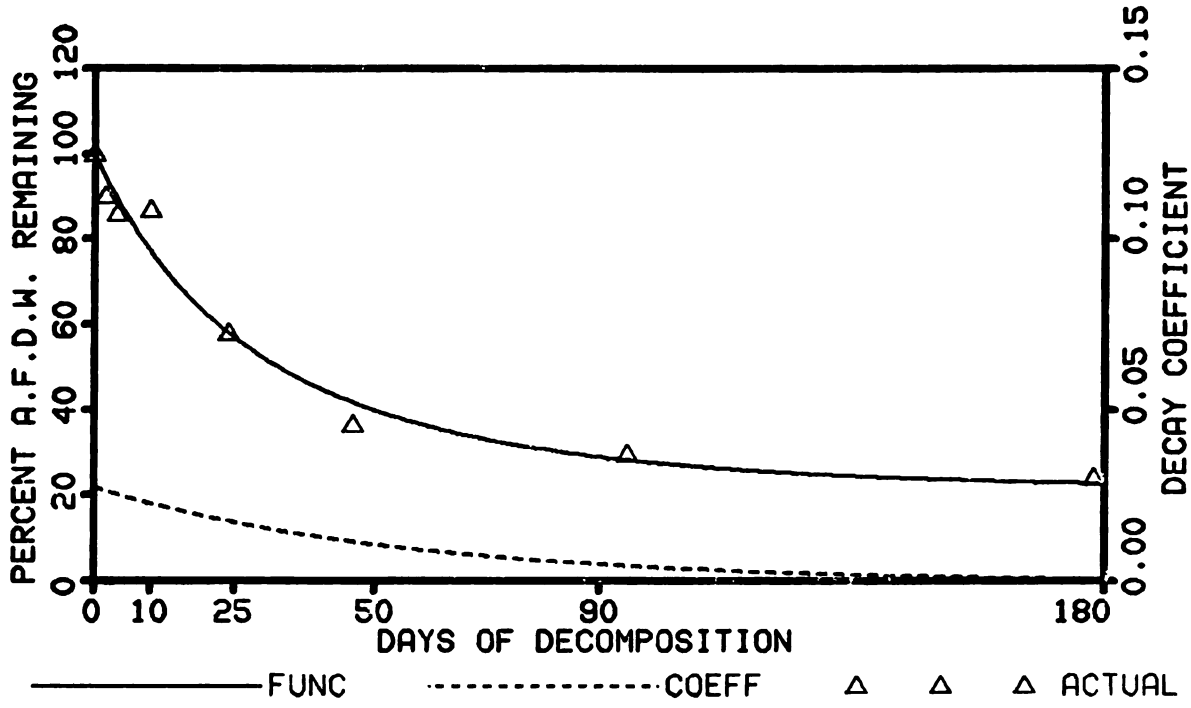
Appendix Figure 114. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



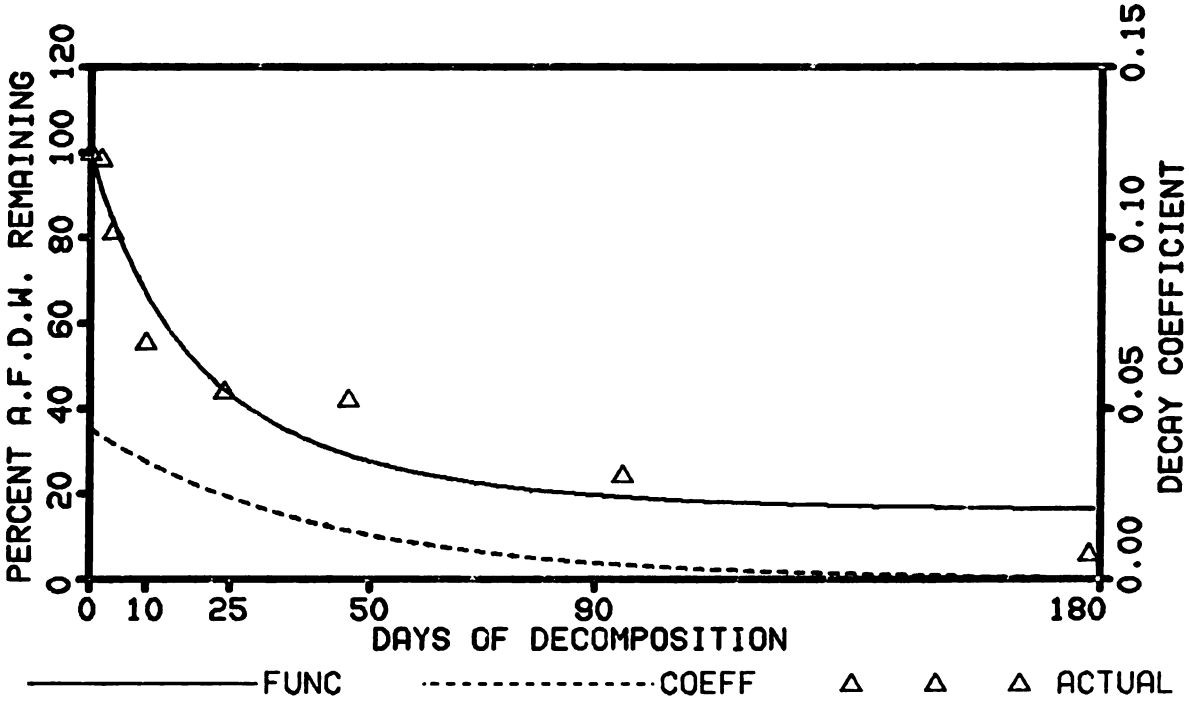
Appendix Figure 115. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



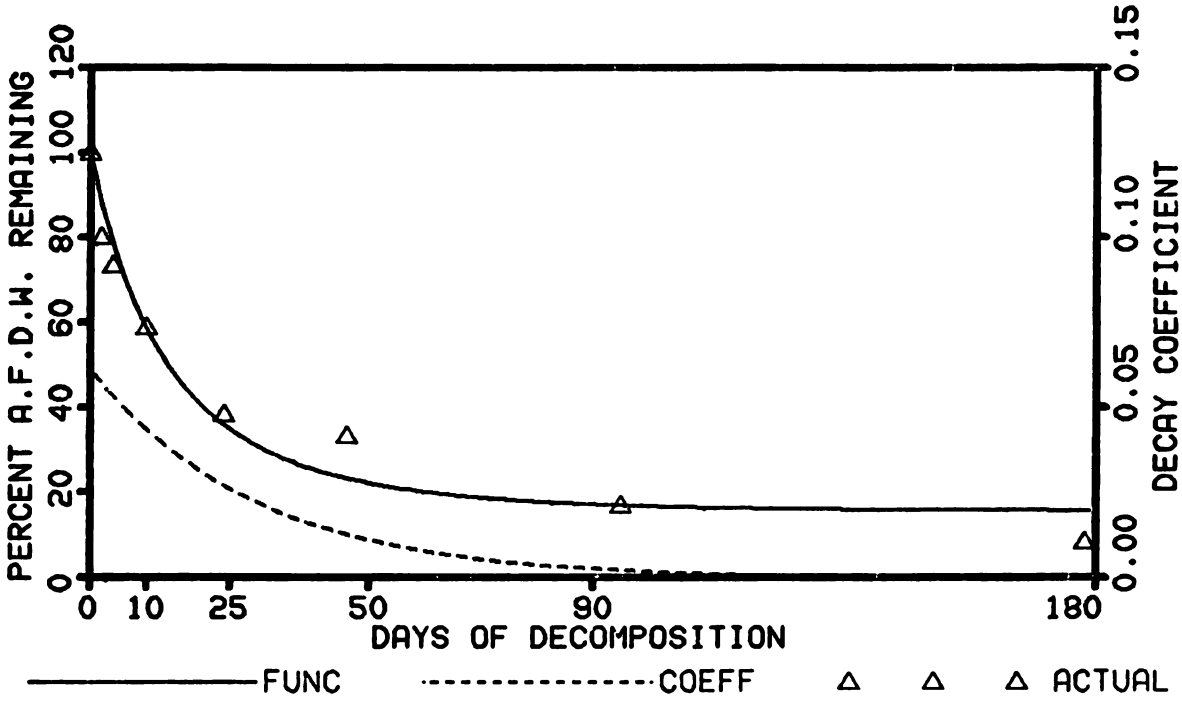
Appendix Figure 116. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



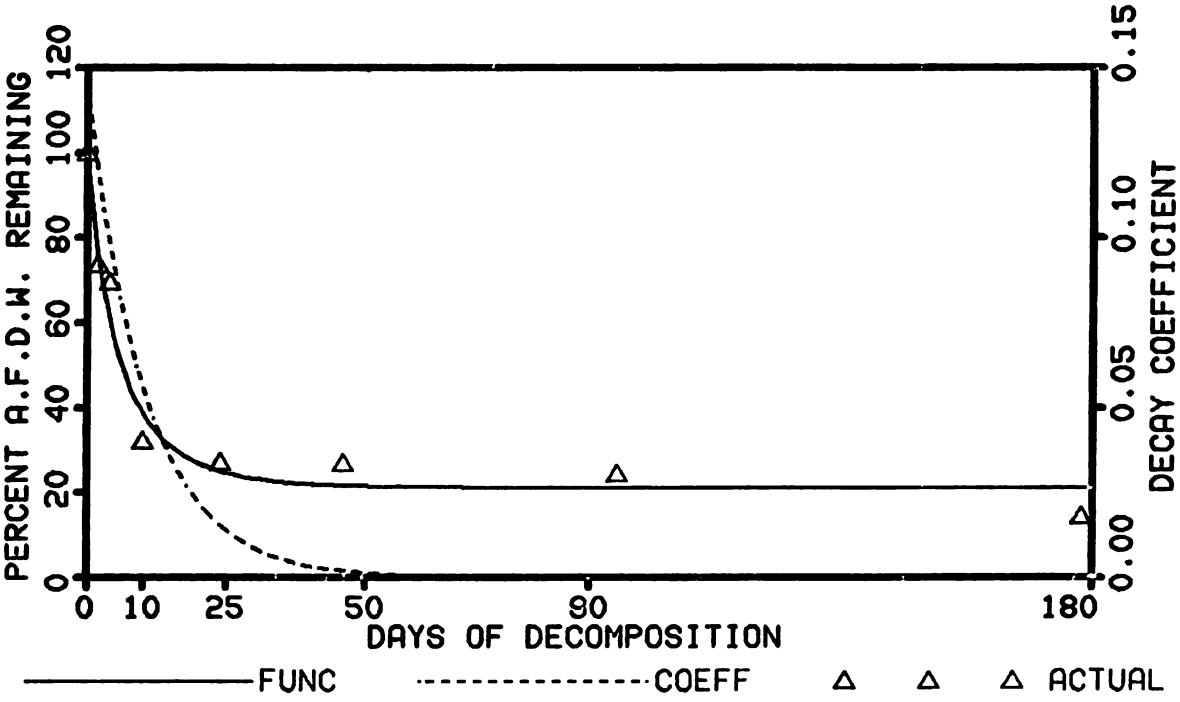
Appendix Figure 117. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



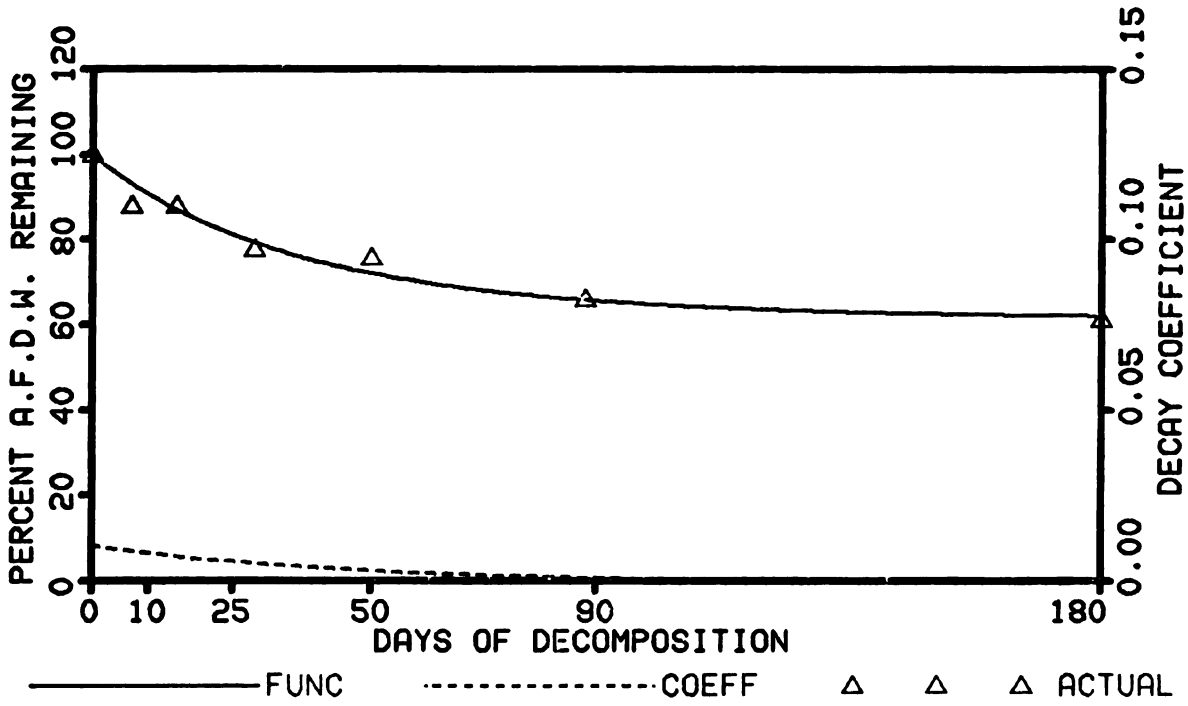
Appendix Figure 118. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



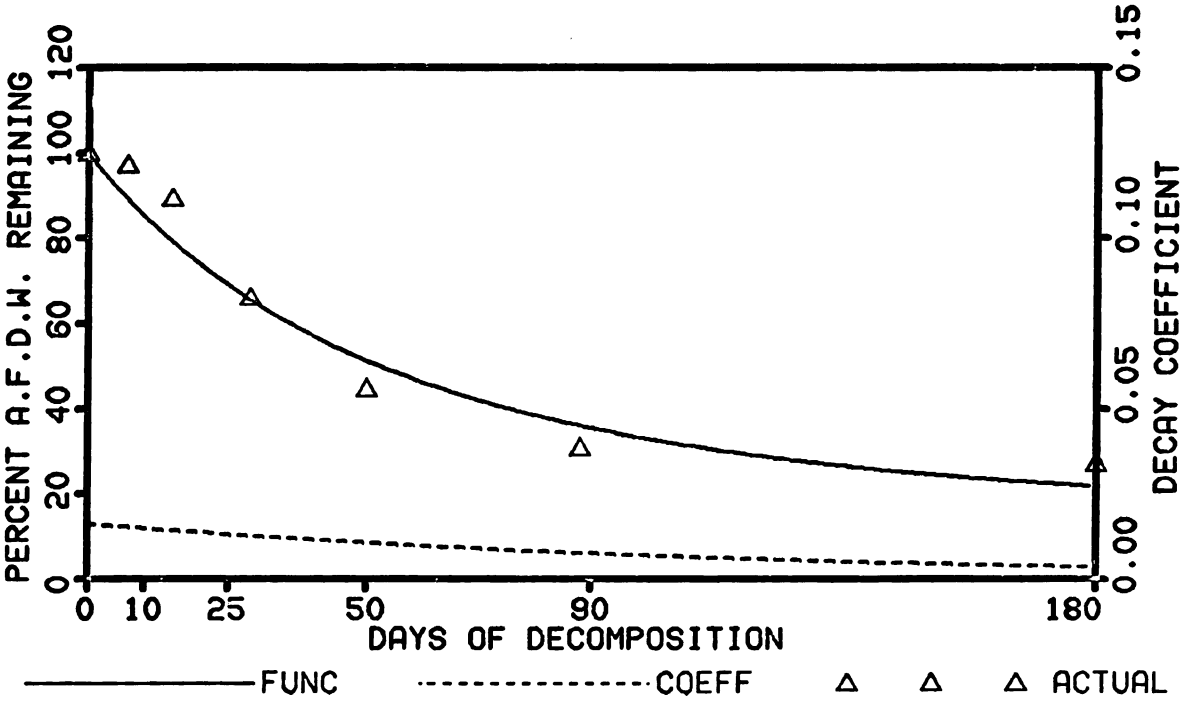
Appendix Figure 119. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



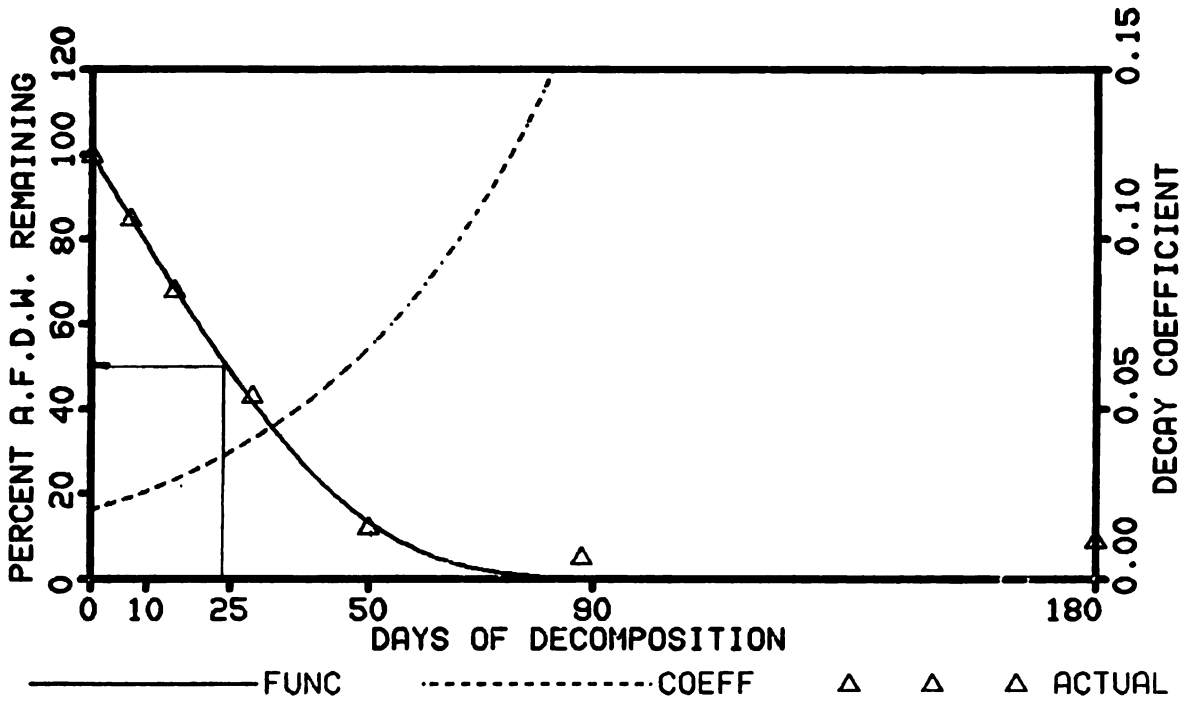
Appendix Figure 120. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



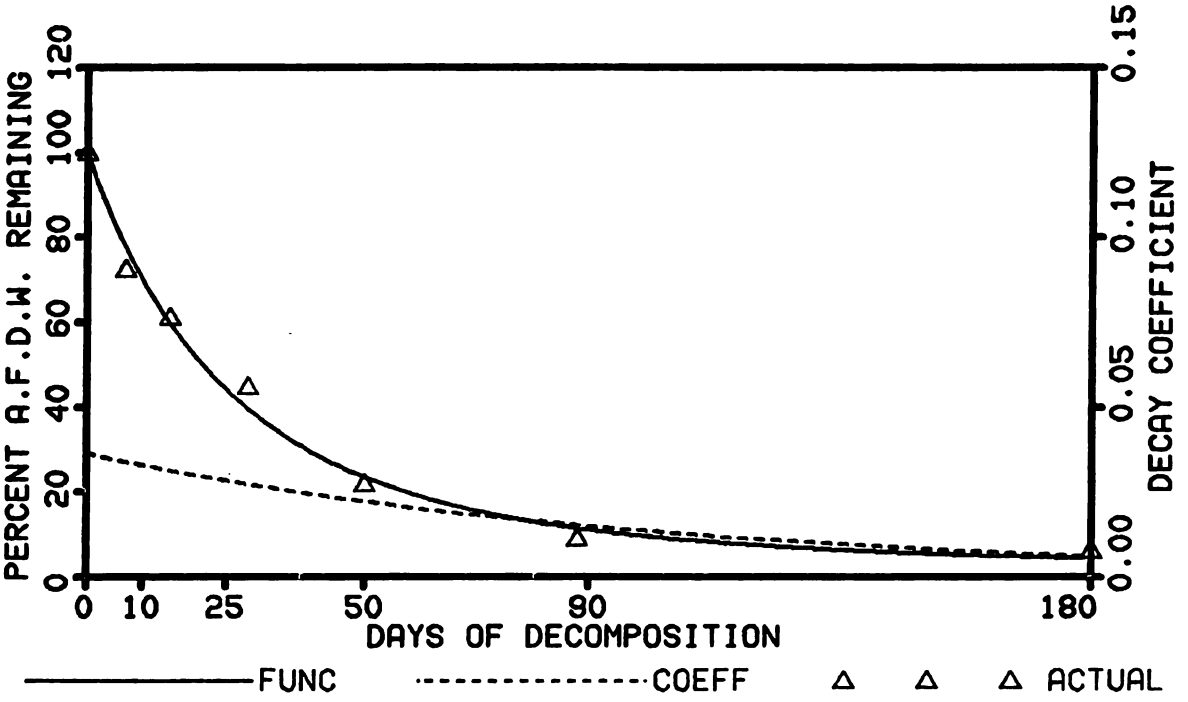
Appendix Figure 121. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during spring and summer. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



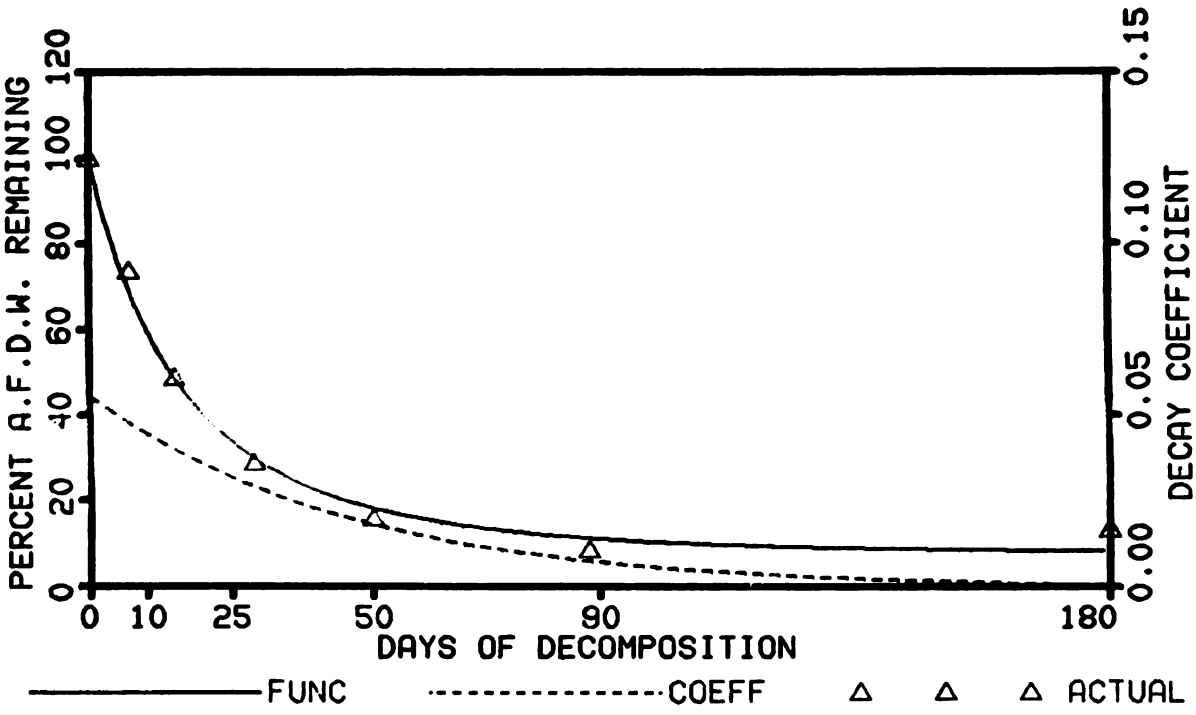
Appendix Figure 122. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during spring and summer. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



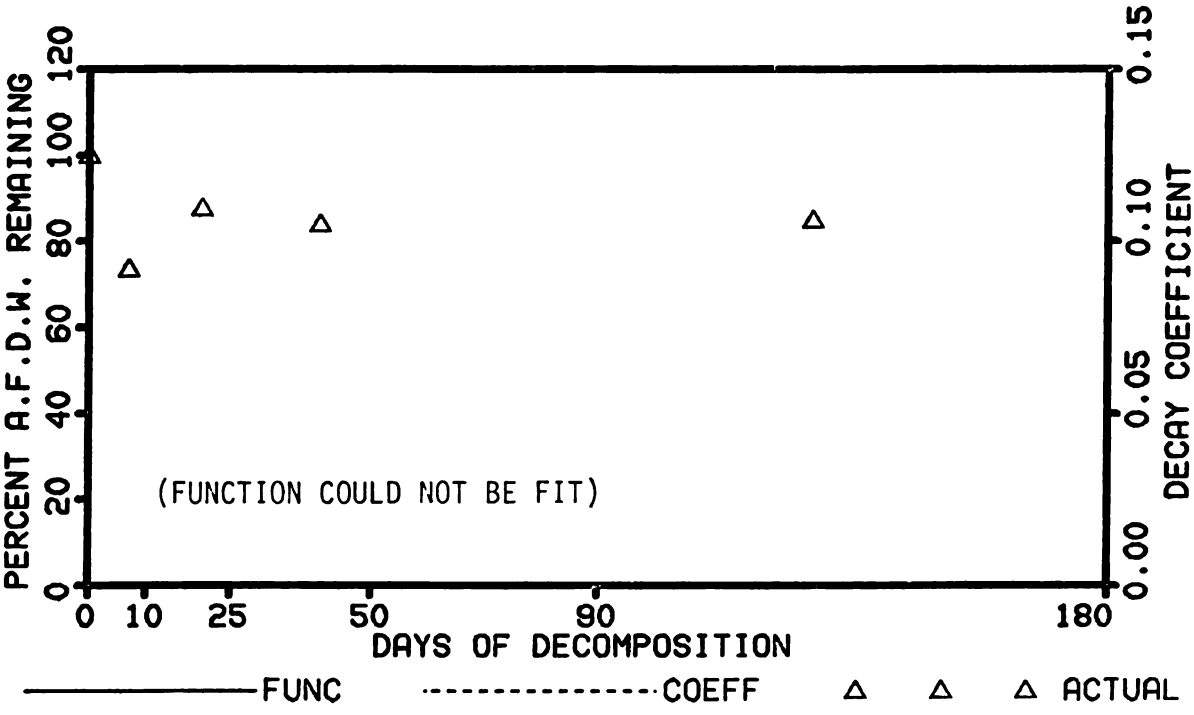
Appendix Figure 123. Decay of *Najas flexilis* in Lawrence Lake littoral zone during spring and summer. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



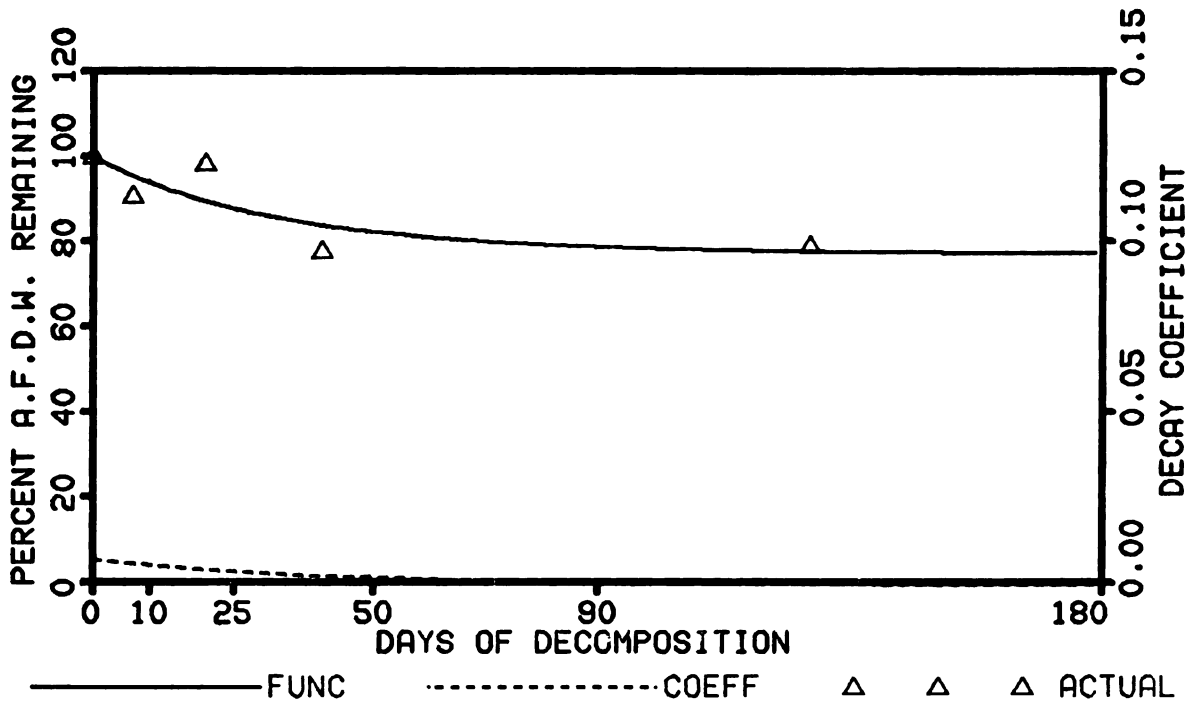
Appendix Figure 124. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during spring and summer. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



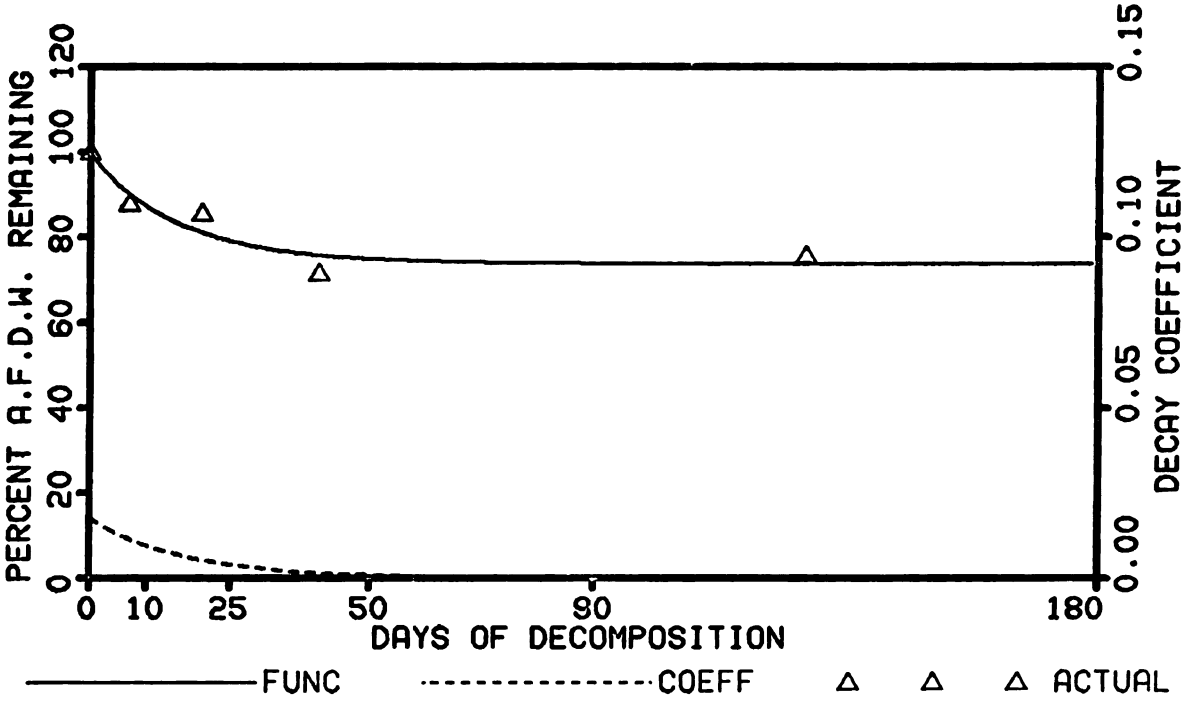
Appendix Figure 125. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during spring and summer. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



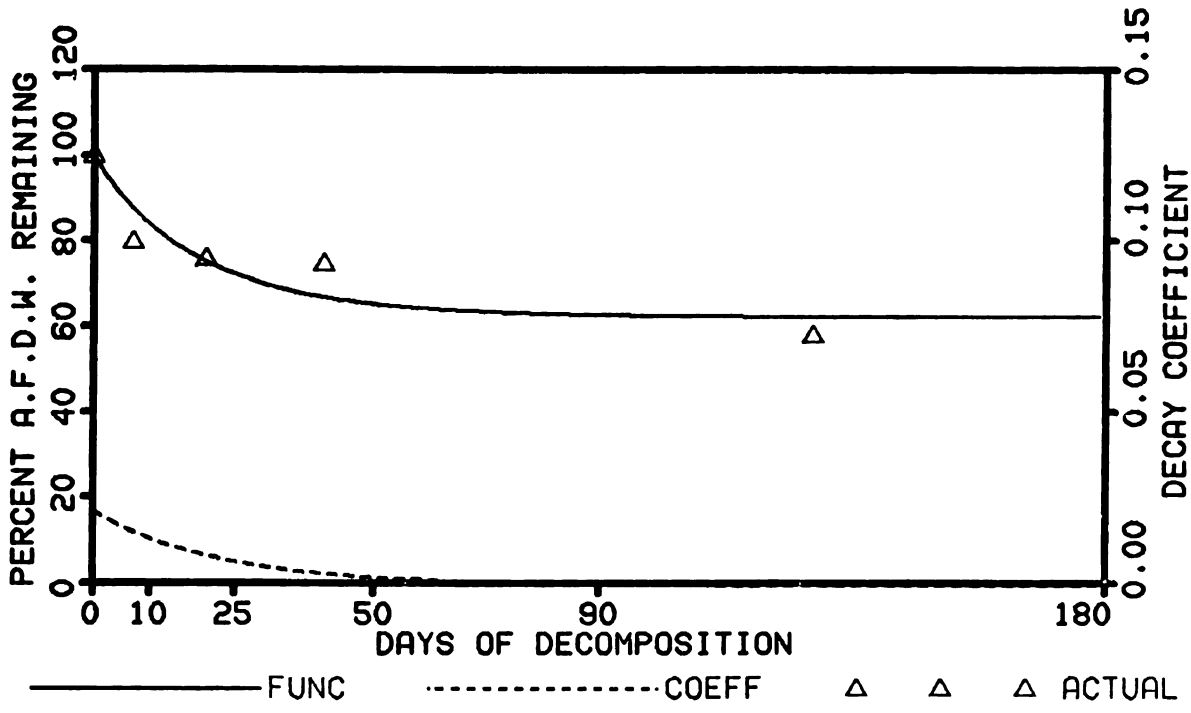
Appendix Figure 126. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



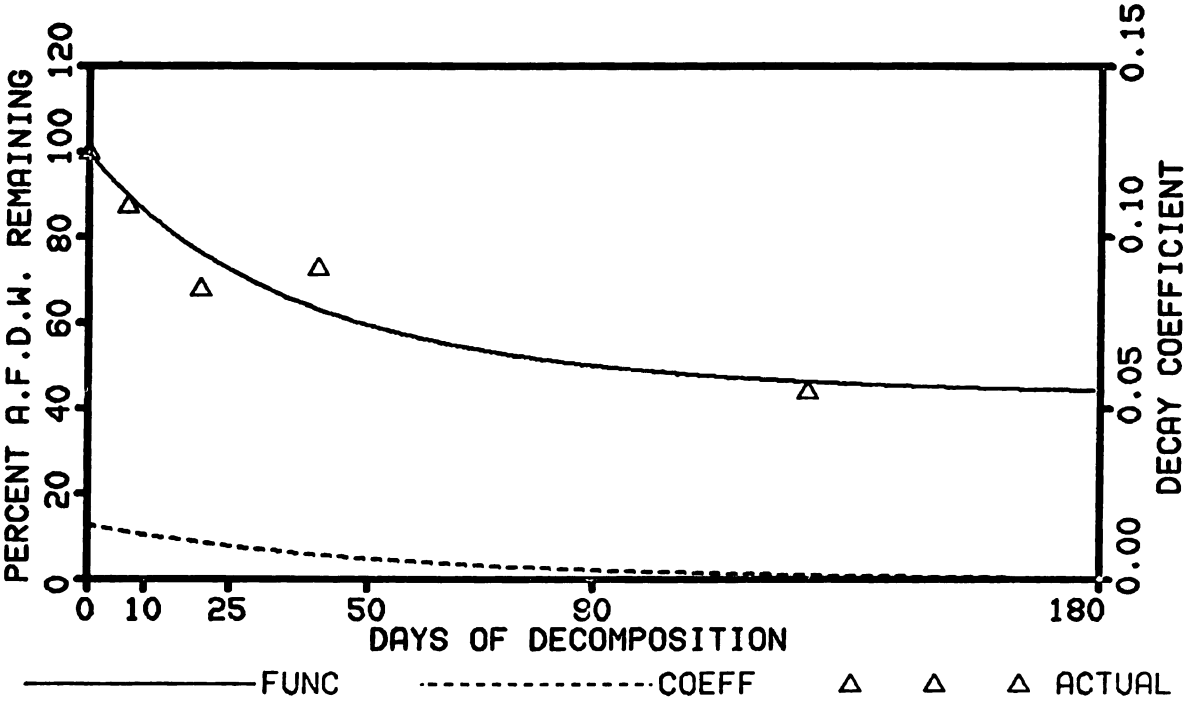
Appendix Figure 127. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



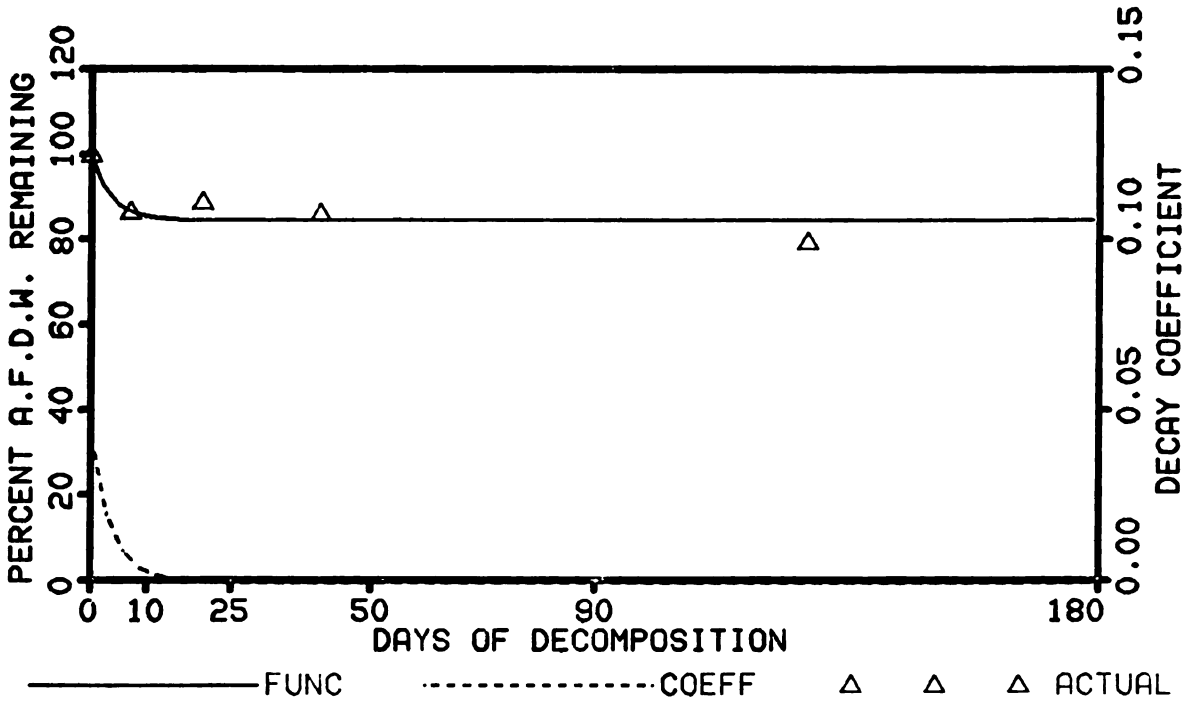
Appendix Figure 128. Decay of *Najas flexilis* in Lawrence Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



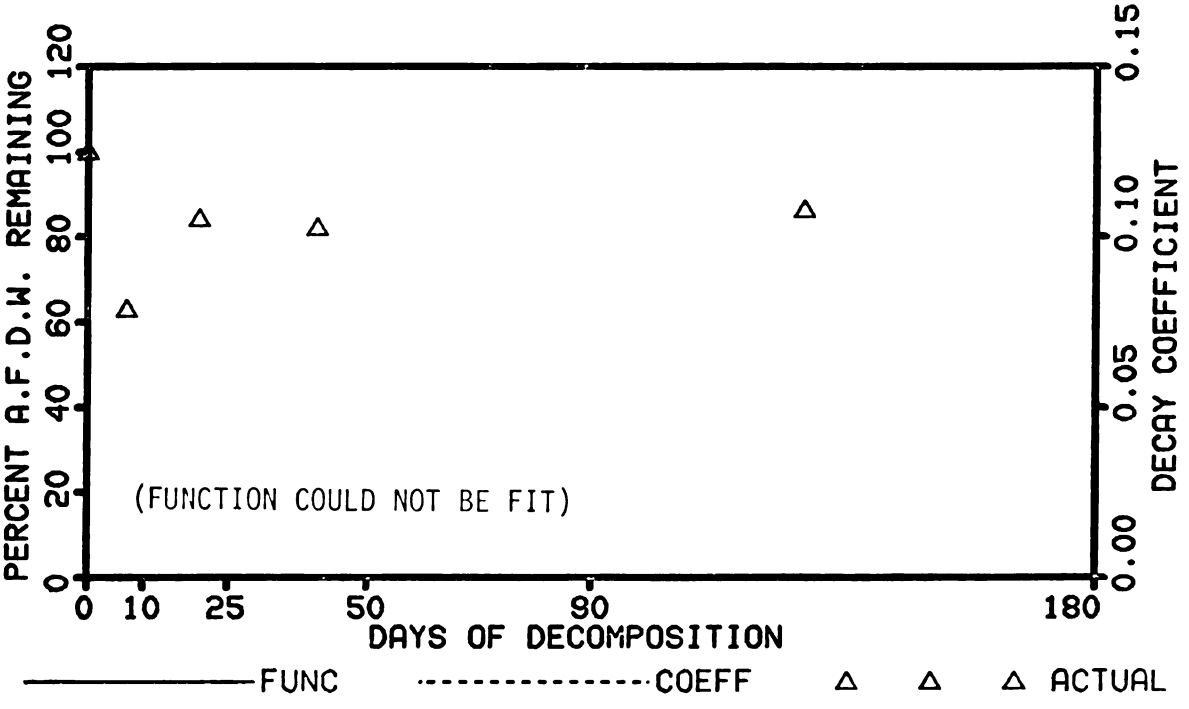
Appendix Figure 129. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



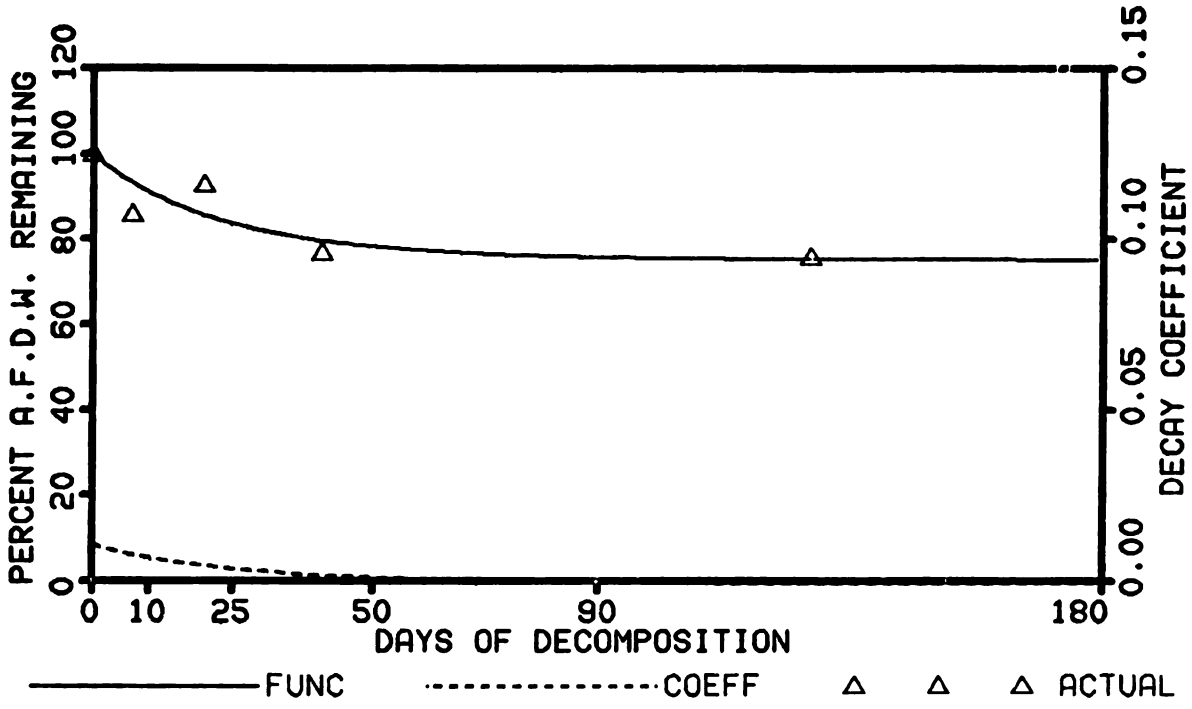
Appendix Figure 130. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



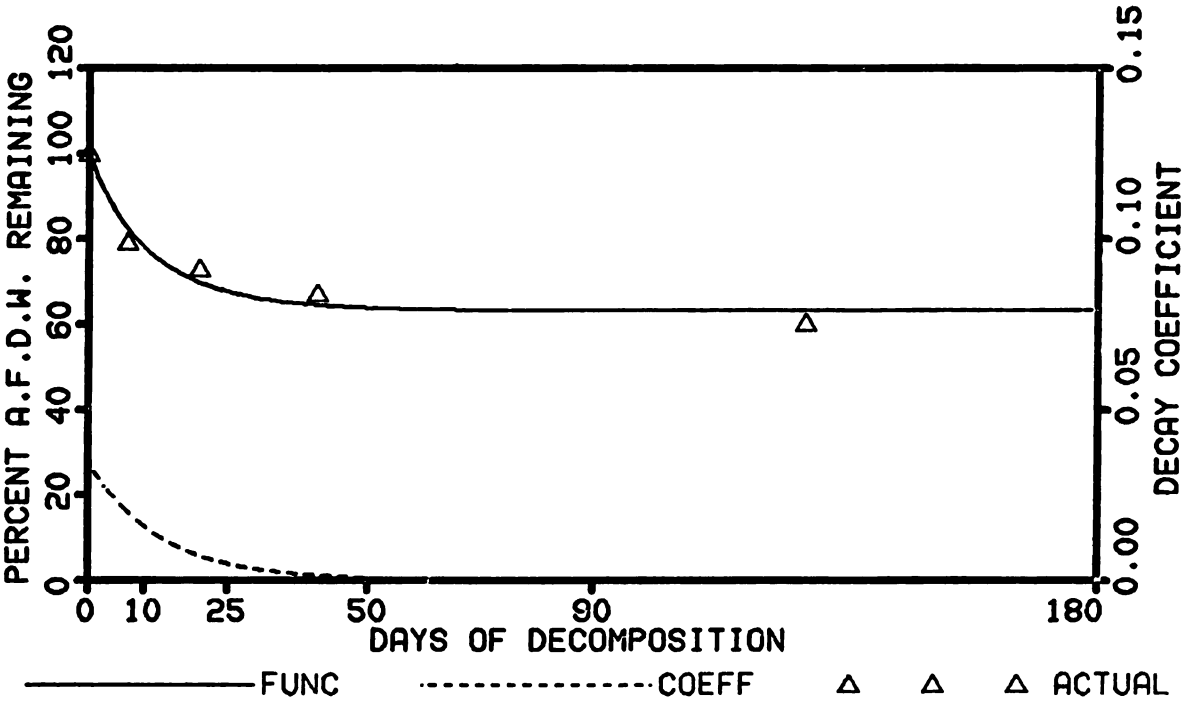
Appendix Figure 131. Decay of *Scirpus acutus* in Lawrence Lake pelagial zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



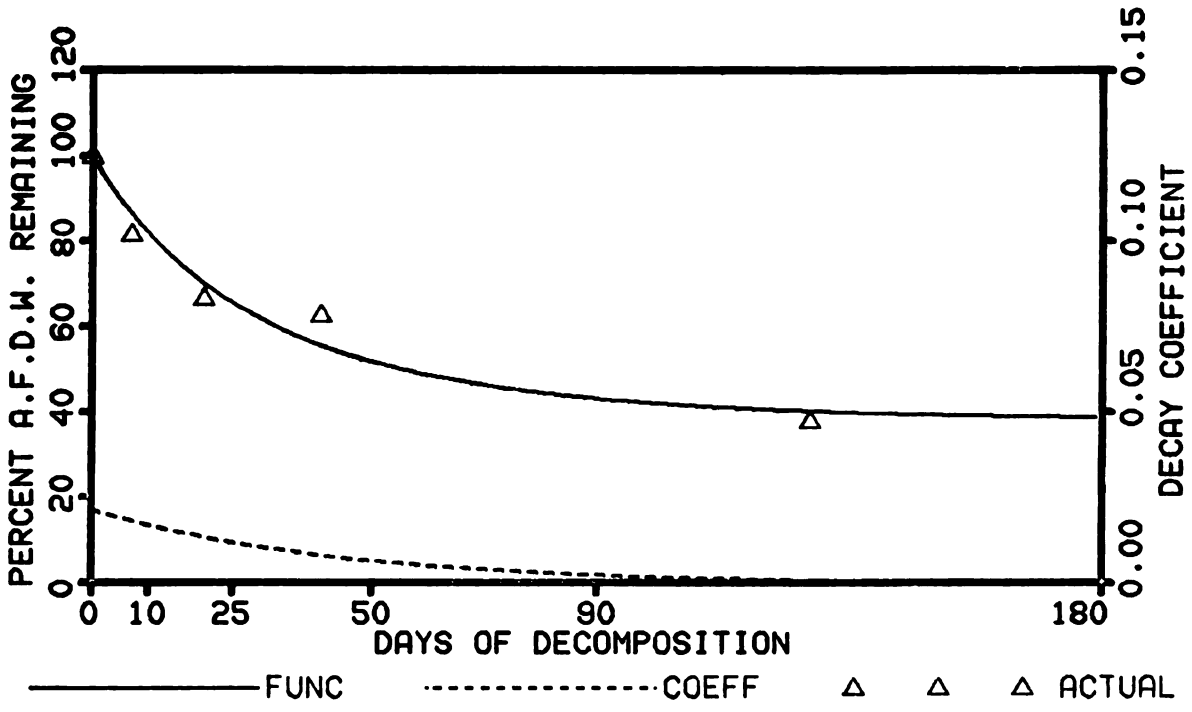
Appendix Figure 132. Decay of *Scirpus subterminalis* in Lawrence Lake pelagial zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



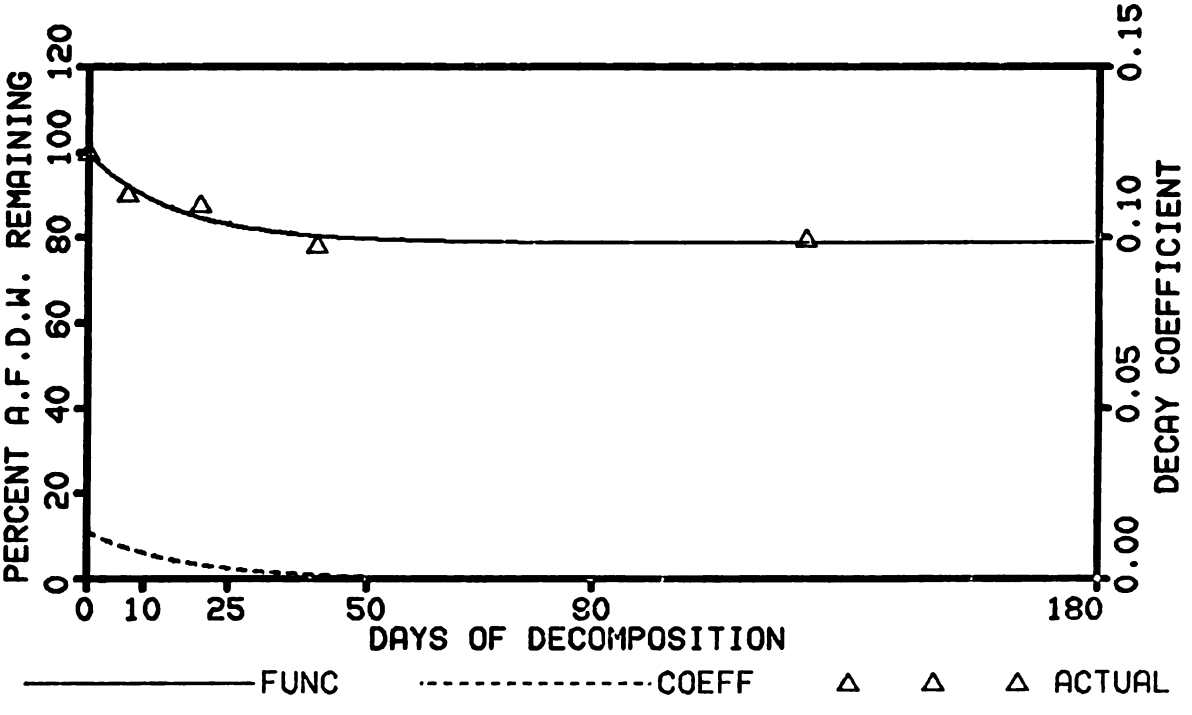
Appendix Figure 133. Decay of *Najas flexilis* in Lawrence Lake pelagial zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



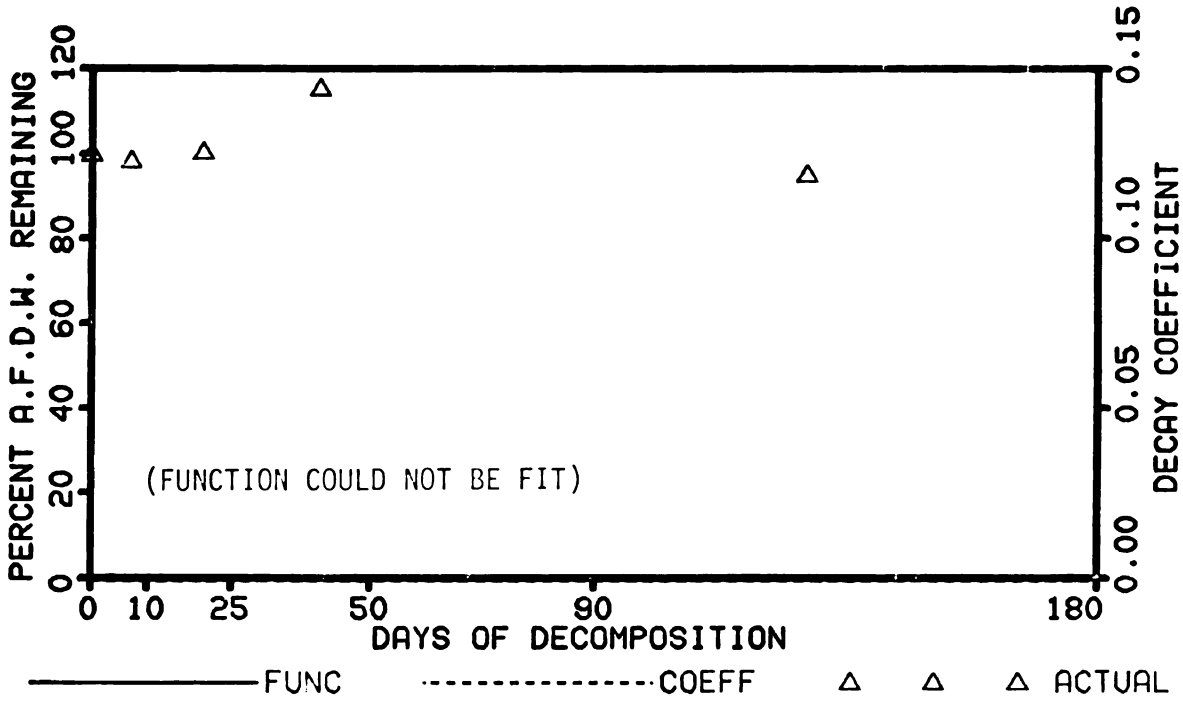
Appendix Figure 134. Decay of *Myriophyllum heterophyllum* in Lawrence Lake pelagial zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



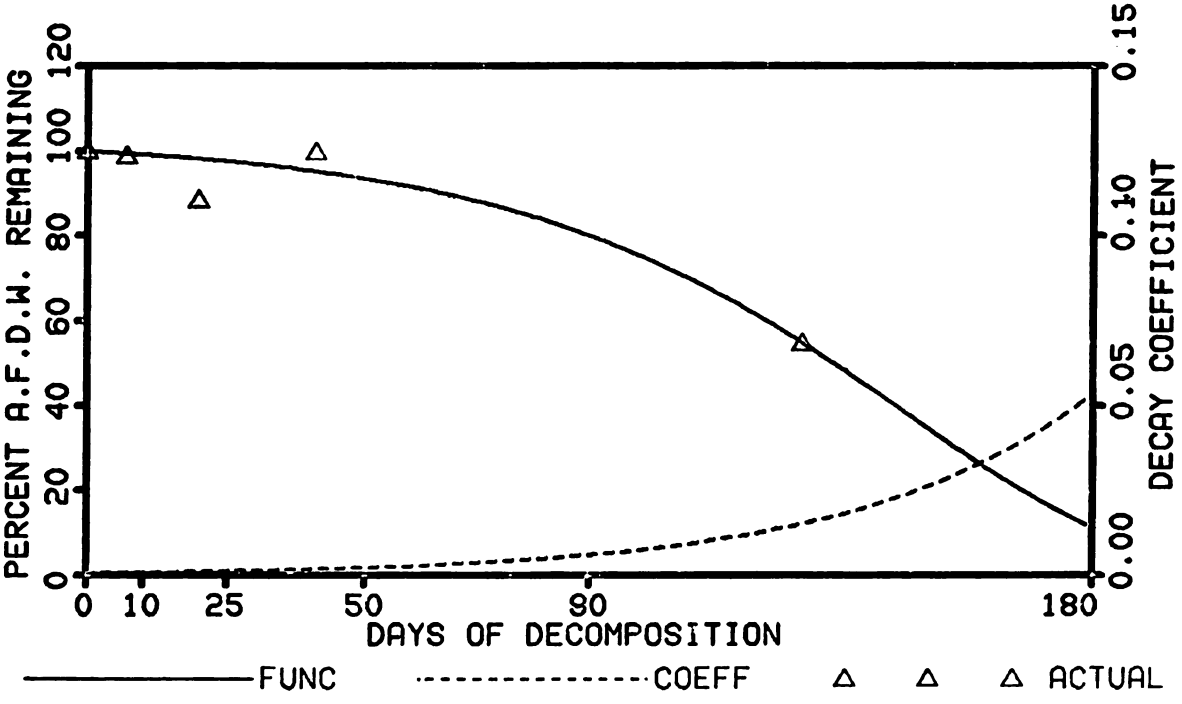
Appendix Figure 135. Decay of *Nuphar variegatum* in Lawrence Lake pelagial zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



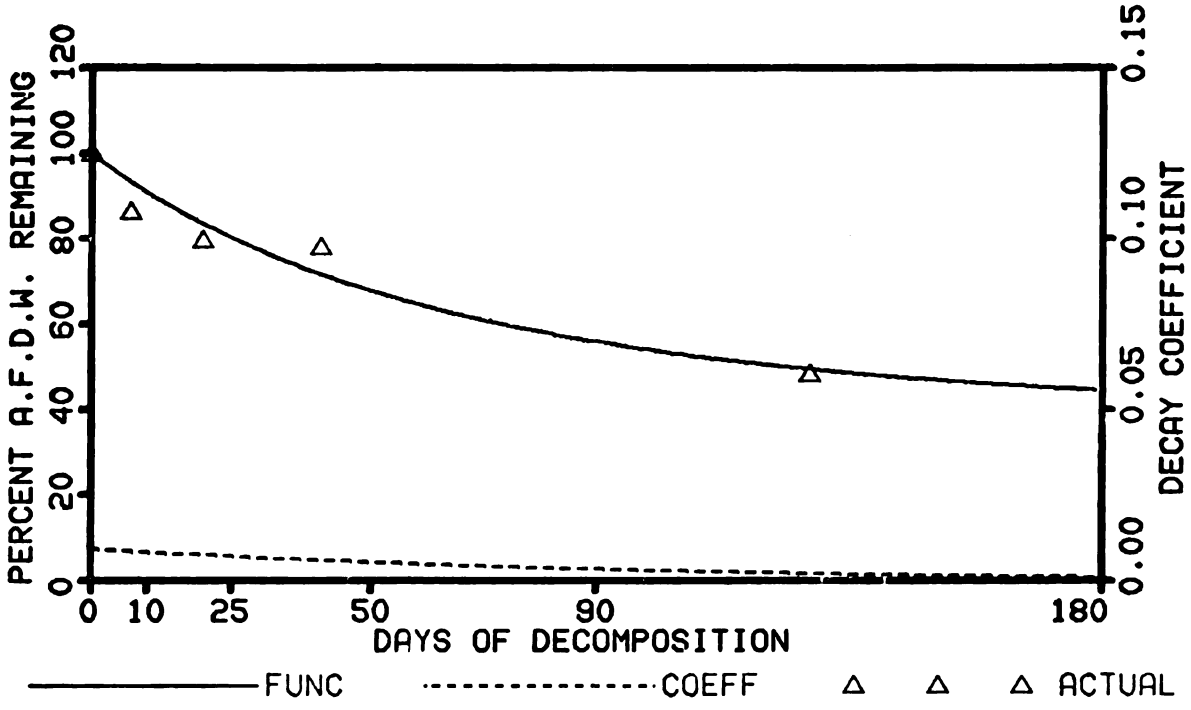
Appendix Figure 136. Decay of *Scirpus acutus* in Wintergreen Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



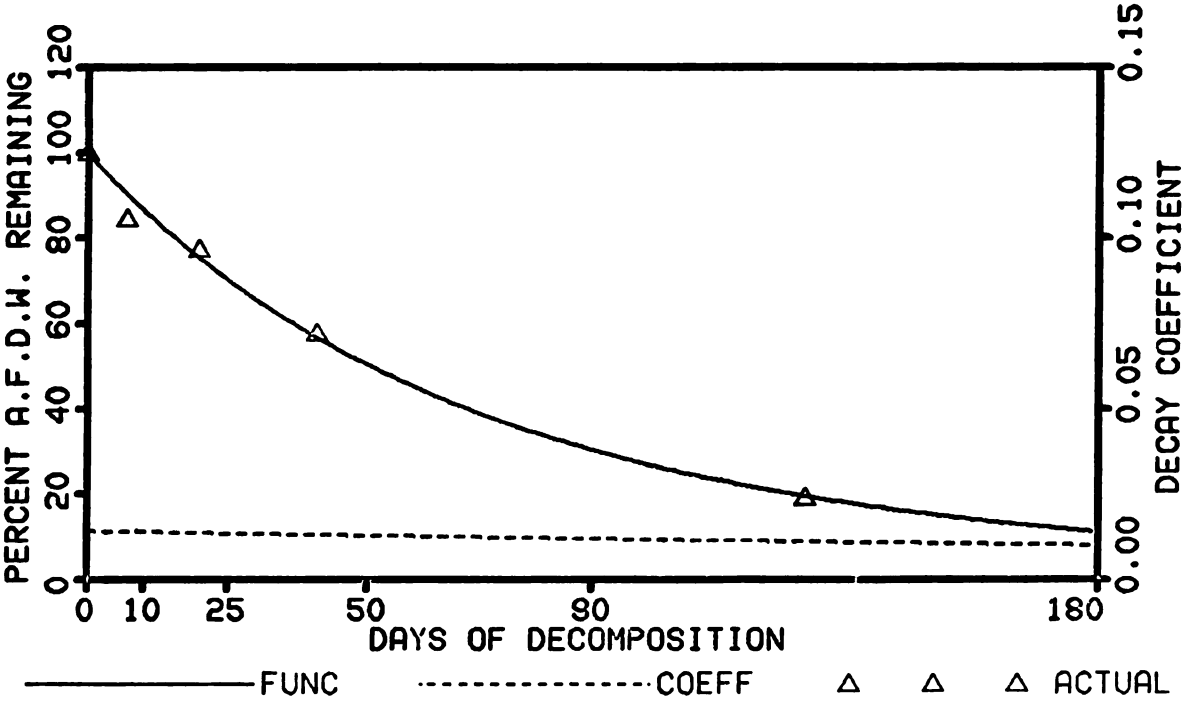
Appendix Figure 137. Decay of *Scirpus subterminalis* in Wintergreen Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



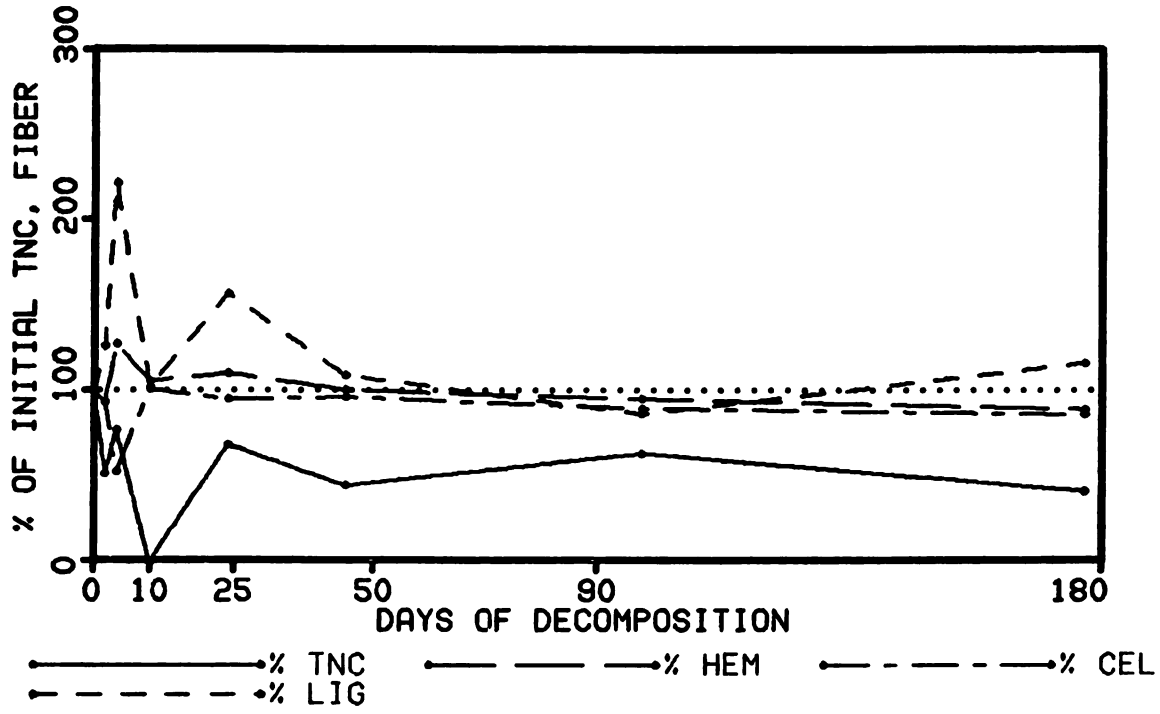
Appendix Figure 138. Decay of *Najas flexilis* in Wintergreen Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



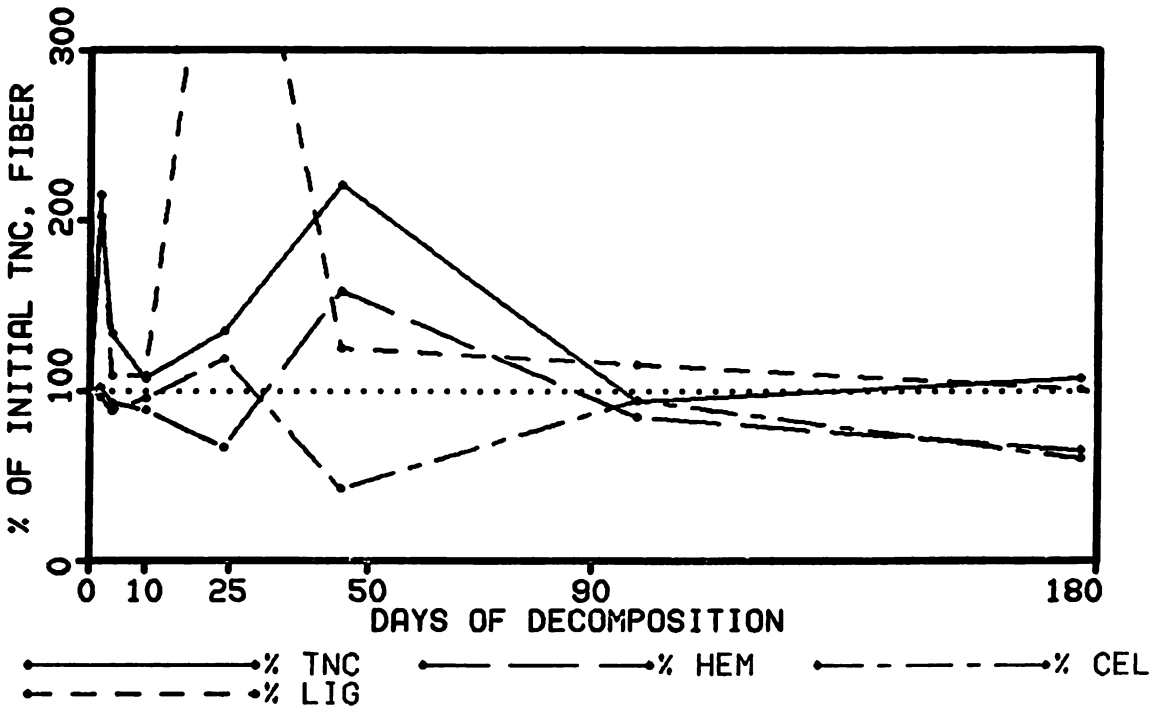
Appendix Figure 139. Decay of *Myriophyllum heterophyllum* in Wintergreen Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



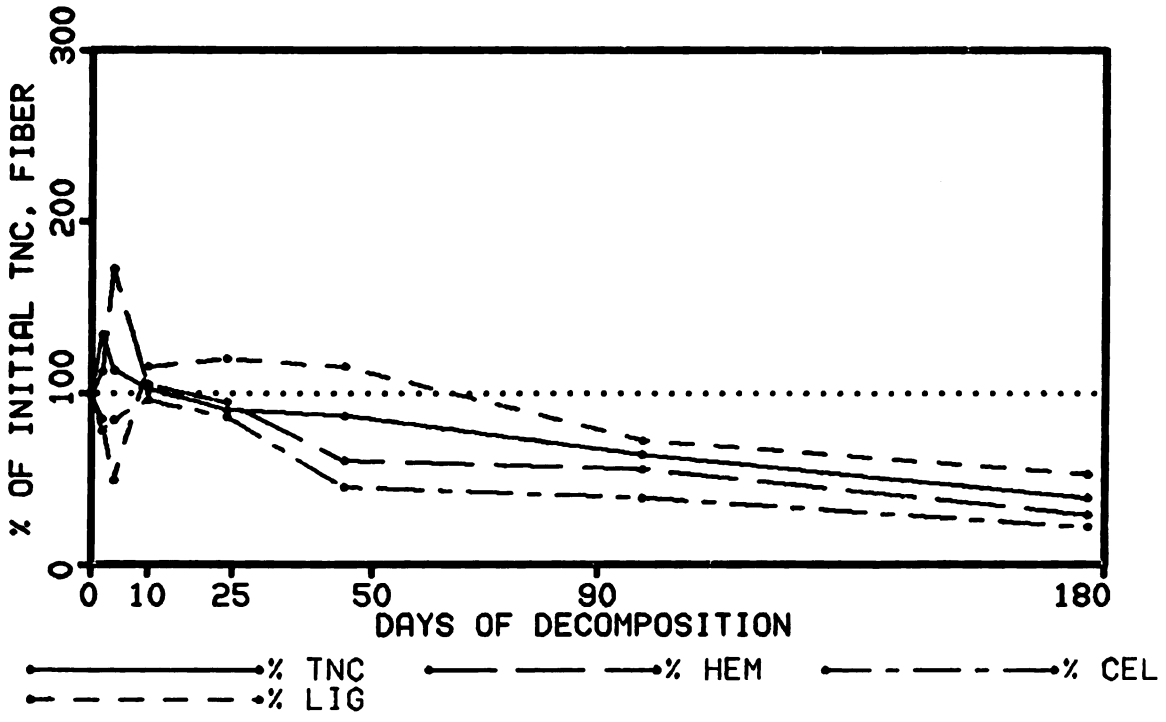
Appendix Figure 140. Decay of *Nuphar variegatum* in Wintergreen Lake littoral zone during fall and winter. Percent of initial ash-free dry weight remaining; actual data, values predicted by exponential function (FUNC), and decay coefficient of the function (COEFF).



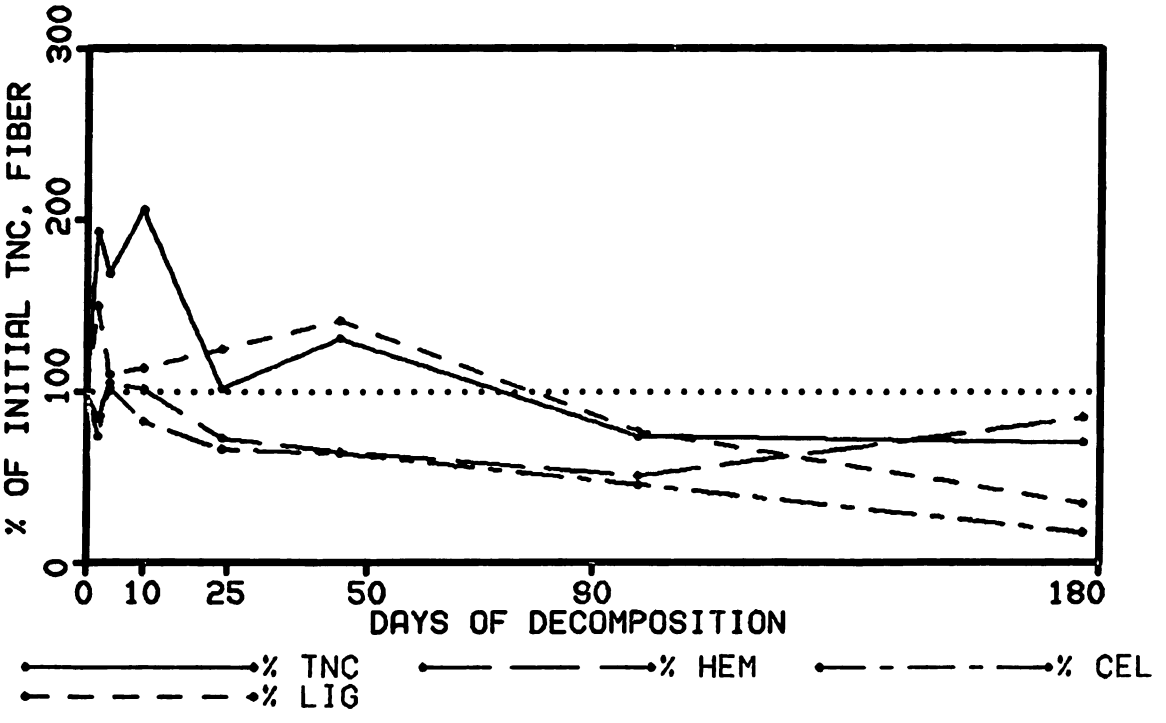
Appendix Figure 141. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



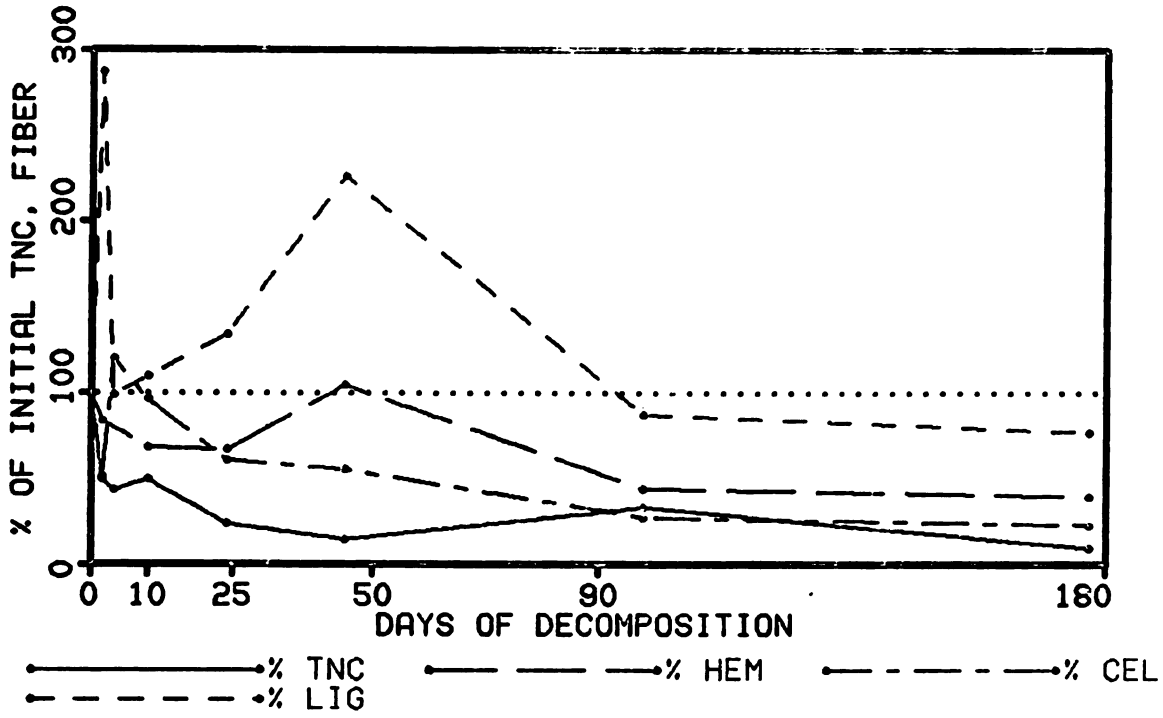
Appendix Figure 142. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



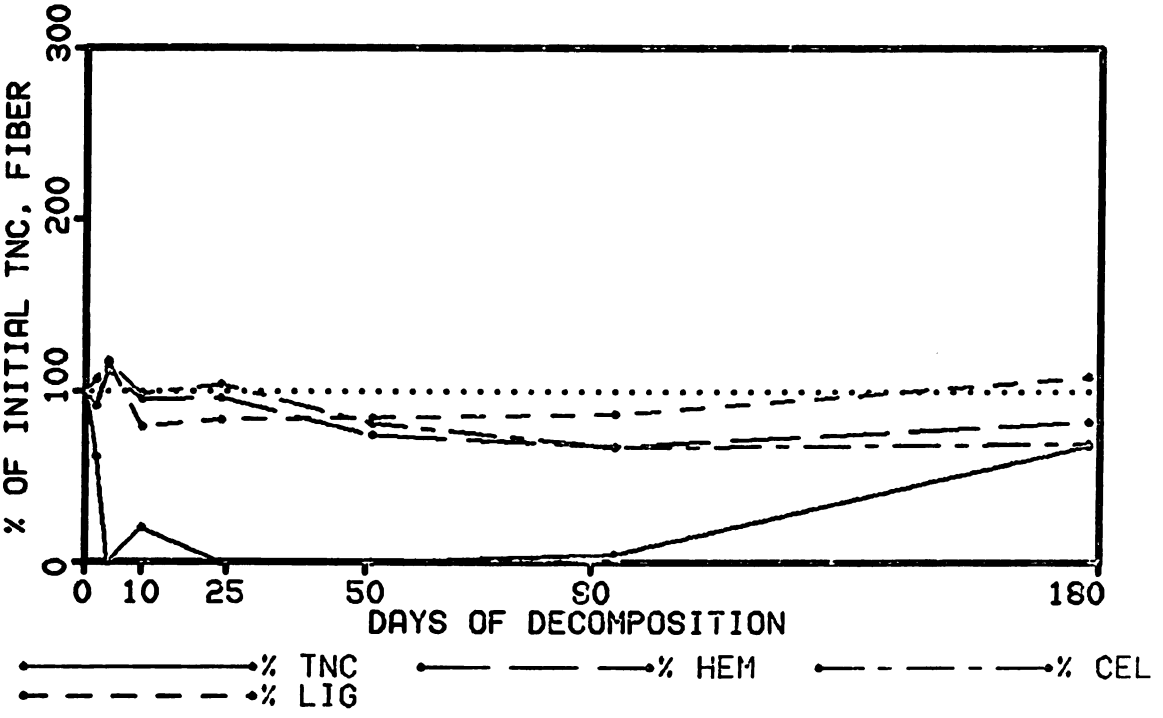
Appendix Figure 143. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



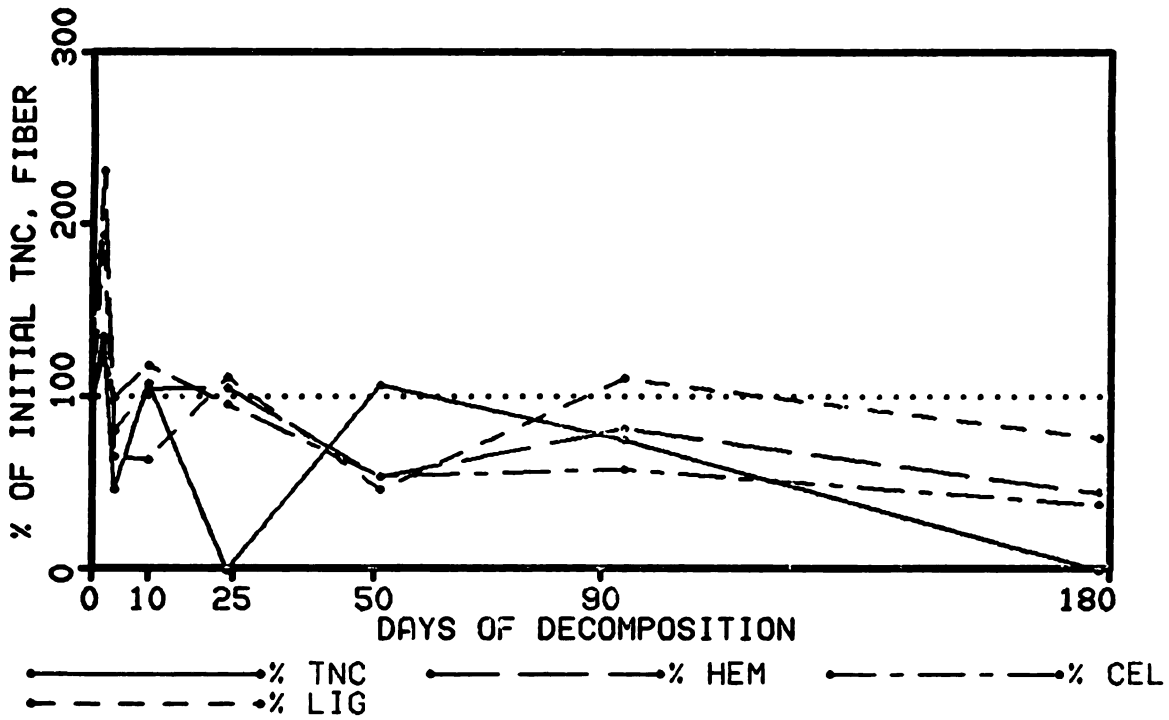
Appendix Figure 144. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



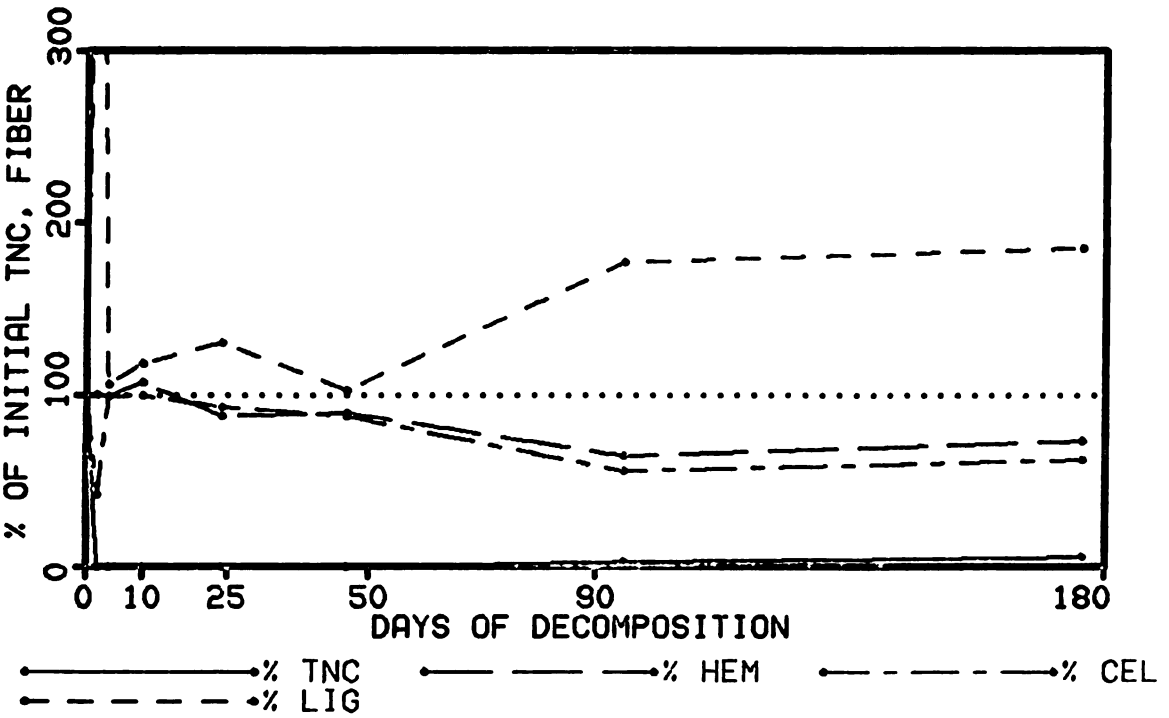
Appendix Figure 145. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



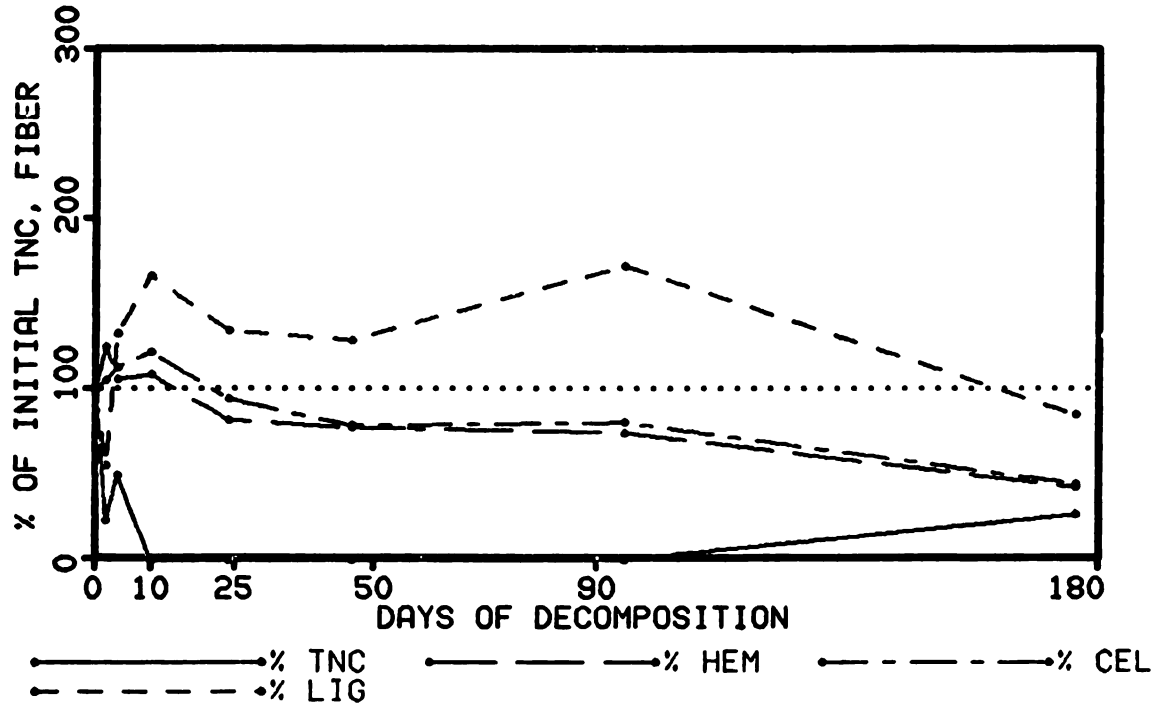
Appendix Figure 146. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



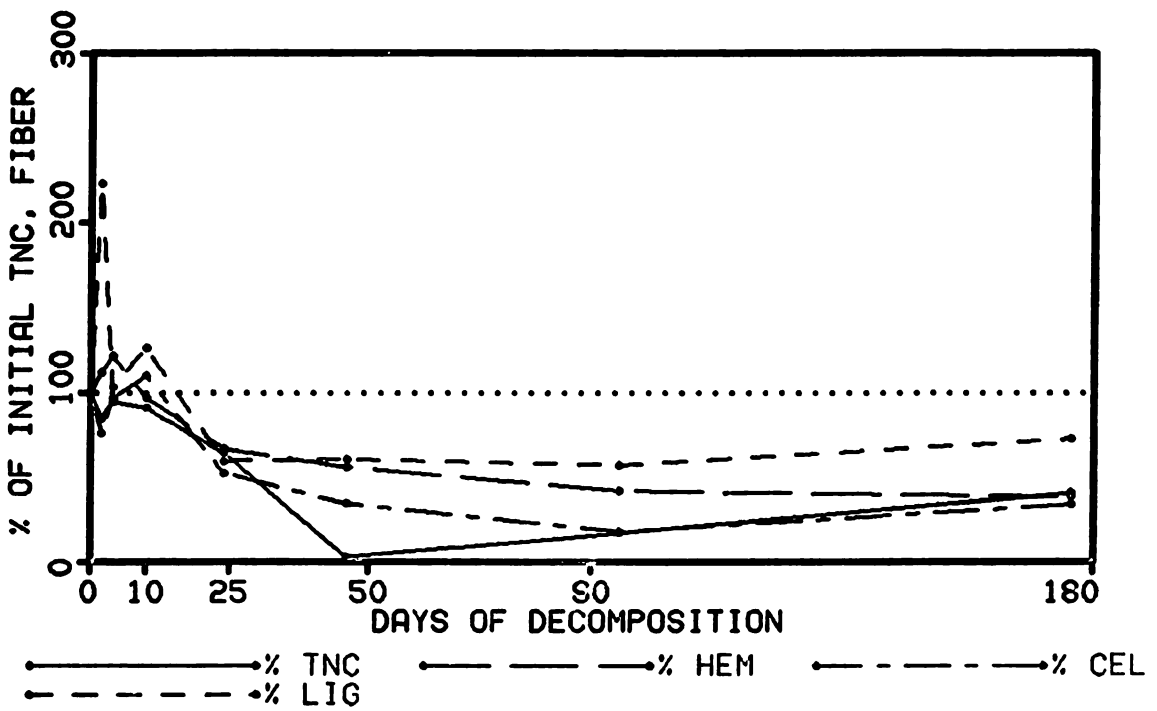
Appendix Figure 147. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



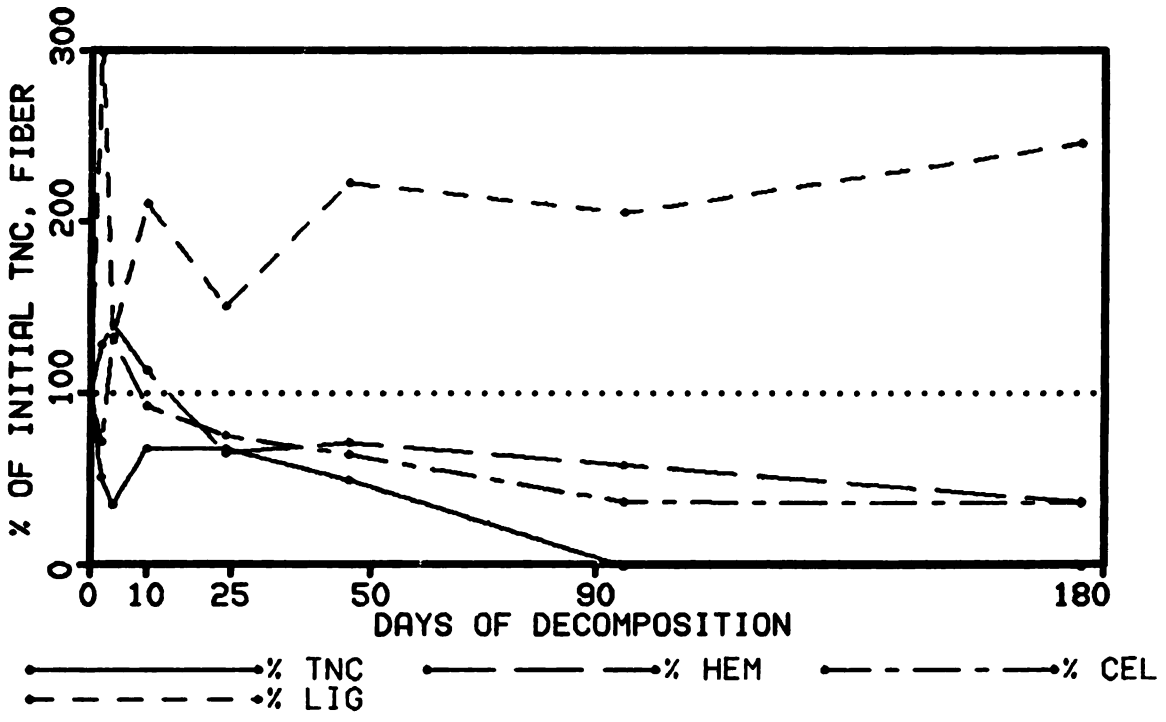
Appendix Figure 148. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



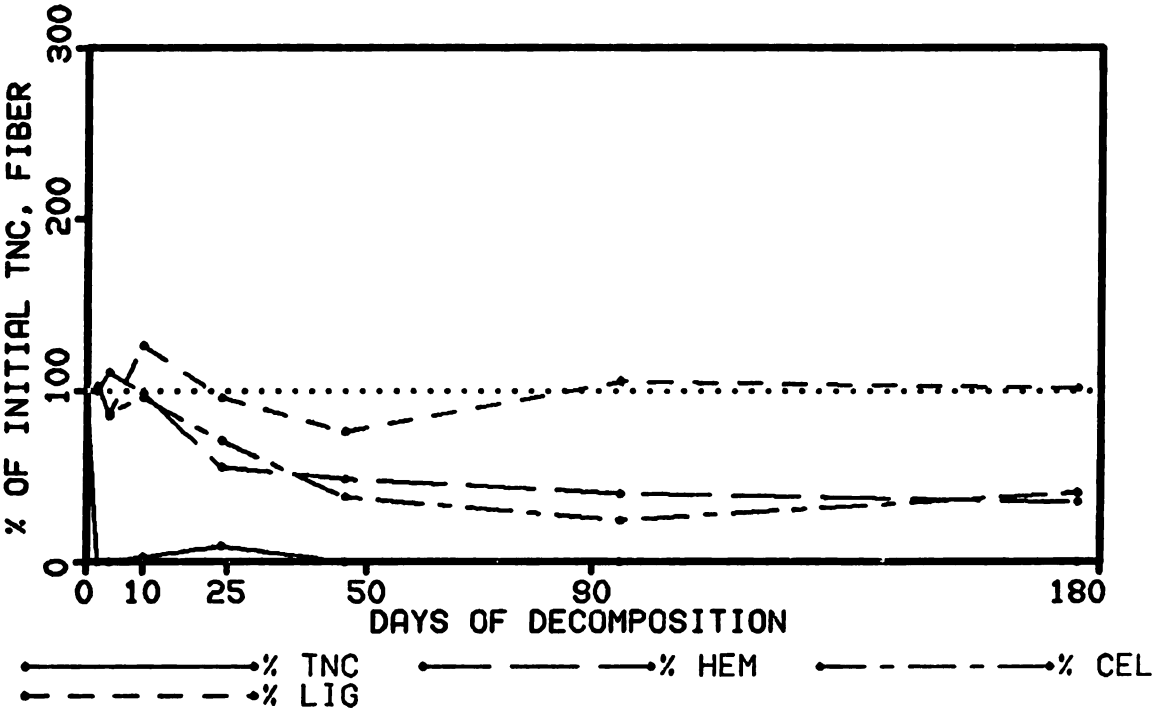
Appendix Figure 149. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



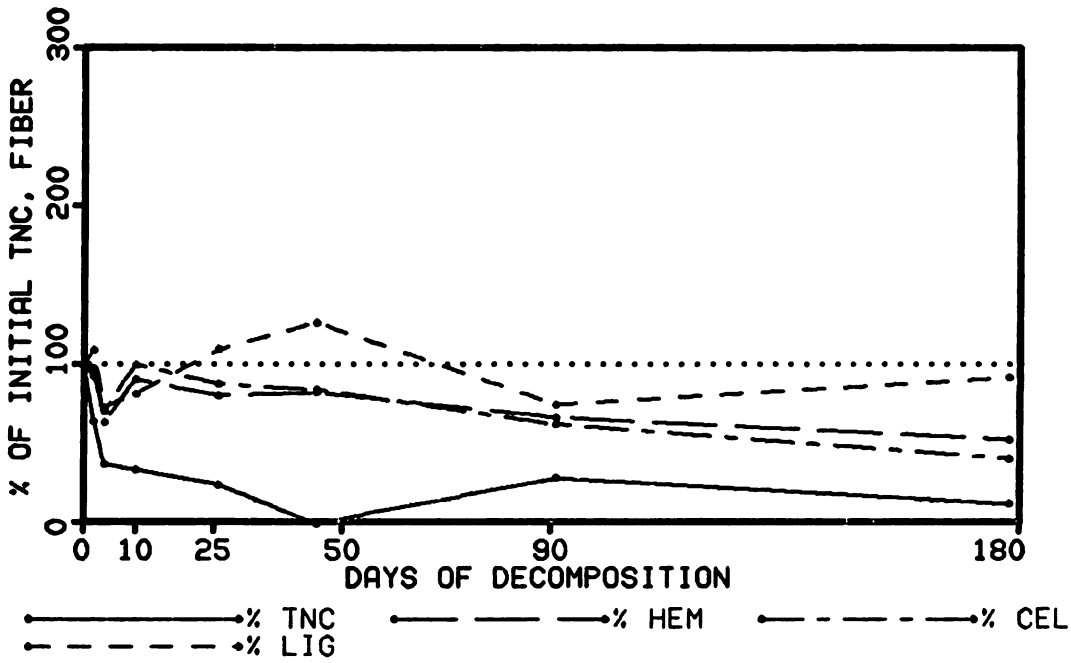
Appendix Figure 150. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



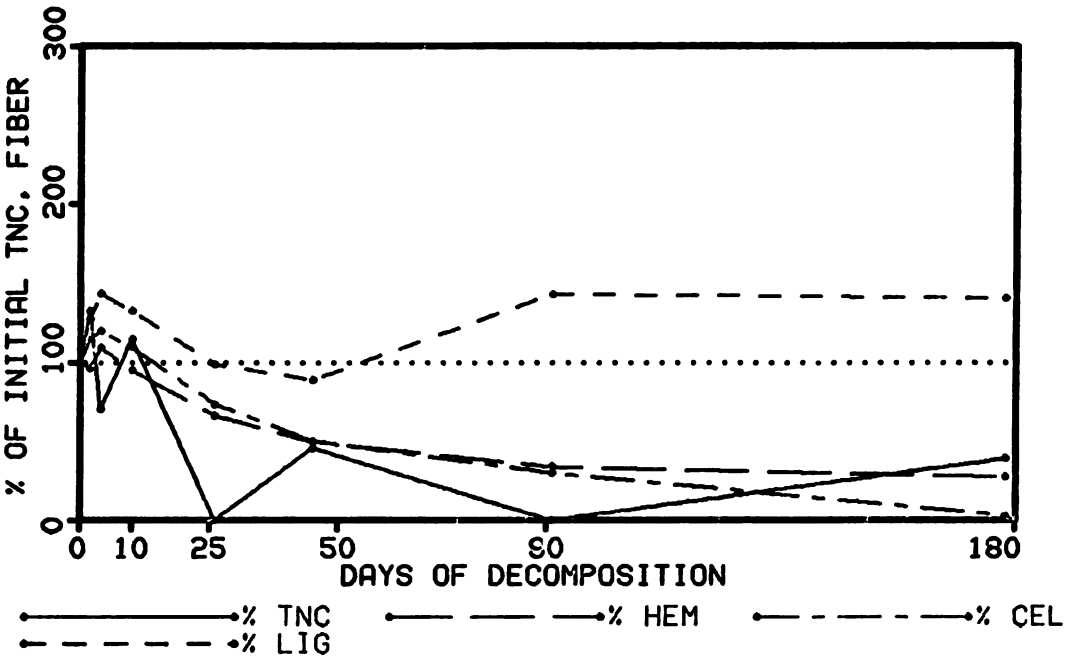
Appendix Figure 151. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



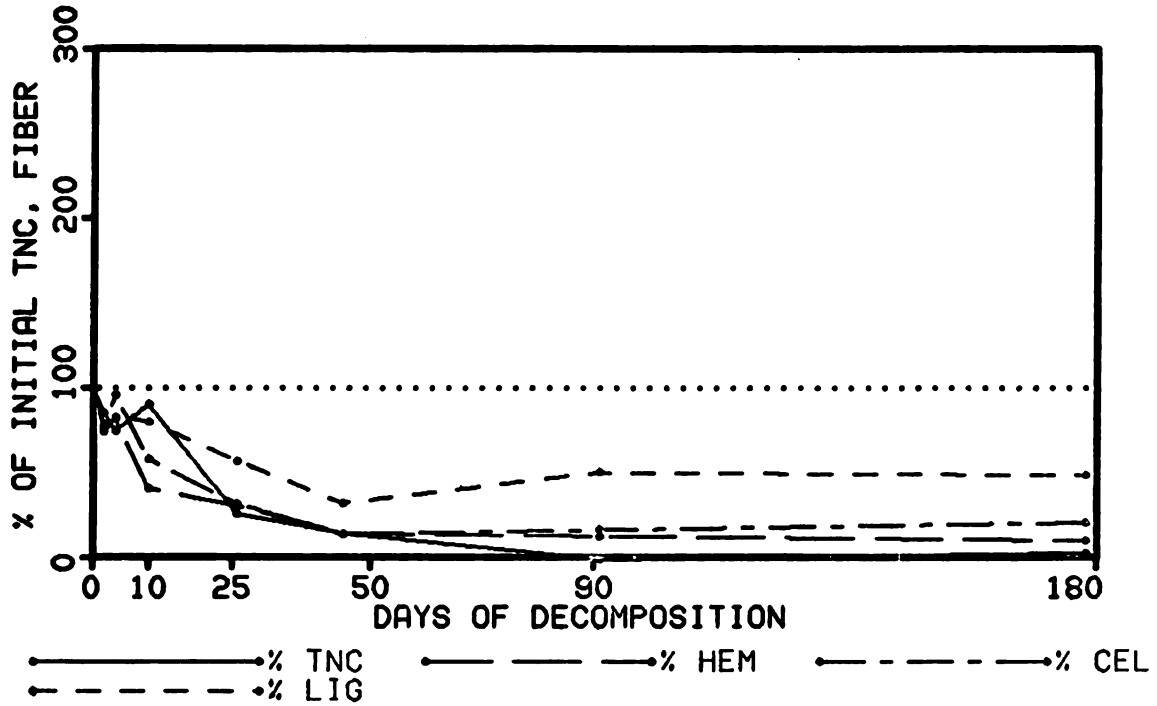
Appendix Figure 152. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



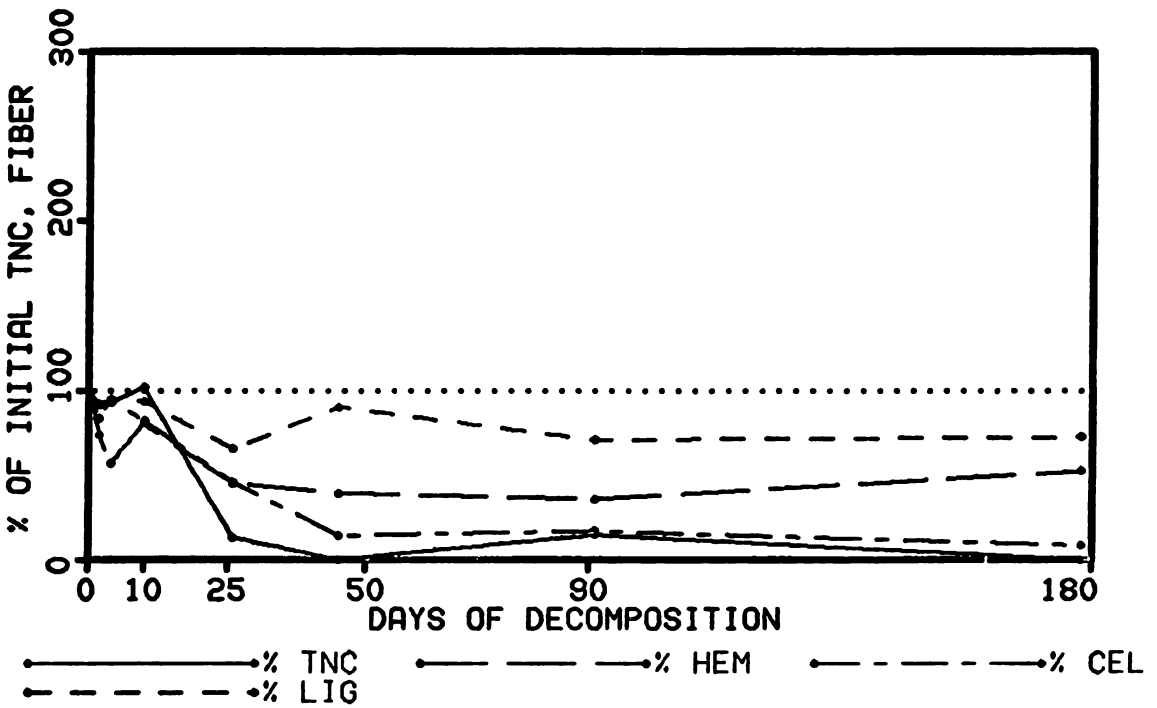
Appendix Figure 153. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



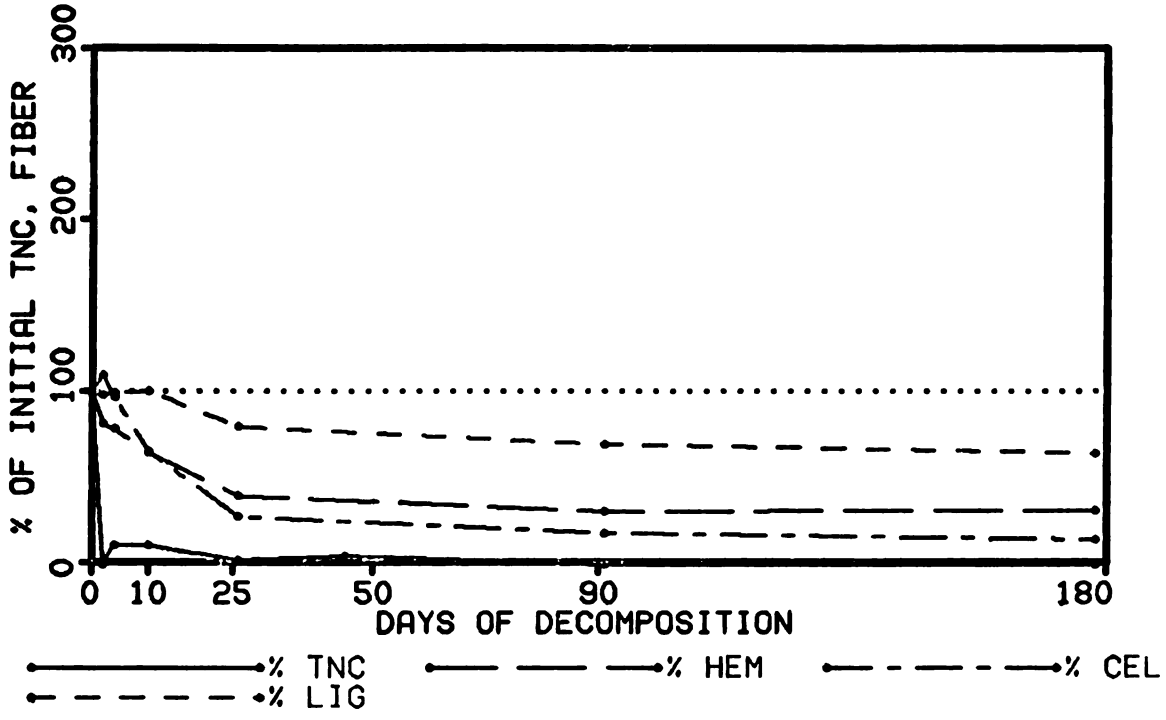
Appendix Figure 154. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



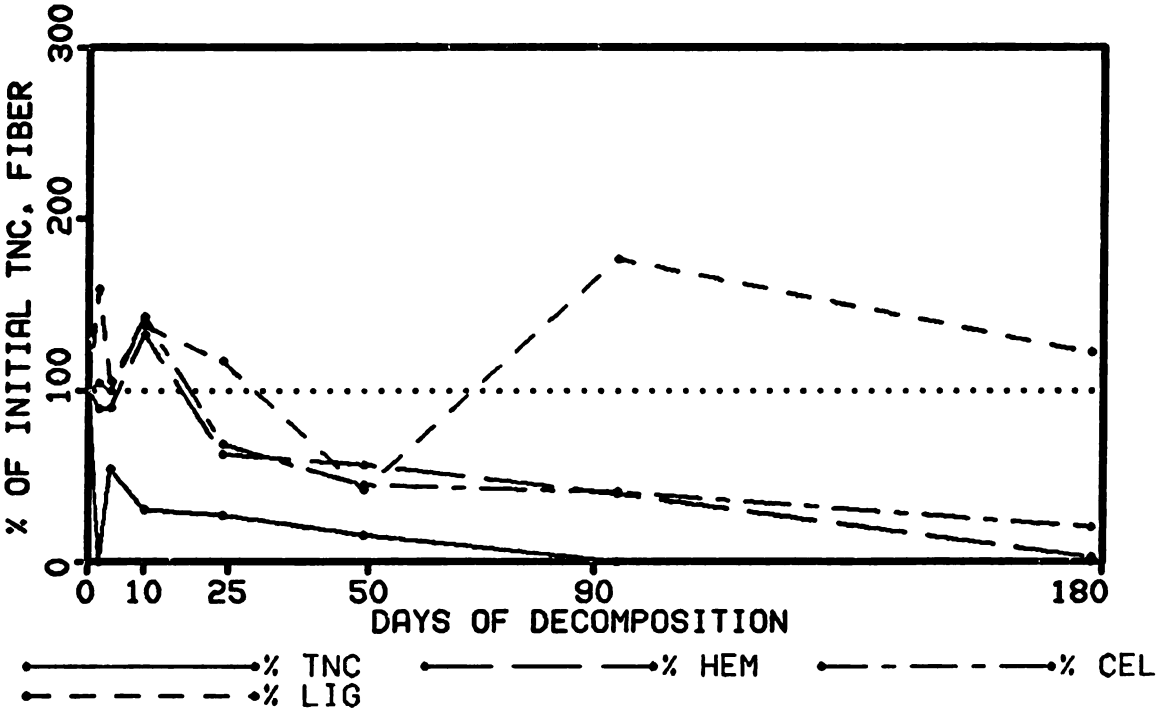
Appendix Figure 155. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



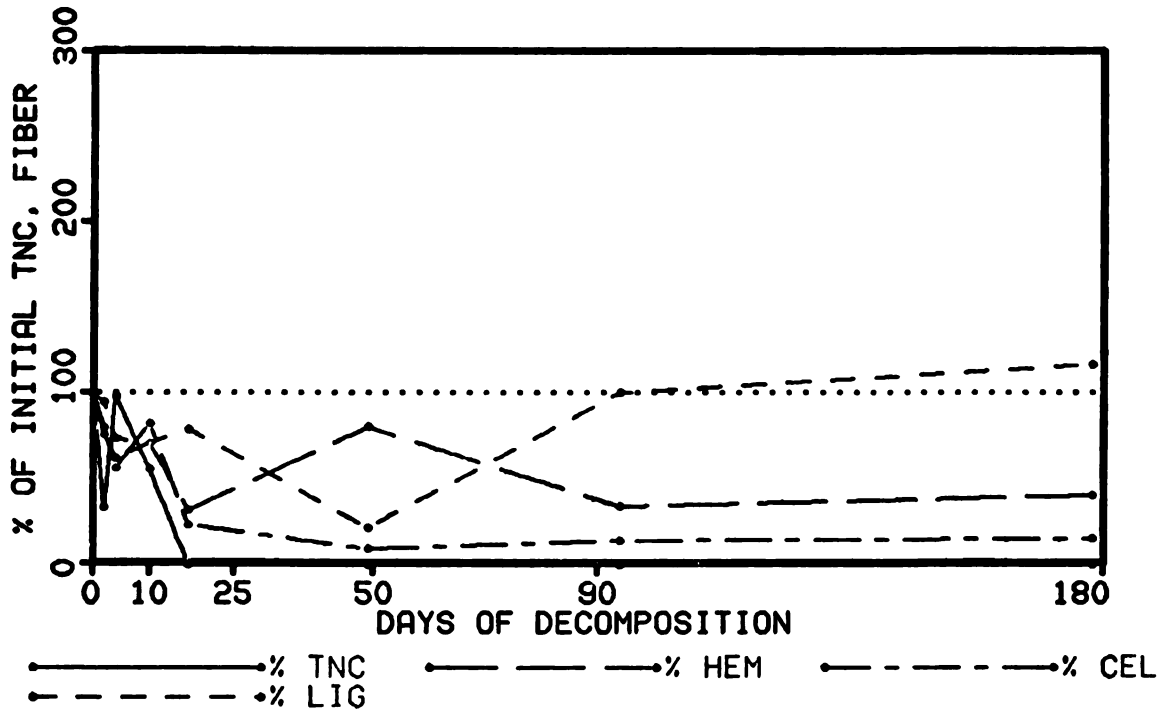
Appendix Figure 156. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



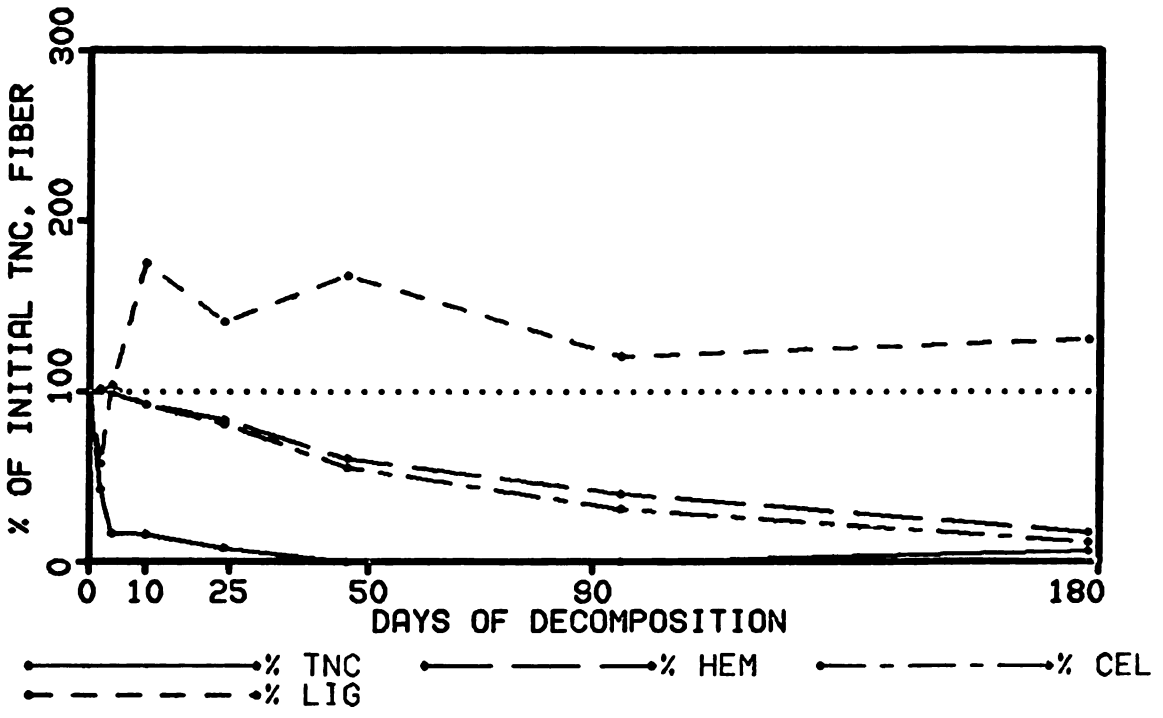
Appendix Figure 157. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



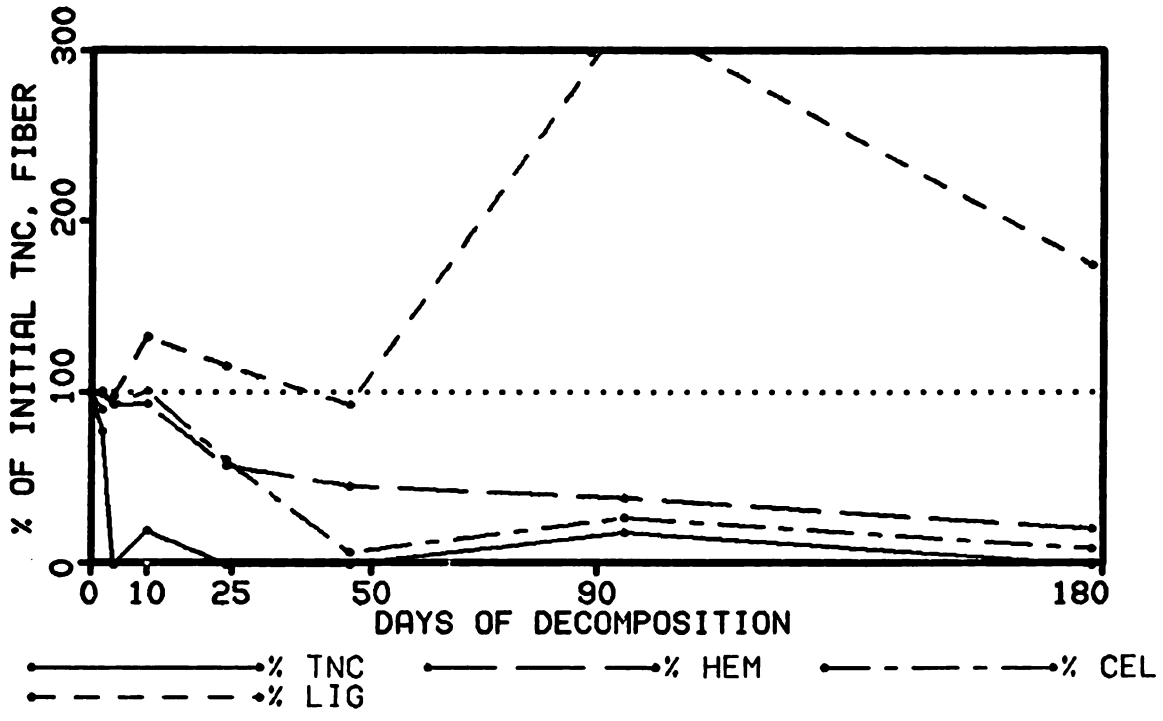
Appendix Figure 158. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



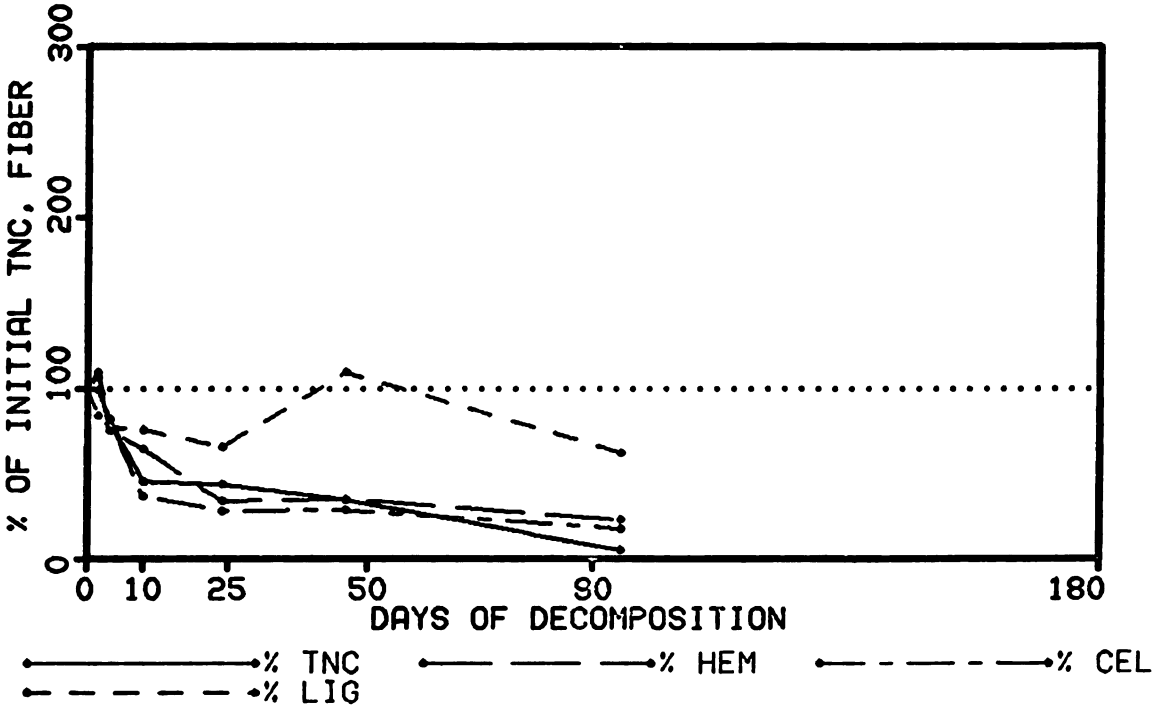
Appendix Figure 159. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



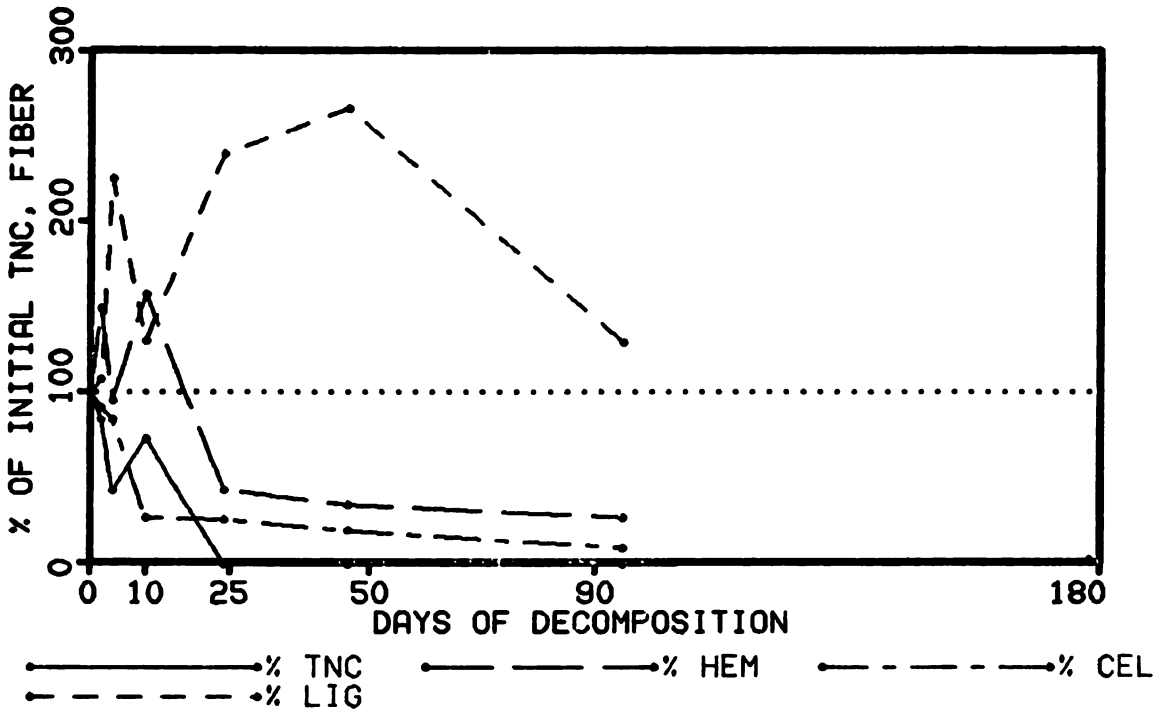
Appendix Figure 160. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



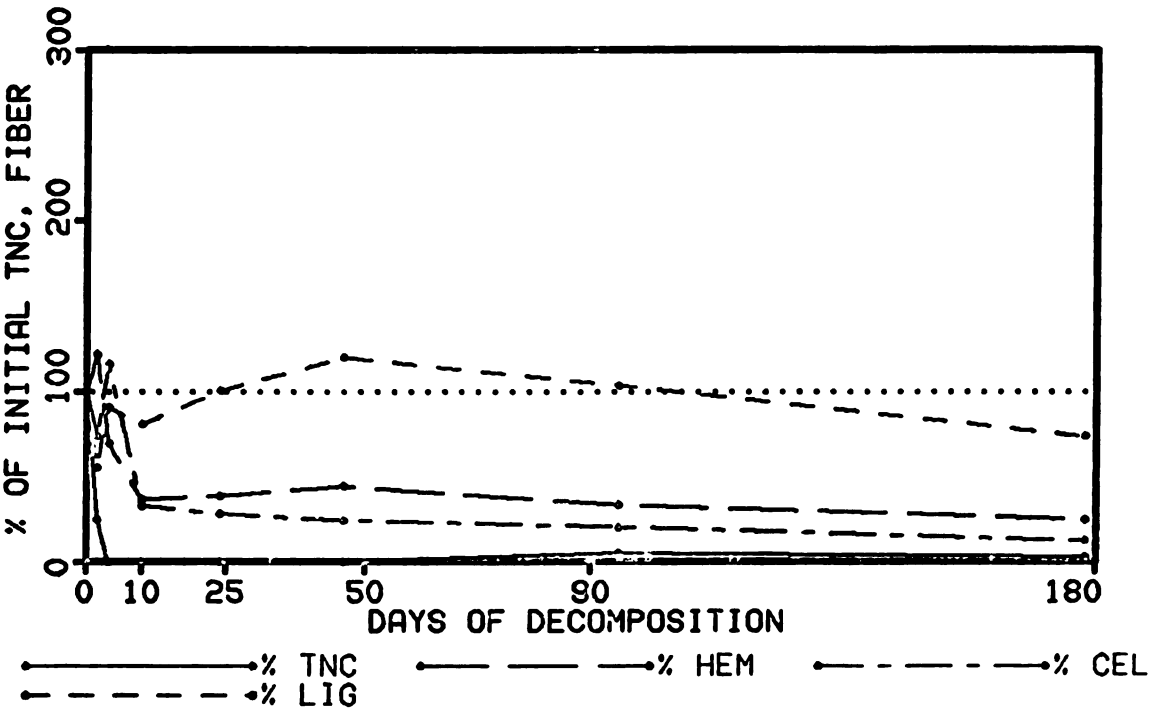
Appendix Figure 161. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



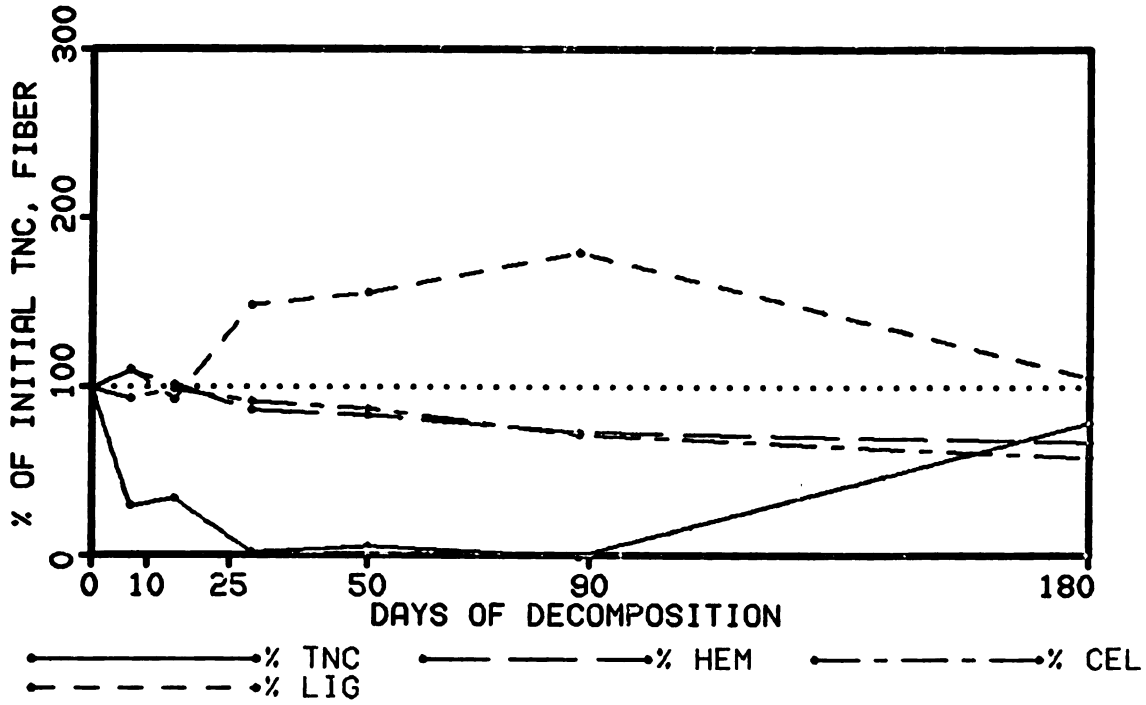
Appendix Figure 162. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



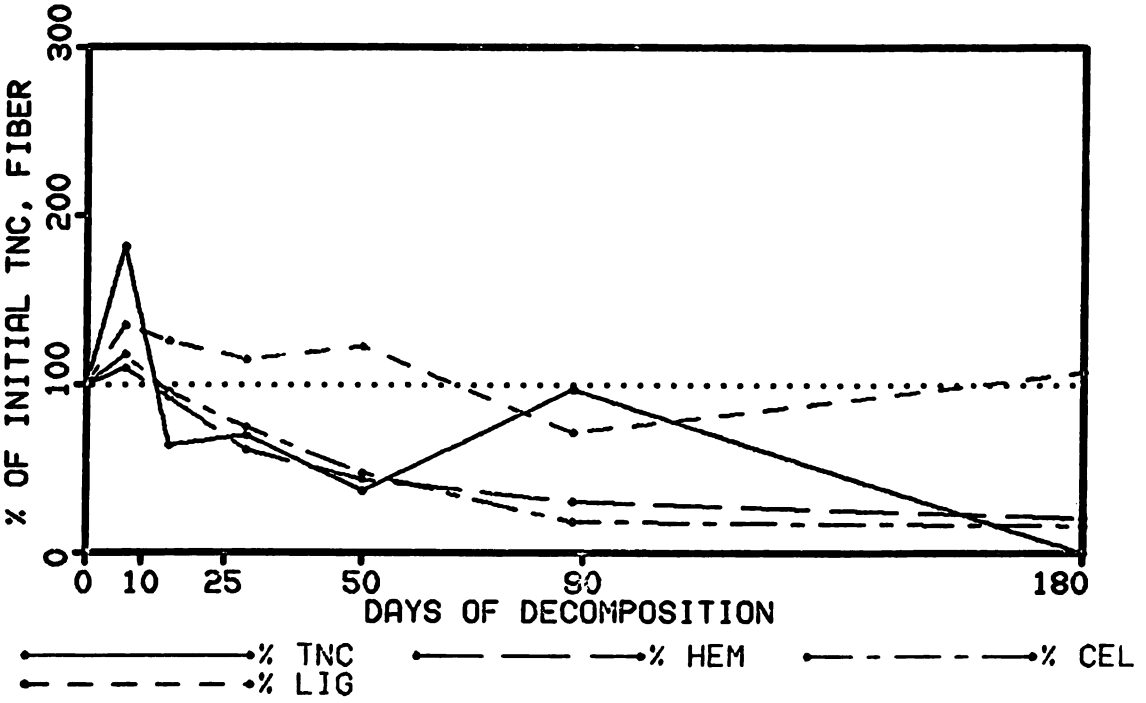
Appendix Figure 163. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



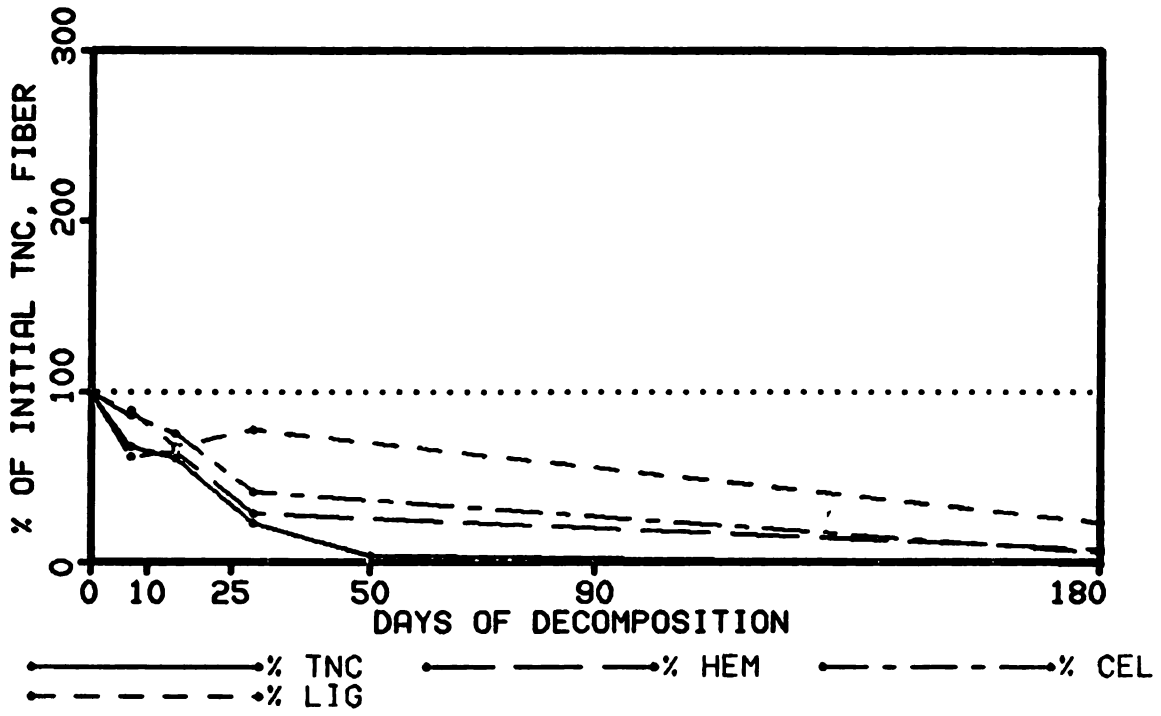
Appendix Figure 164. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



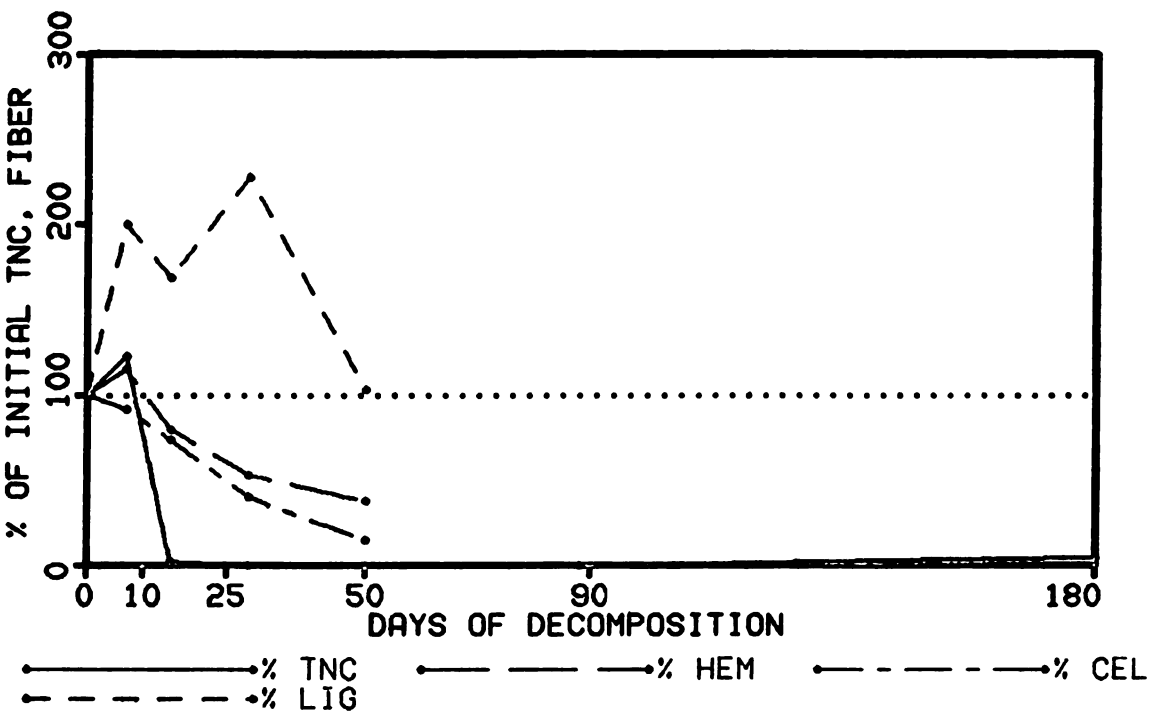
Appendix Figure 165. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during spring and summer. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



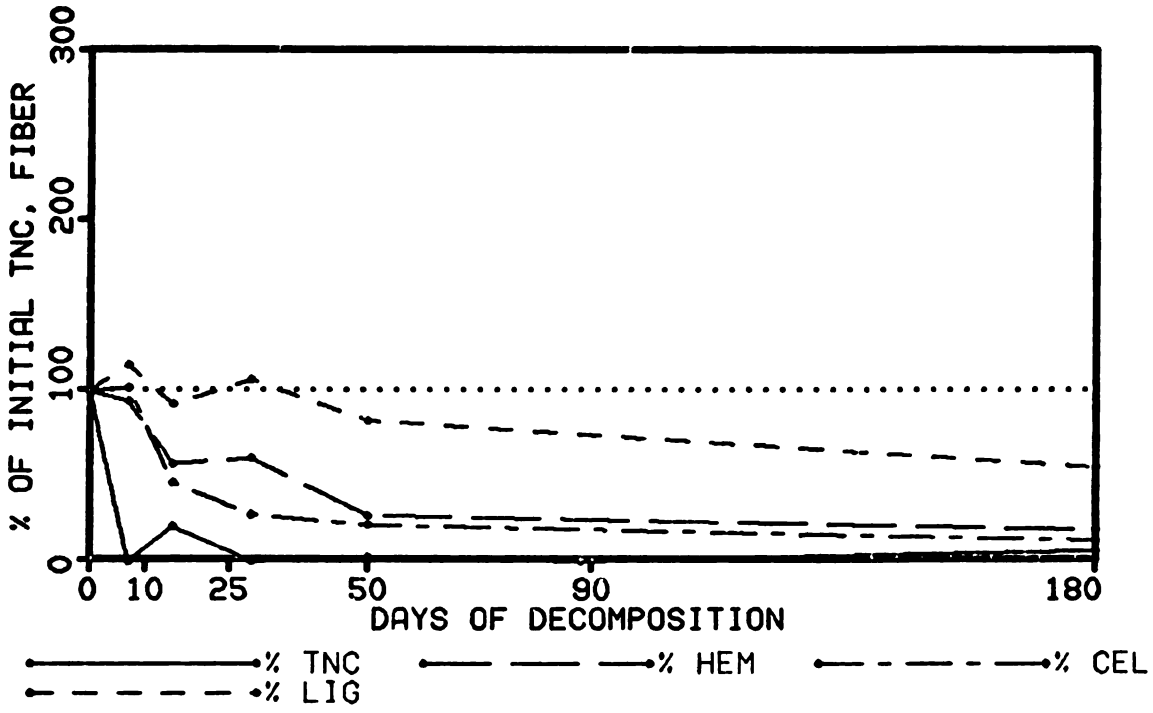
Appendix Figure 166. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during spring and summer. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



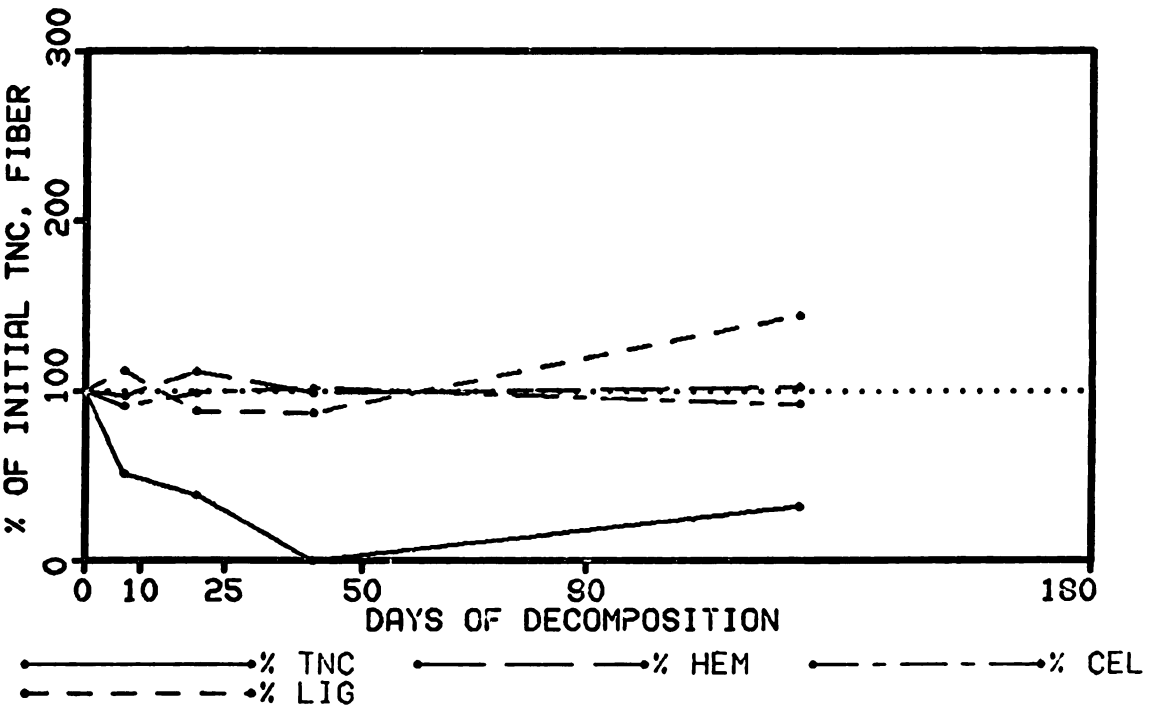
Appendix Figure 167. Decay of *Najas flexilis* in Lawrence Lake littoral zone during spring and summer. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



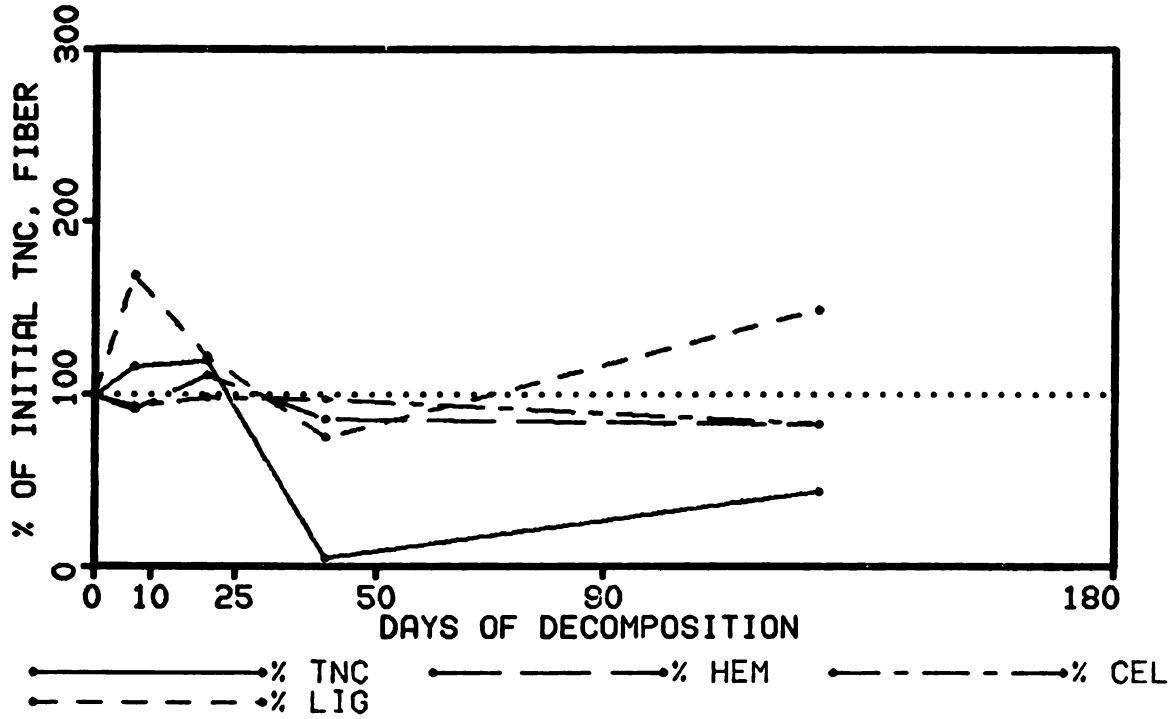
Appendix Figure 168. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during spring and summer. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



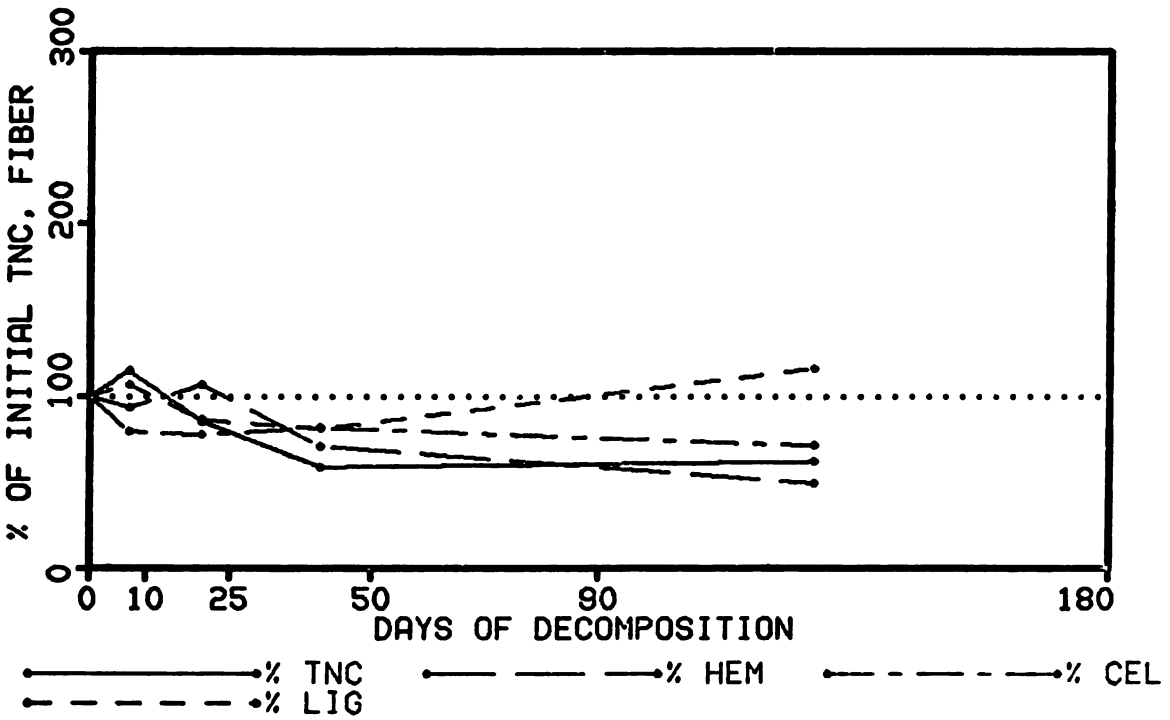
Appendix Figure 169. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during spring and summer. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



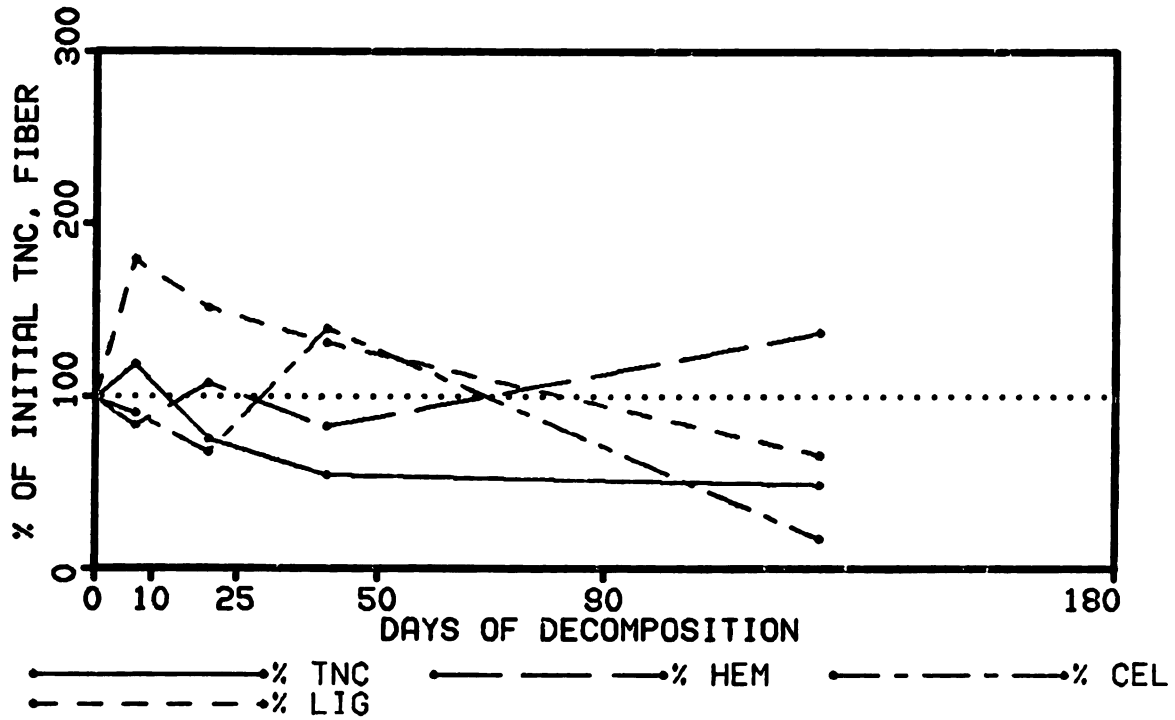
Appendix Figure 170. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



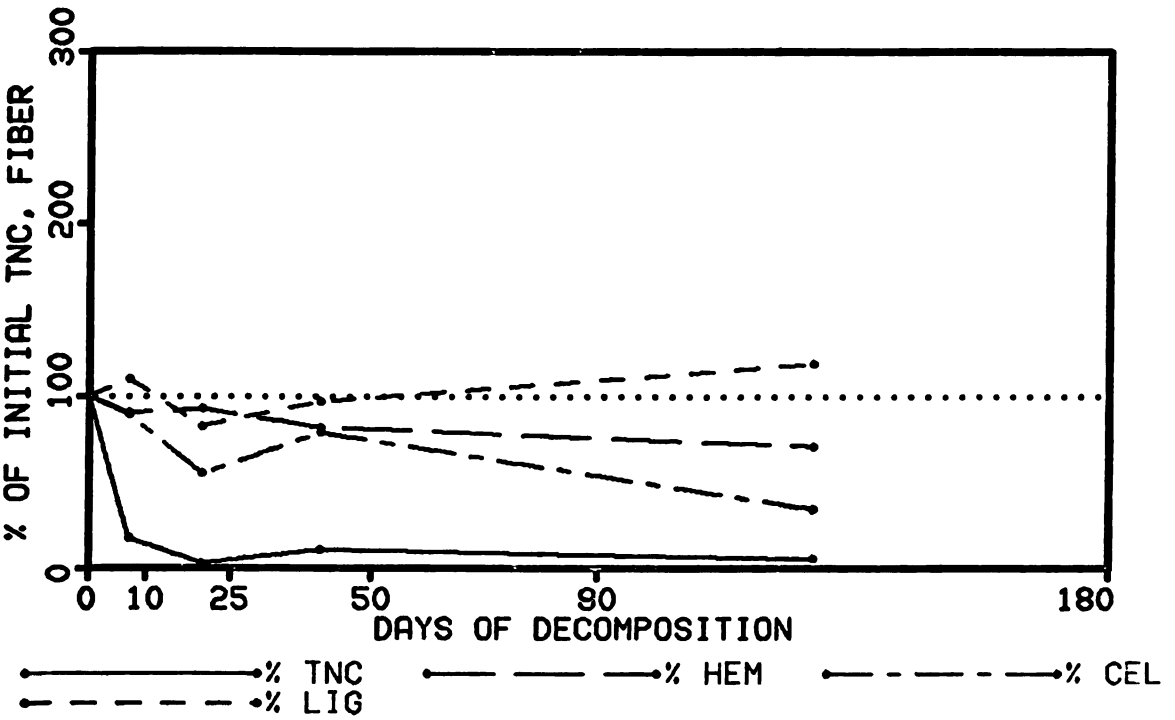
Appendix Figure 171. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



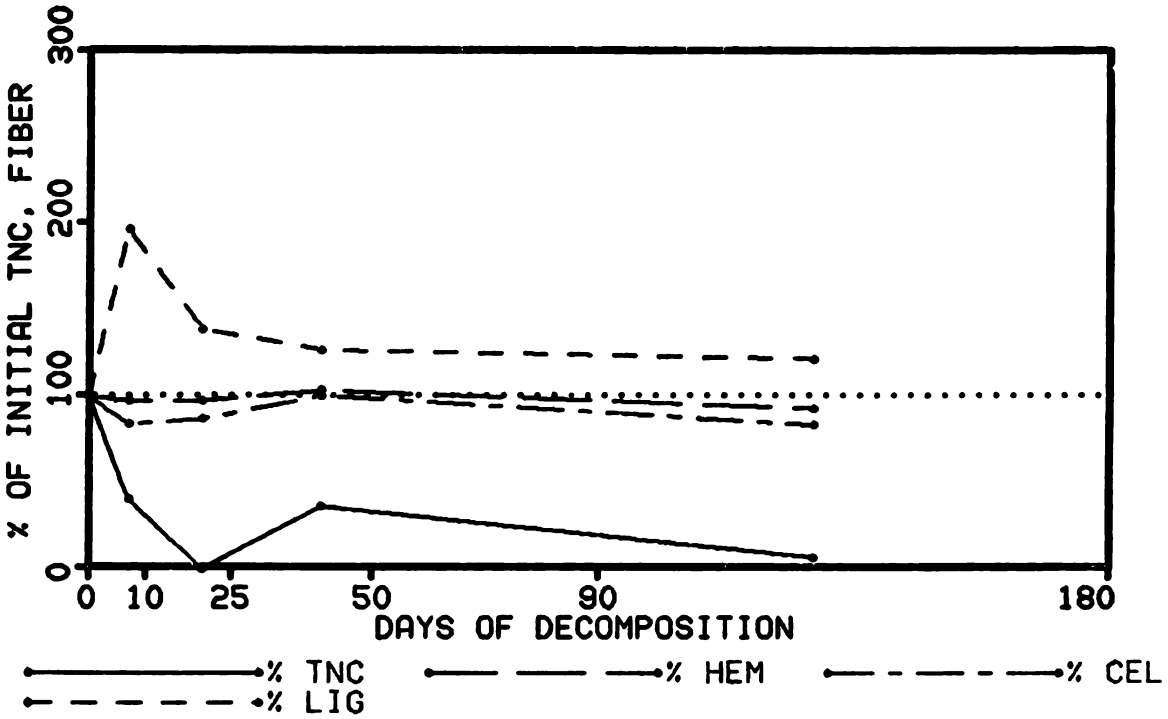
Appendix Figure 172. Decay of *Najas flexilis* in Lawrence Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



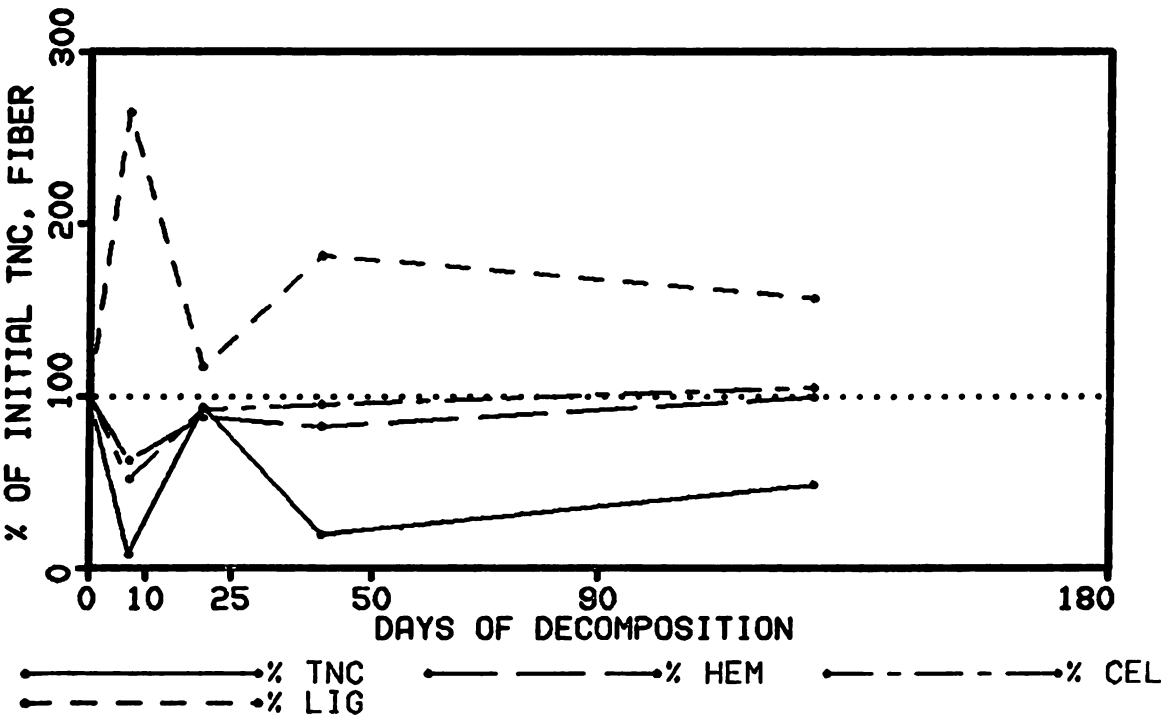
Appendix Figure 173. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



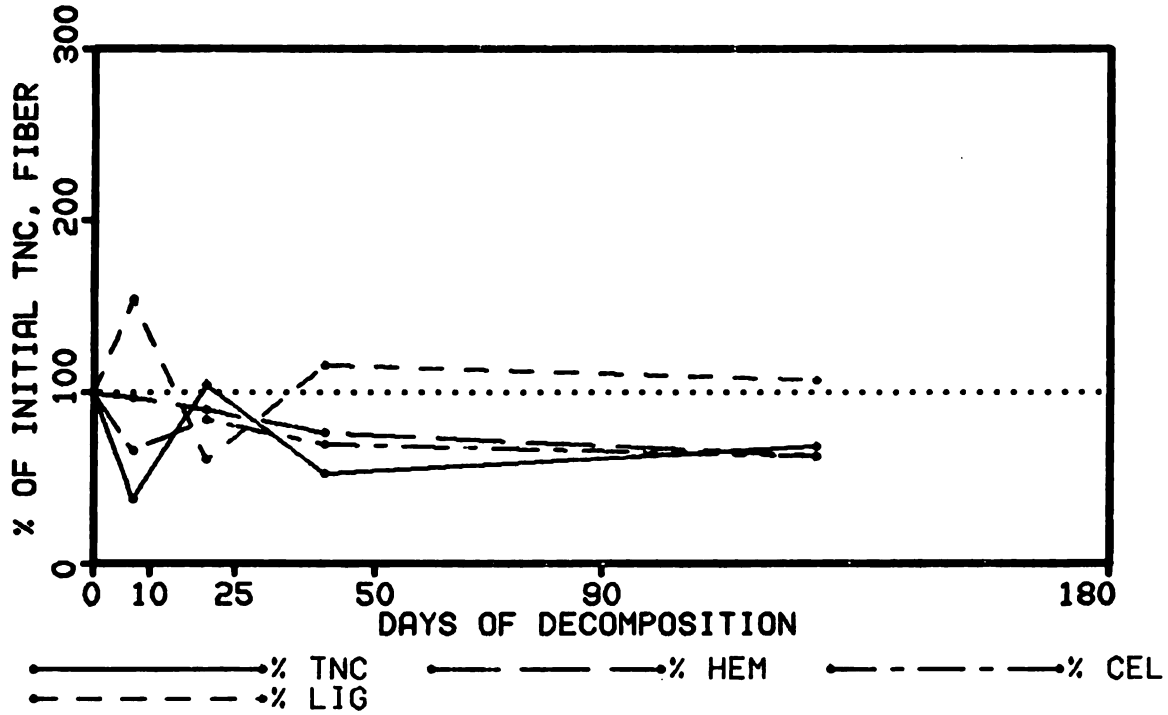
Appendix Figure 174. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



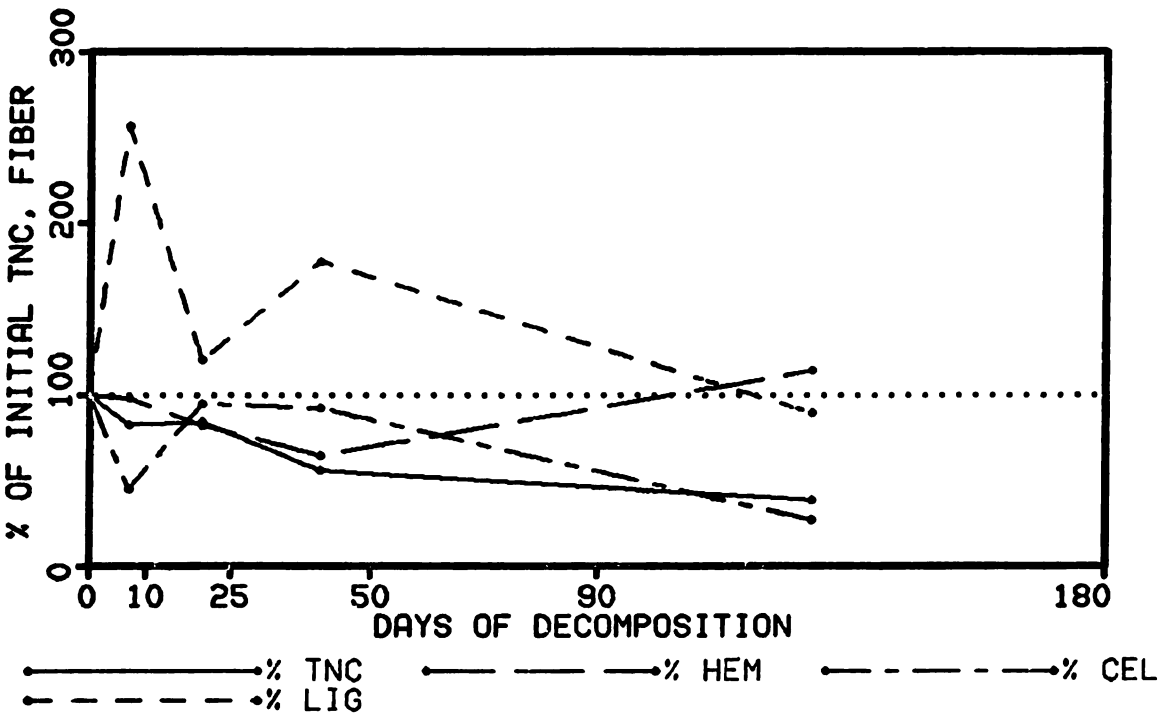
Appendix Figure 175. Decay of *Scirpus acutus* in Lawrence Lake pelagial zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



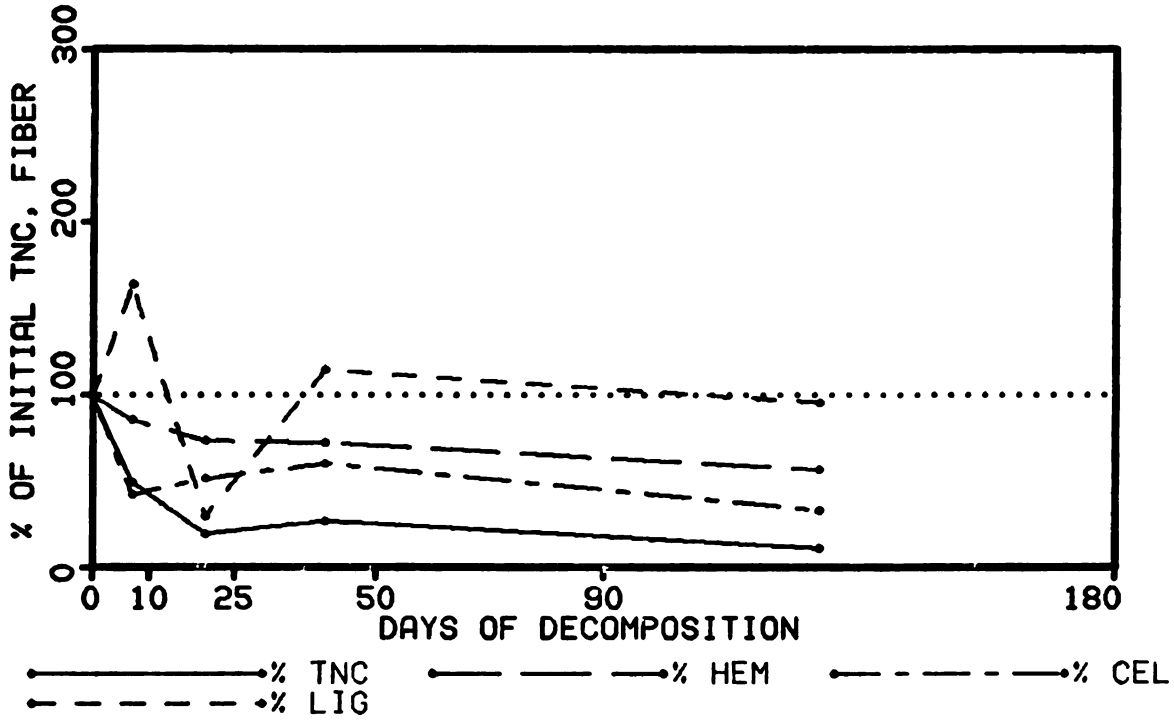
Appendix Figure 176. Decay of *Scirpus subterminalis* in Lawrence Lake pelagial zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



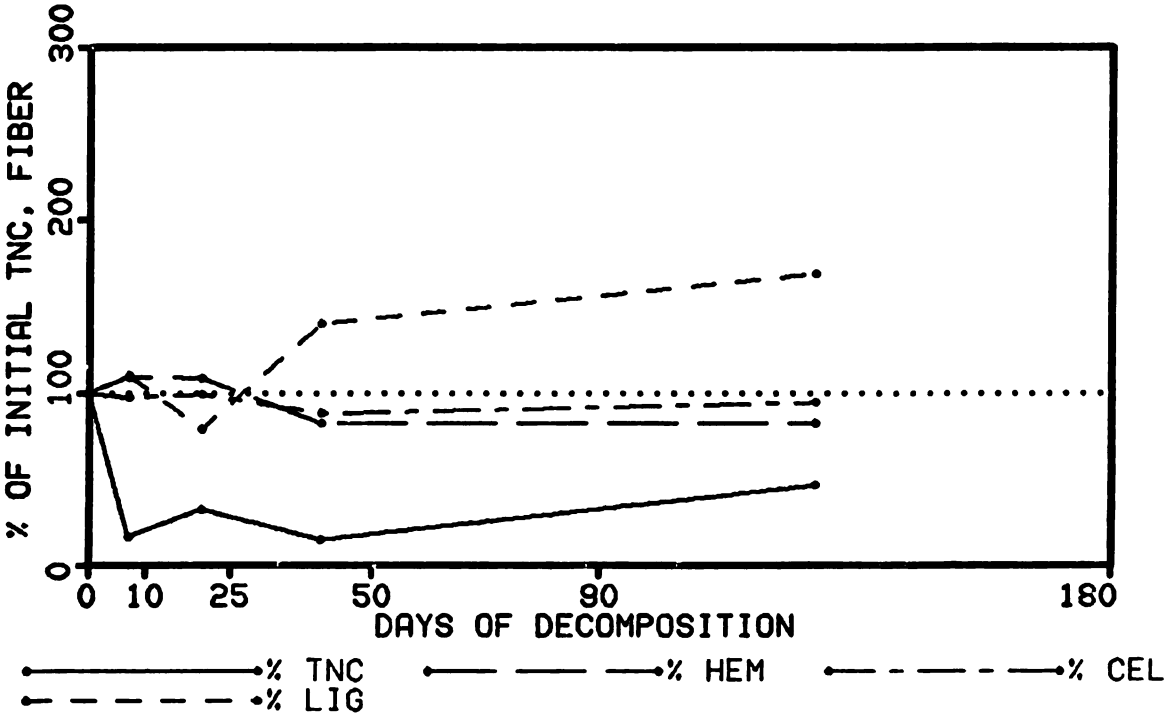
Appendix Figure 177. Decay of *Najas flexilis* in Lawrence Lake pelagial zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



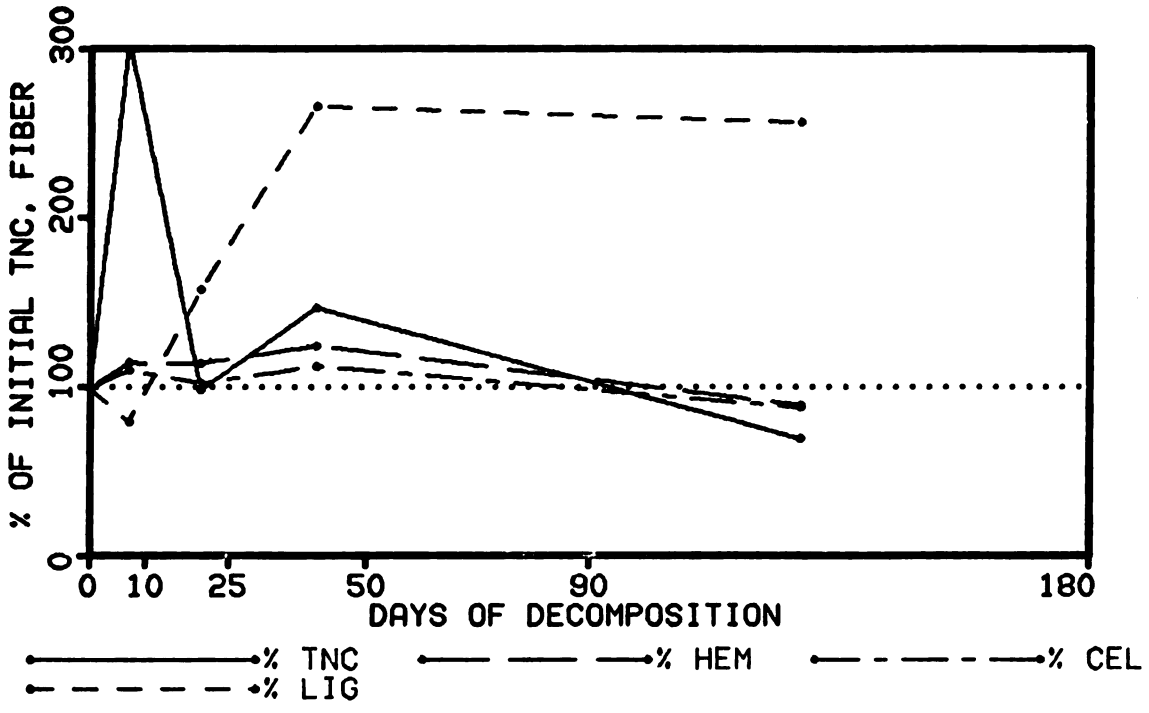
Appendix Figure 178. Decay of *Myriophyllum heterophyllum* in Lawrence Lake pelagial zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



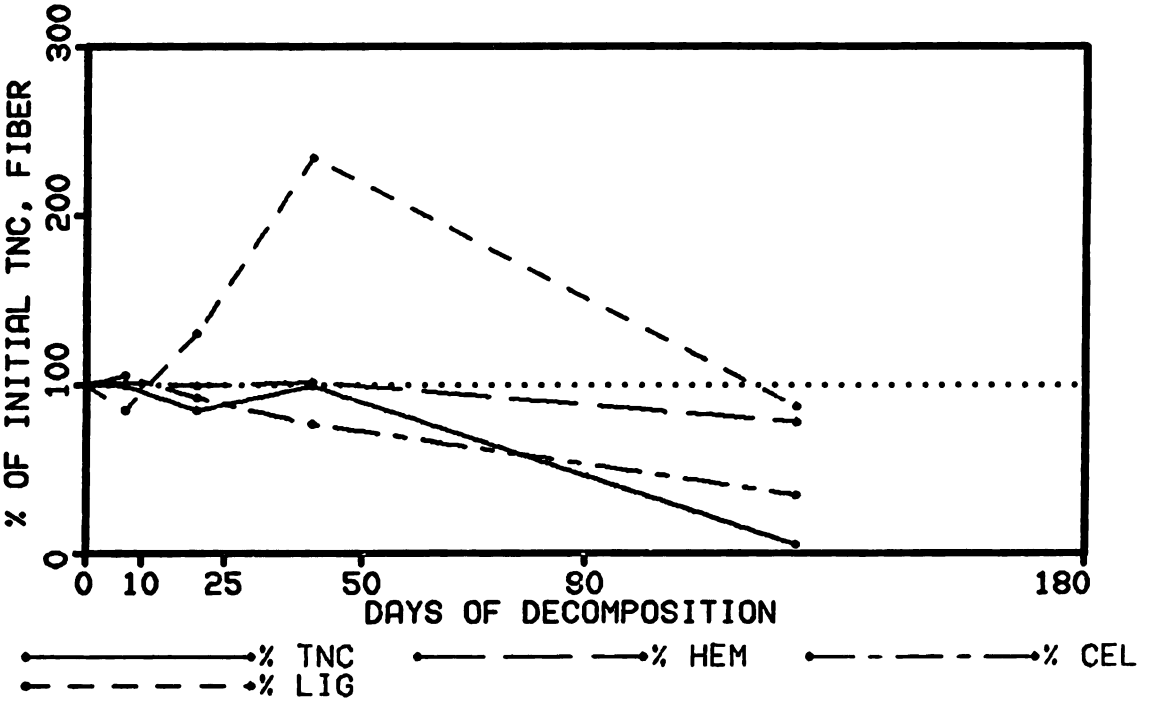
Appendix Figure 179. Decay of *Nuphar variegatum* in Lawrence Lake pelagial zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



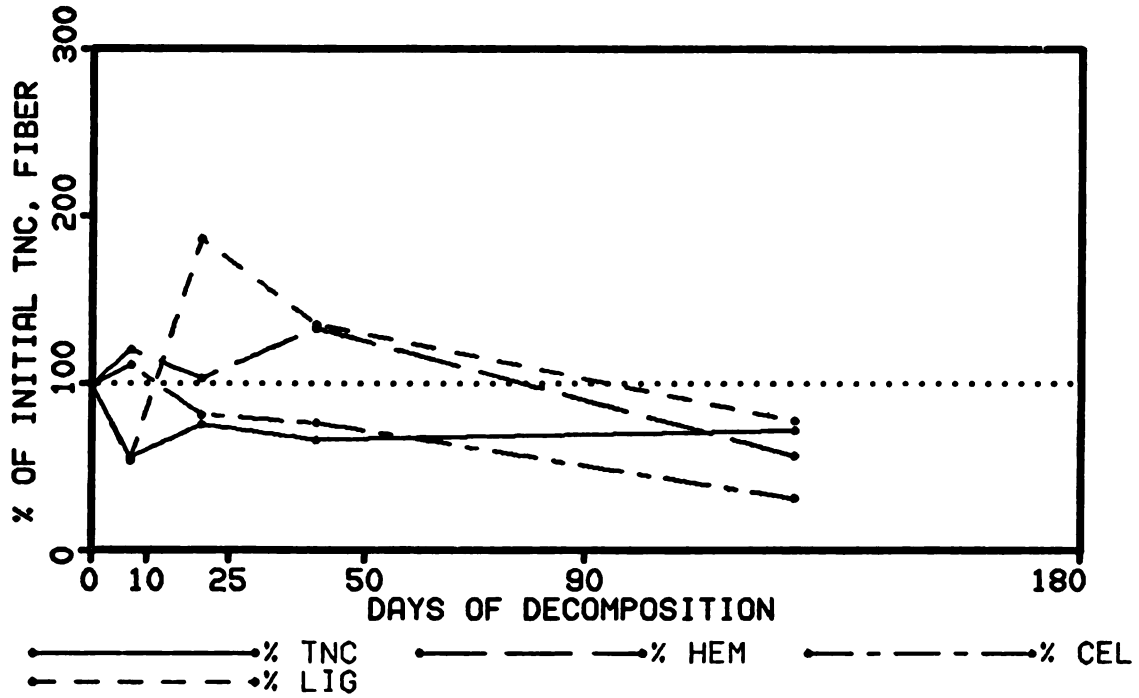
Appendix Figure 180. Decay of *Scirpus acutus* in Wintergreen Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



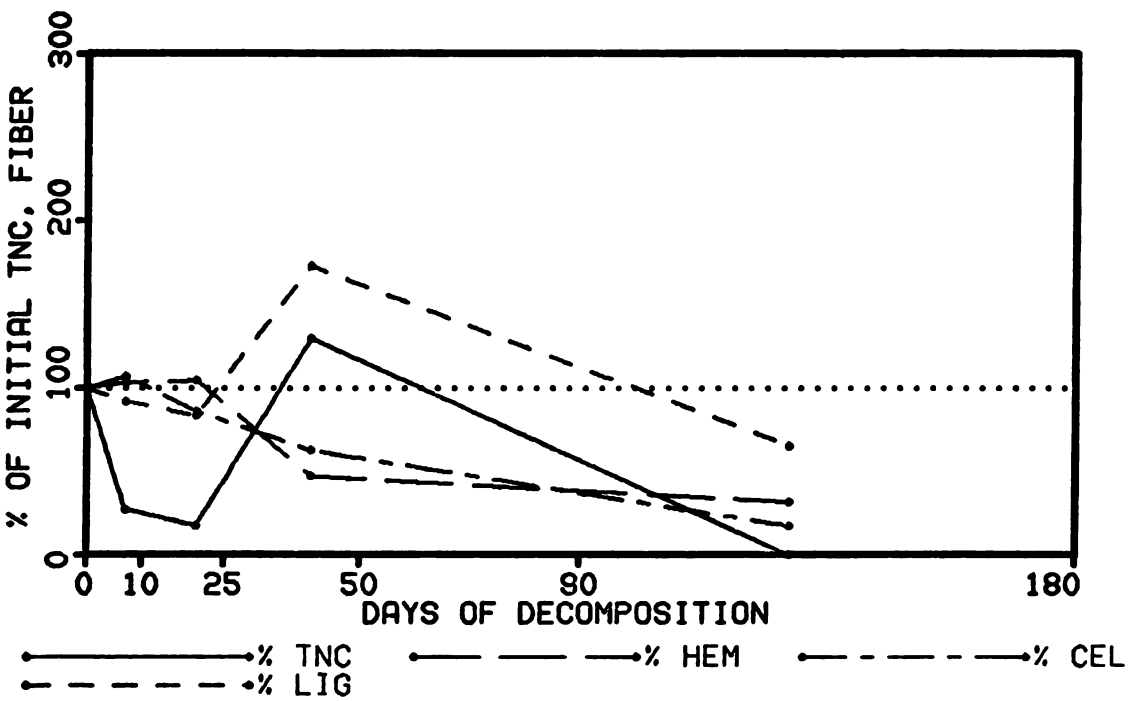
Appendix Figure 181. Decay of *Scirpus subterminalis* in Wintergreen Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



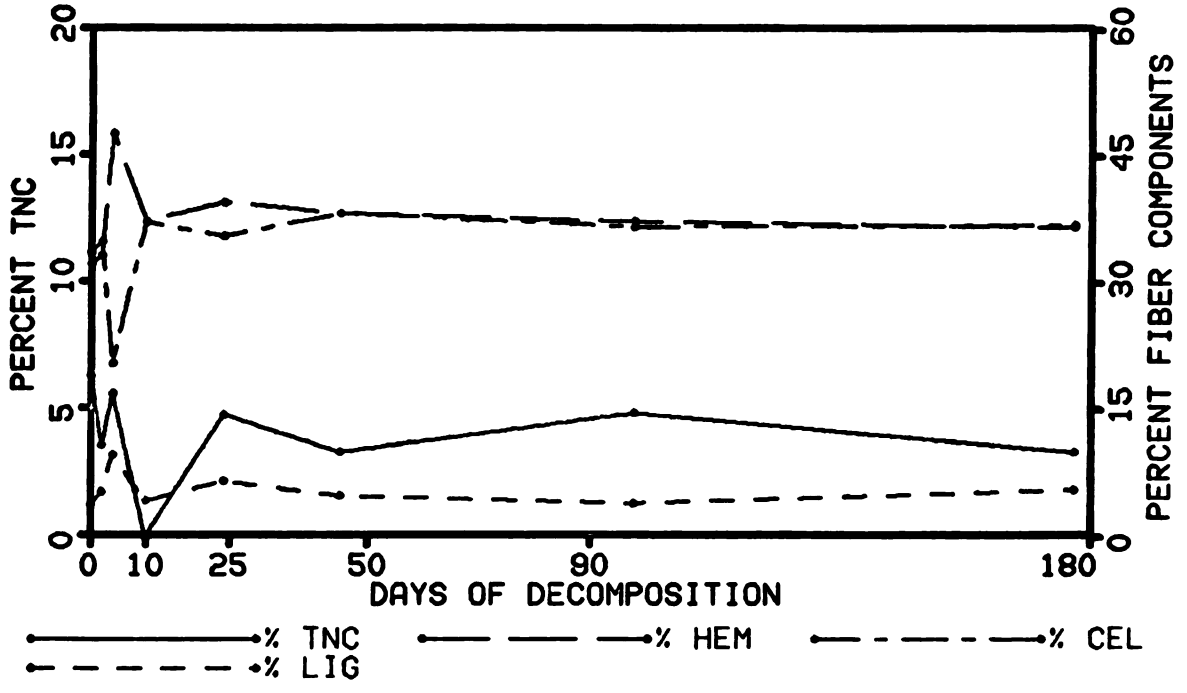
Appendix Figure 182. Decay of *Najas flexilis* in Wintergreen Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



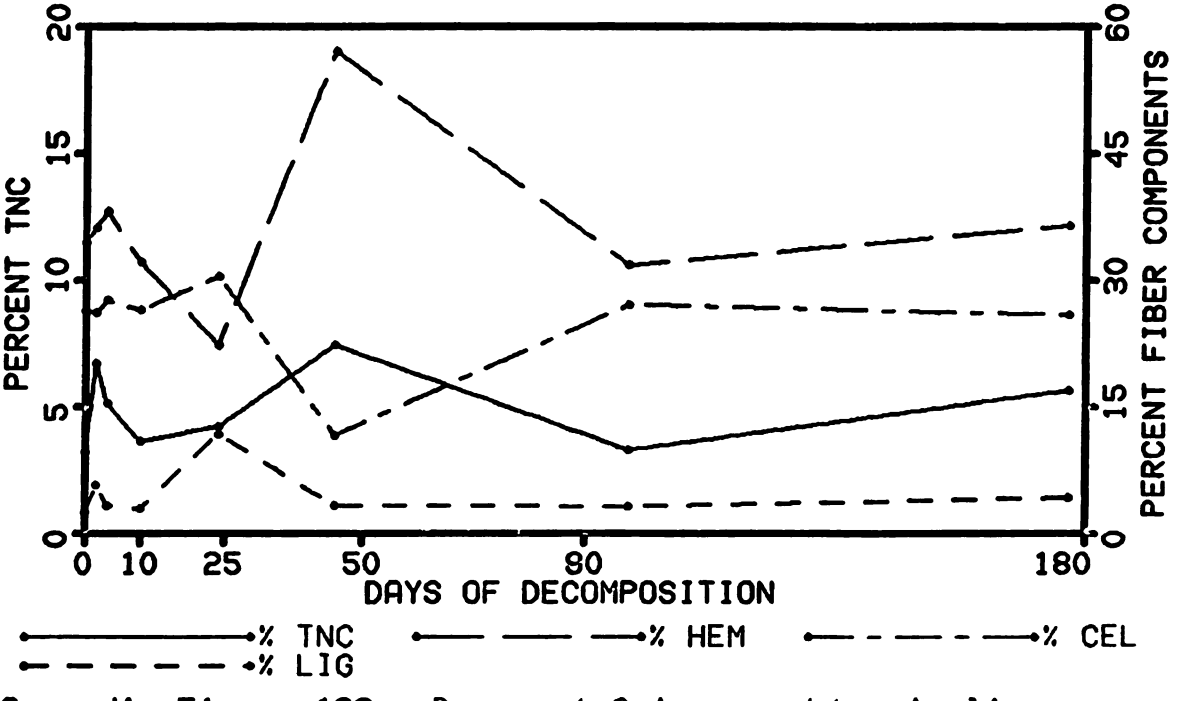
Appendix Figure 183. Decay of *Myriophyllum heterophyllum* in Wintergreen Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



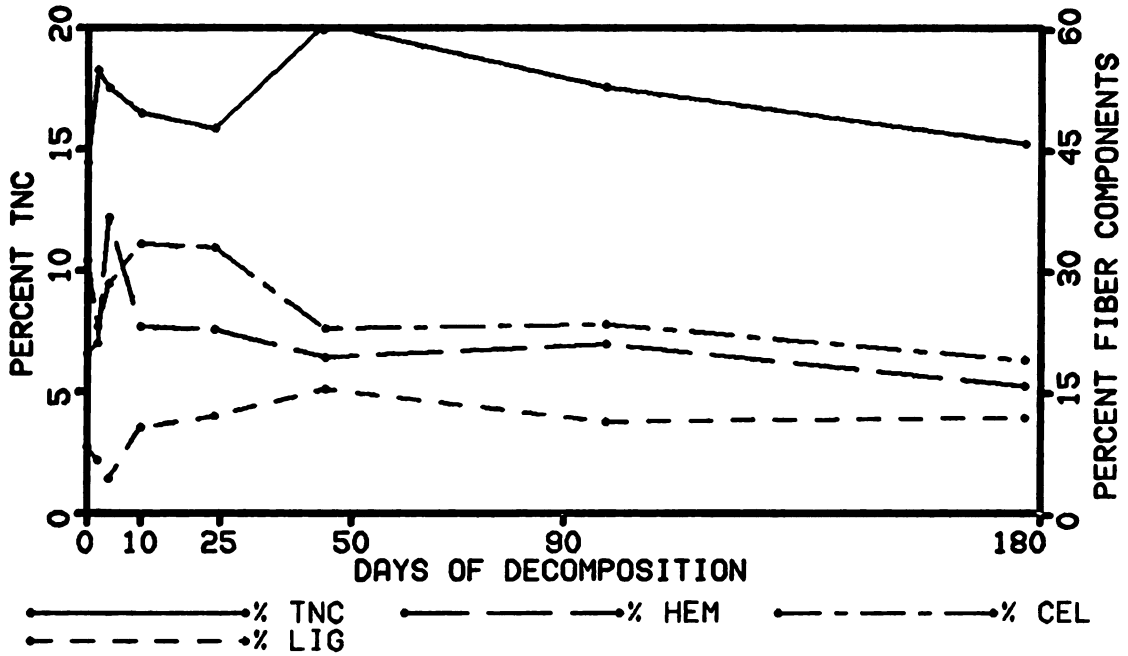
Appendix Figure 184. Decay of *Nuphar variegatum* in Wintergreen Lake littoral zone during fall and winter. Percent of initial content, on ash-free dry weight basis, of total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG) in tissue.



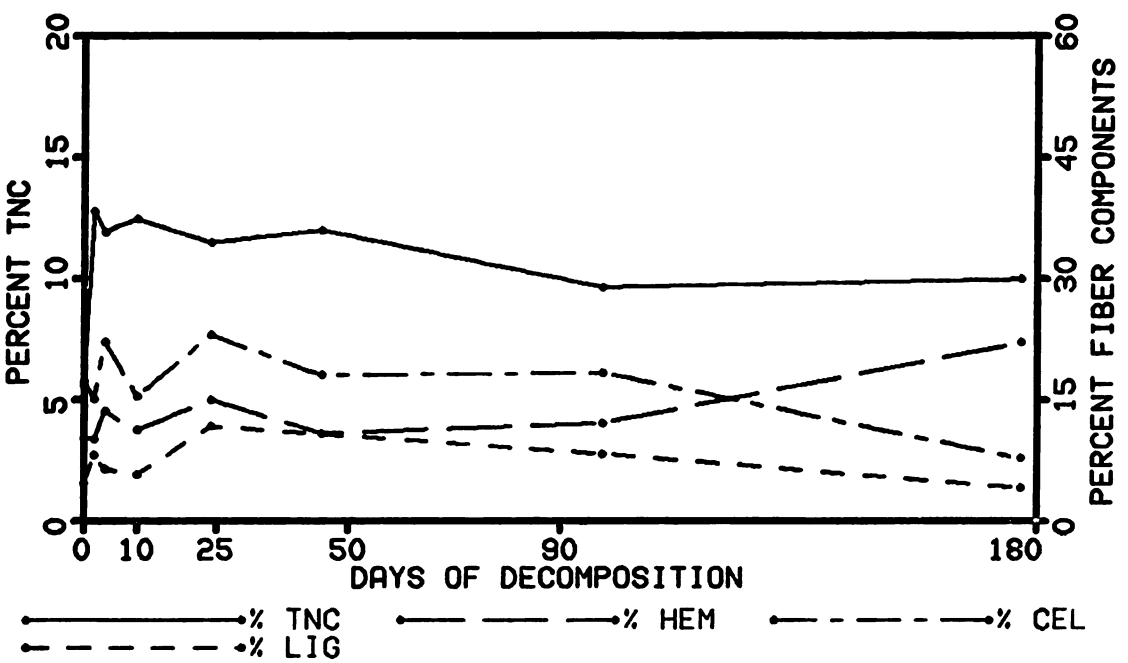
Appendix Figure 185. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



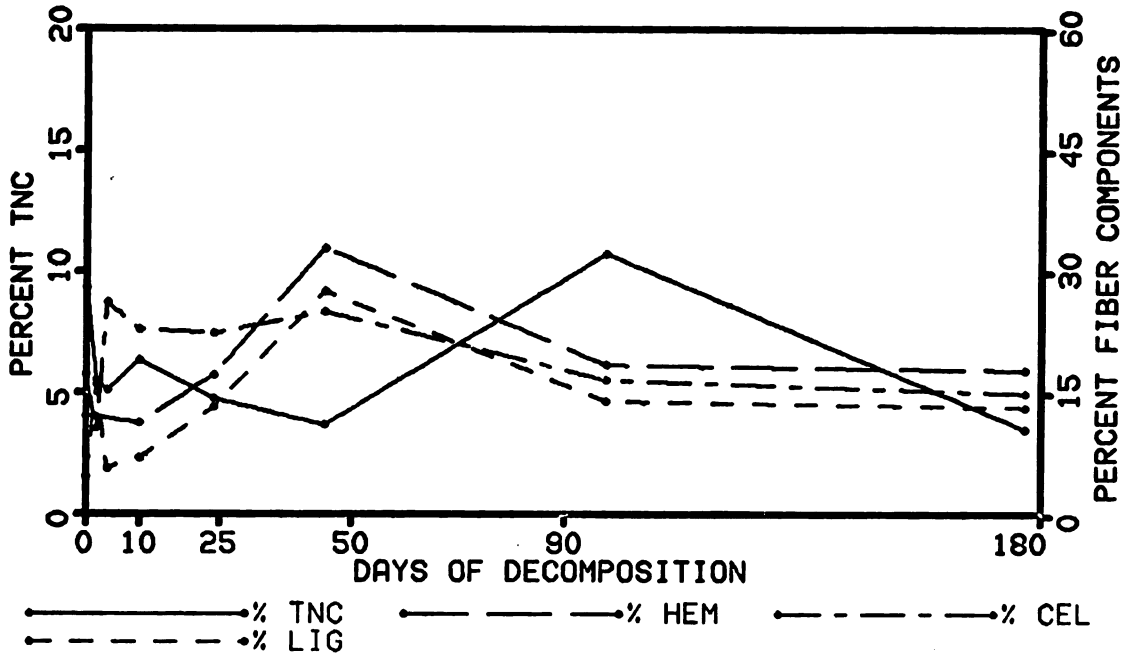
Appendix Figure 186. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



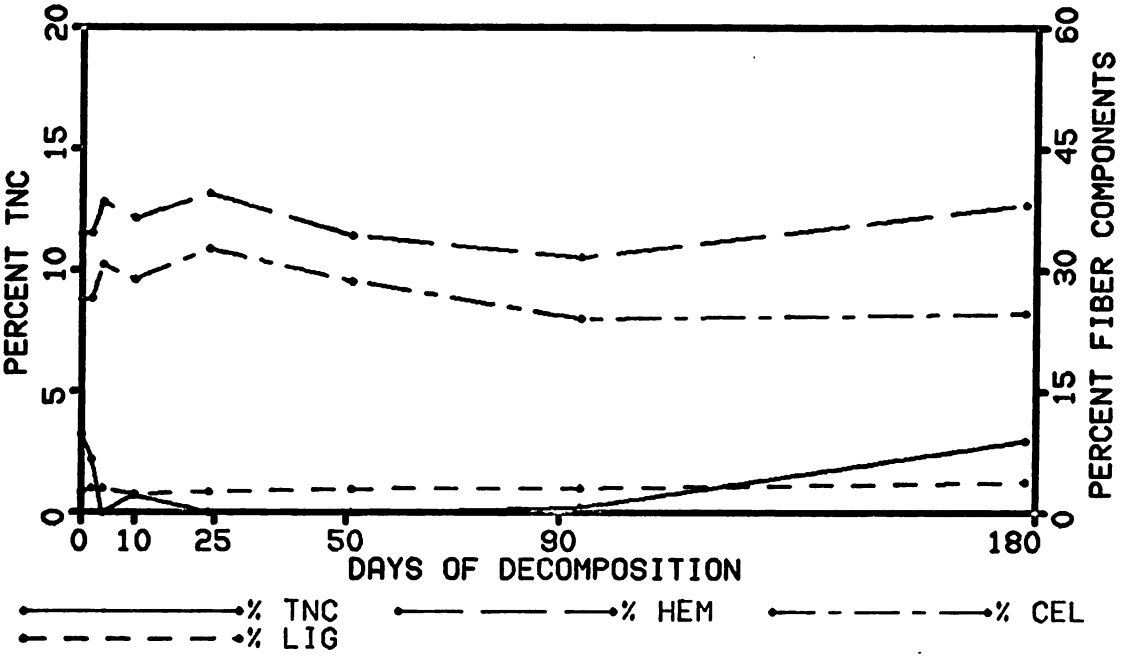
Appendix Figure 187. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



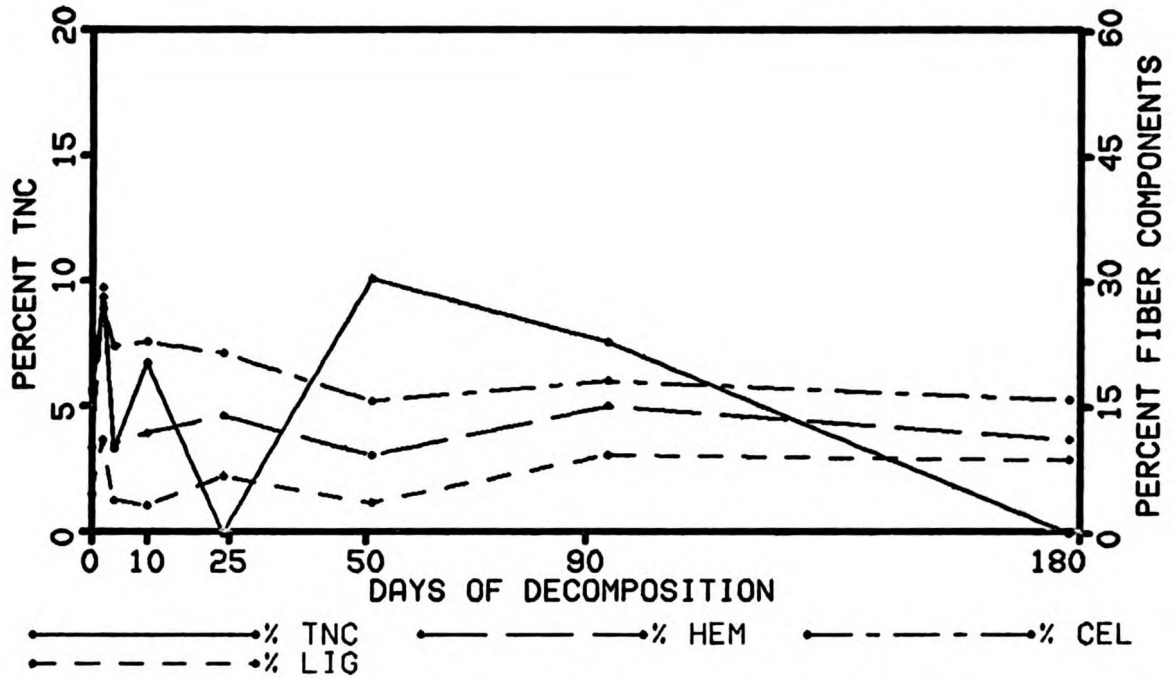
Appendix Figure 188. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



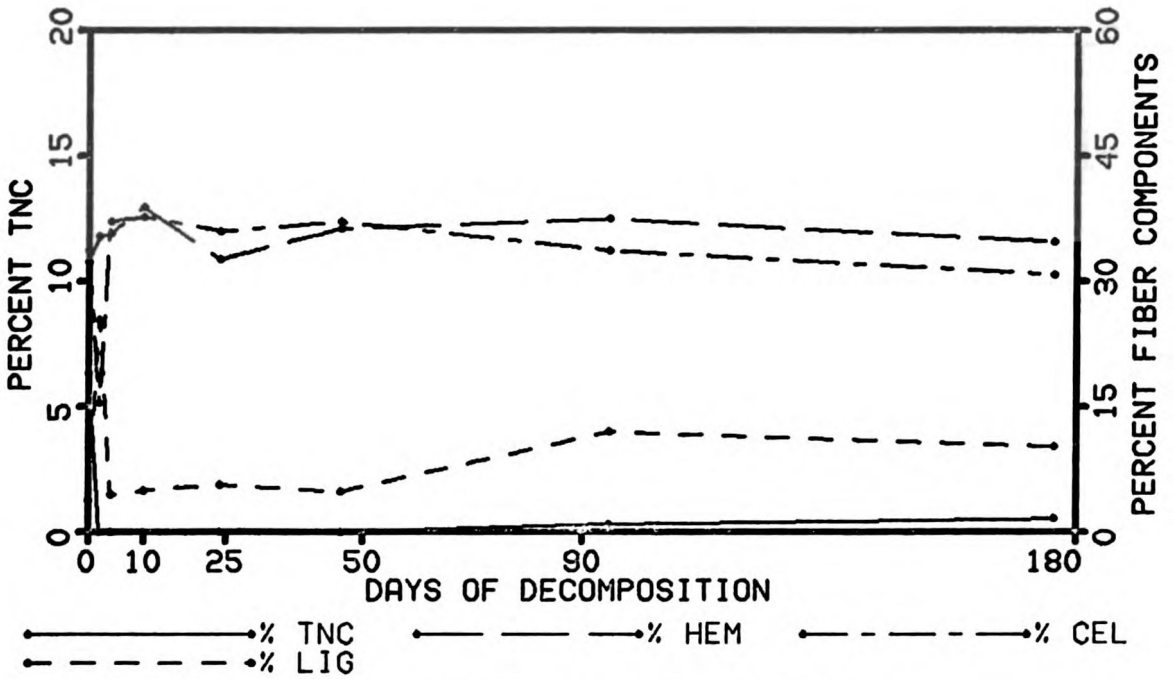
Appendix Figure 189. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



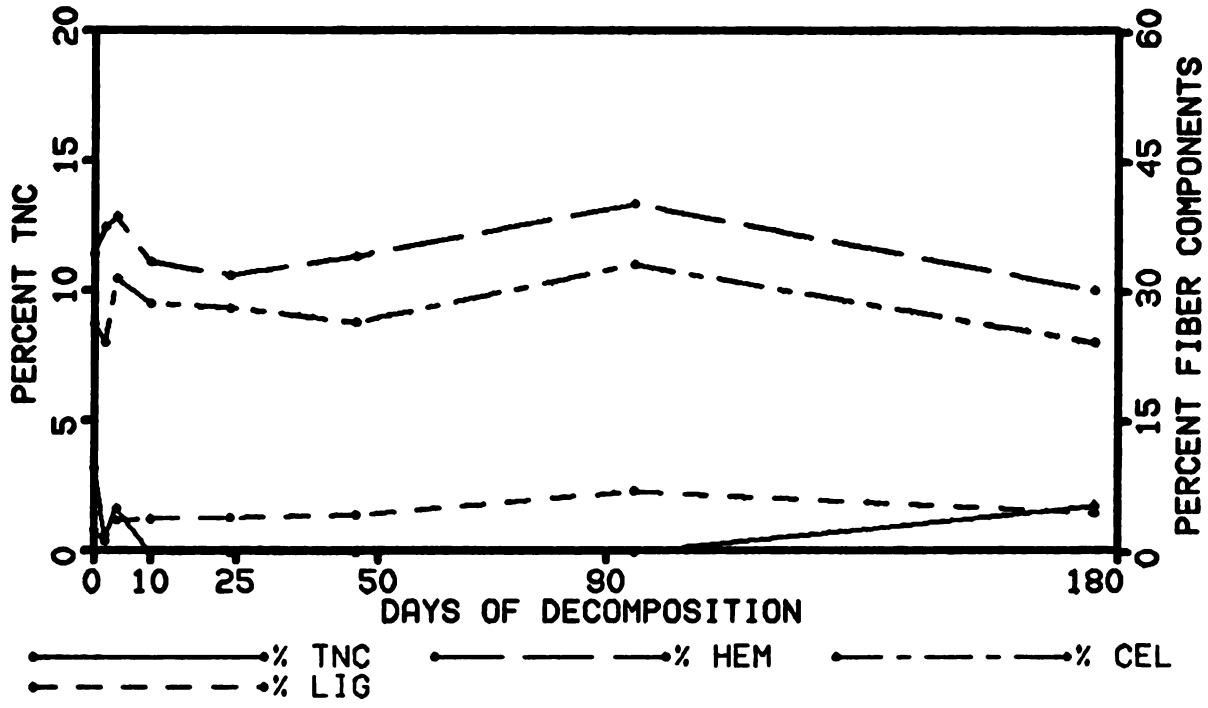
Appendix Figure 190. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



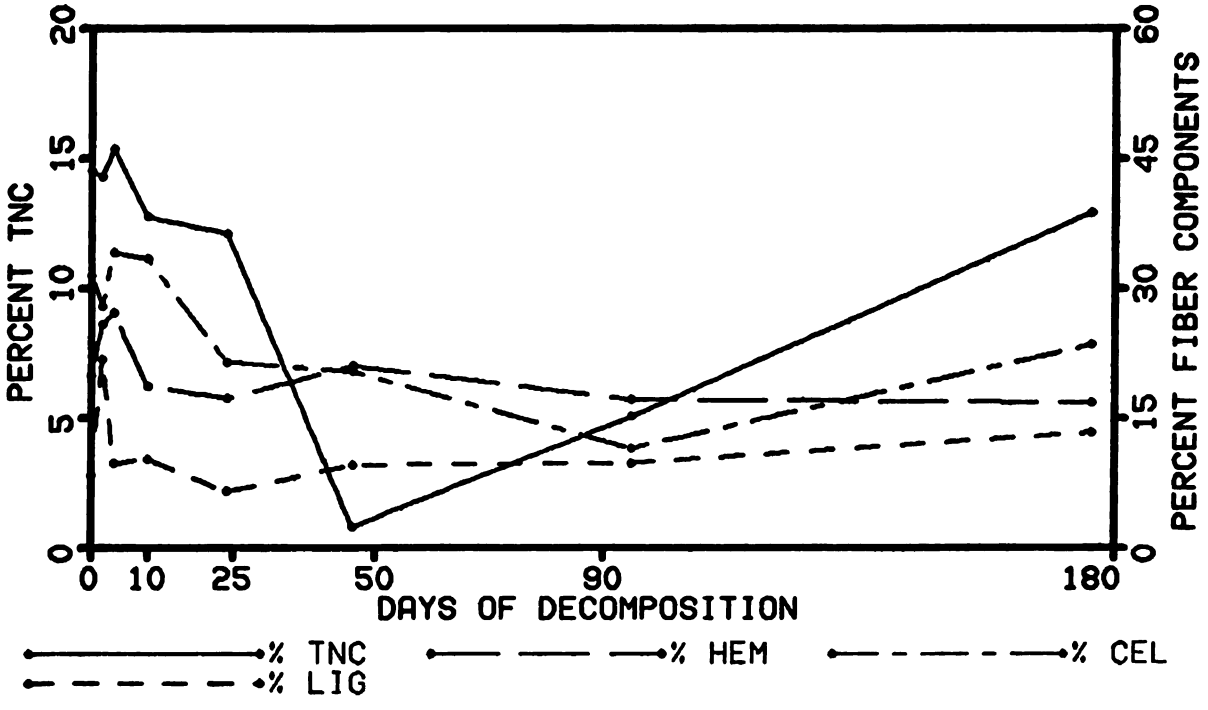
Appendix Figure 191. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



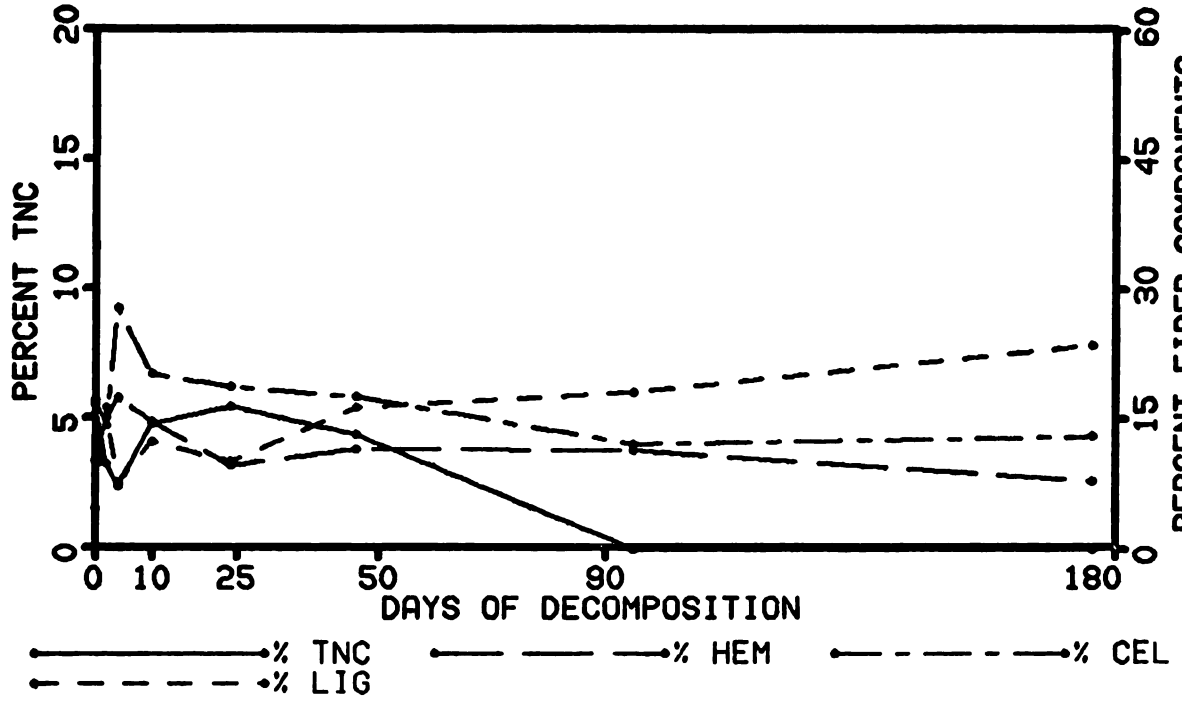
Appendix Figure 192. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



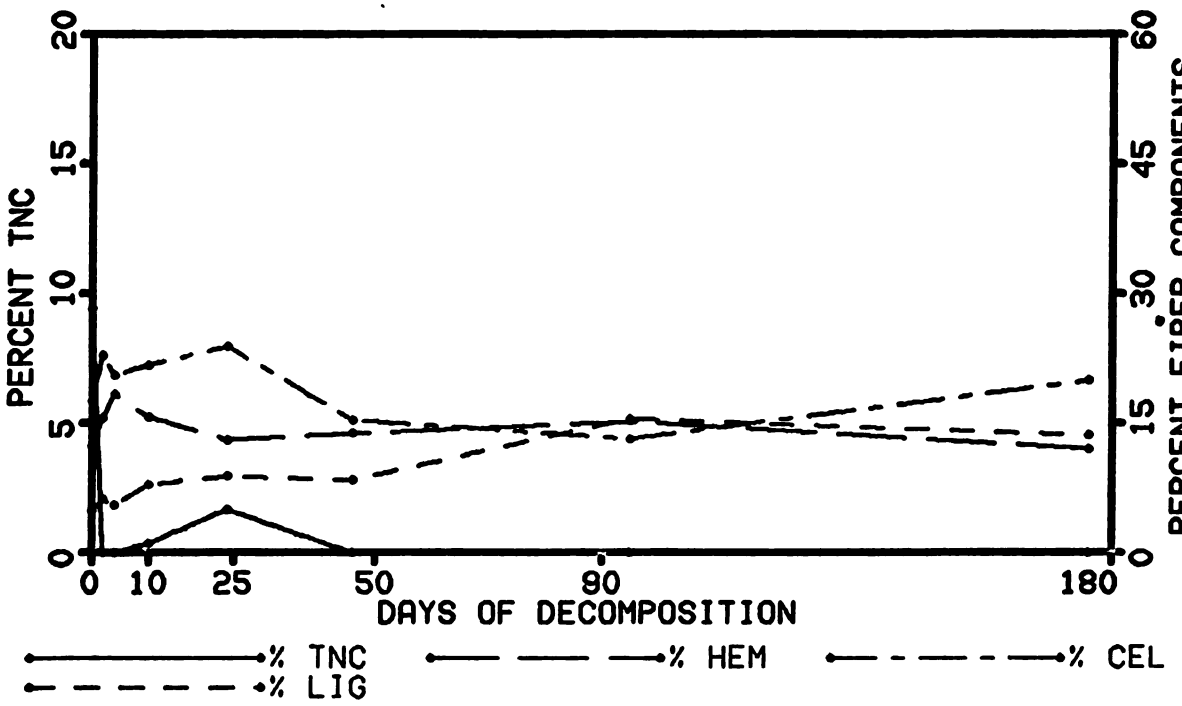
Appendix Figure 193. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



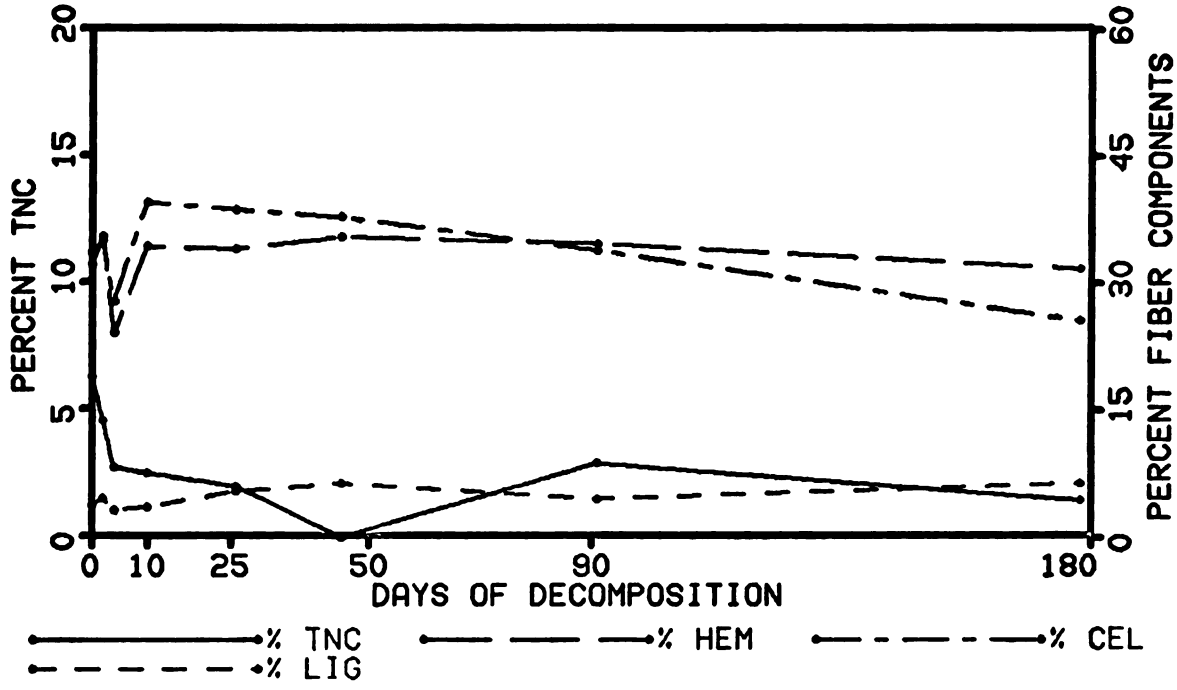
Appendix Figure 194. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



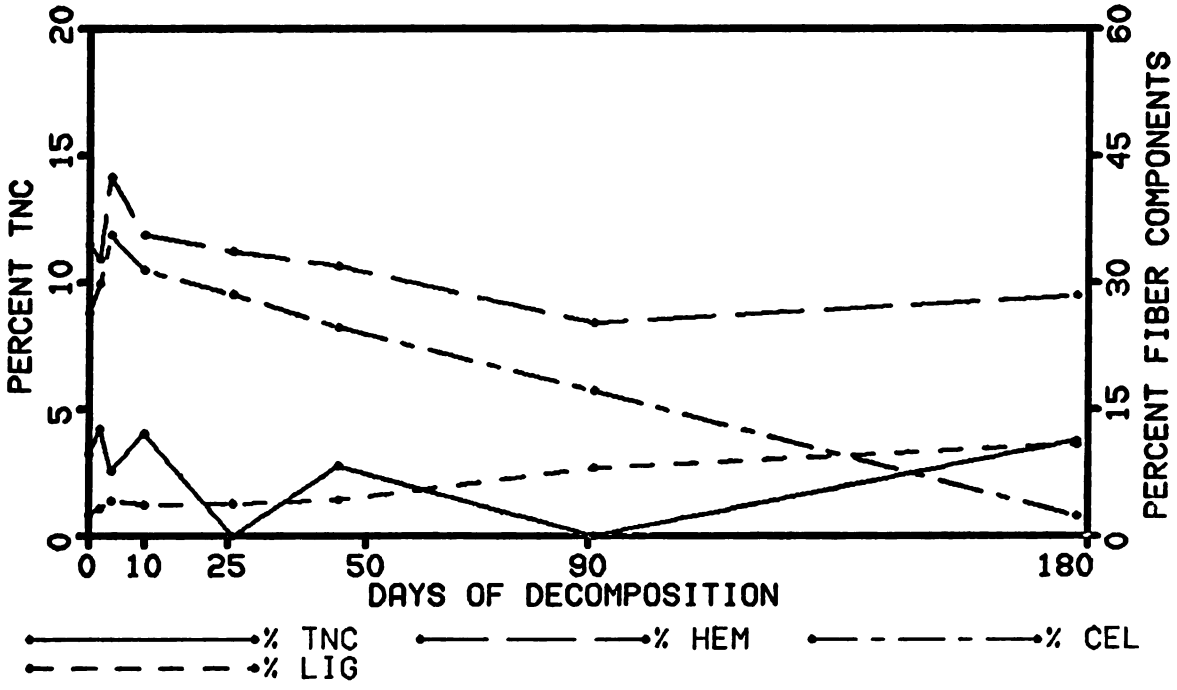
Appendix Figure 195. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



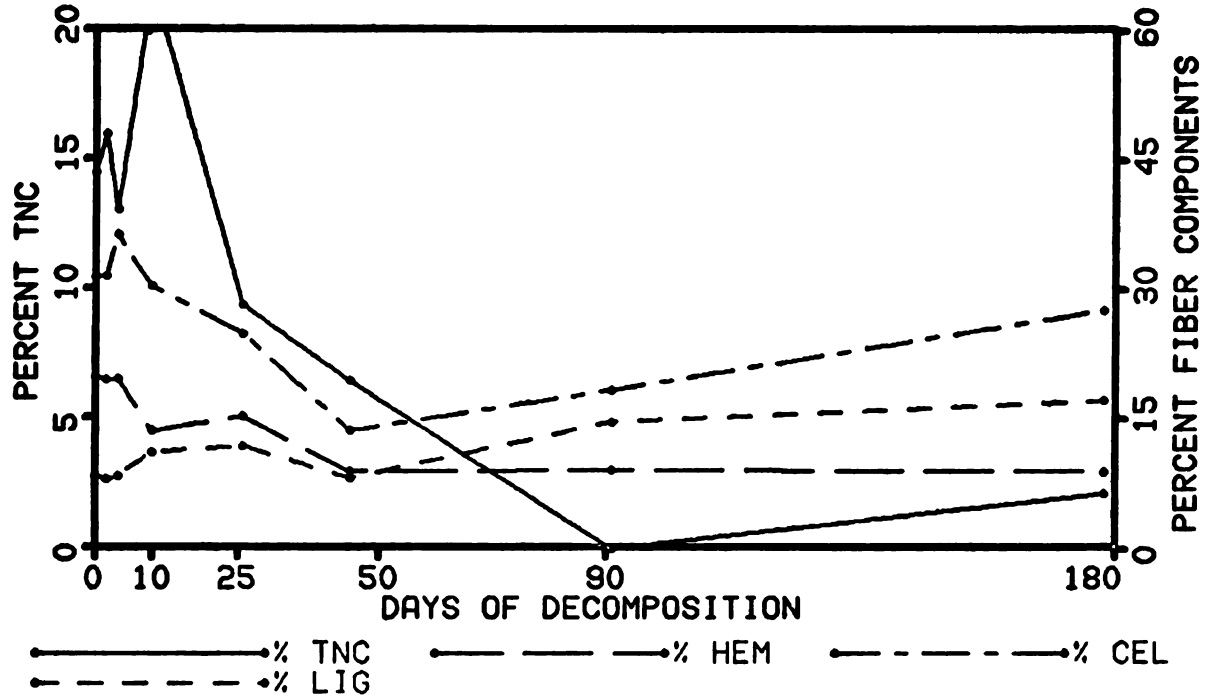
Appendix Figure 196. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



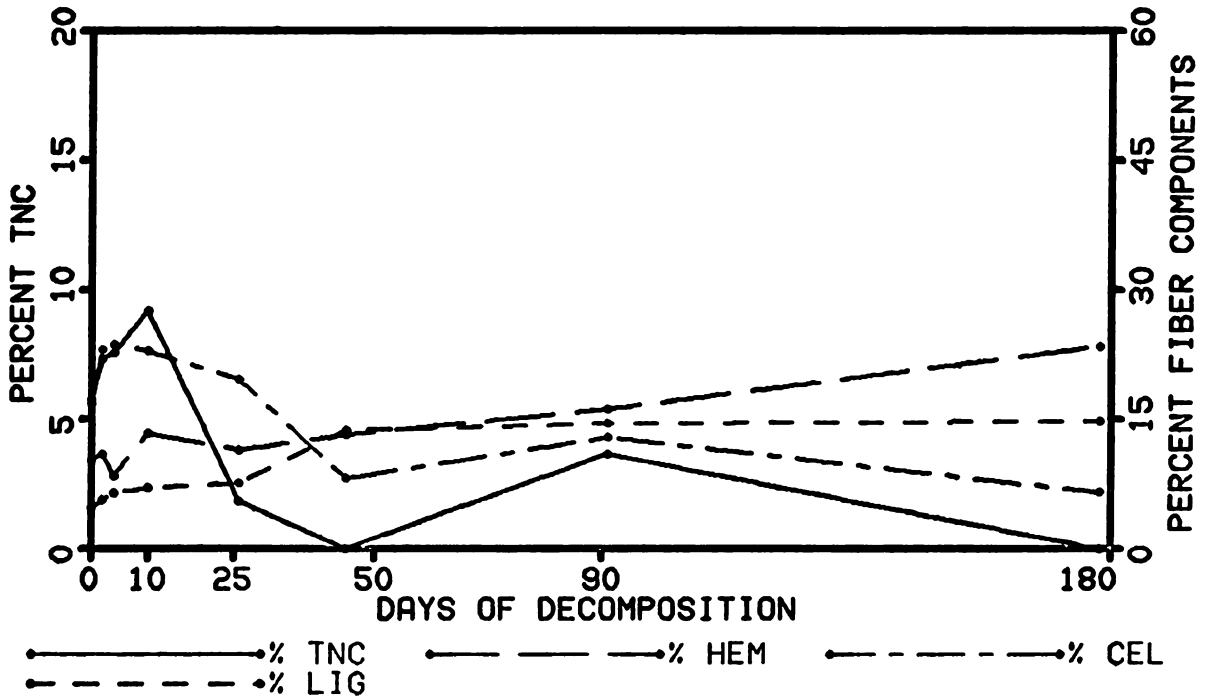
Appendix Figure 197. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



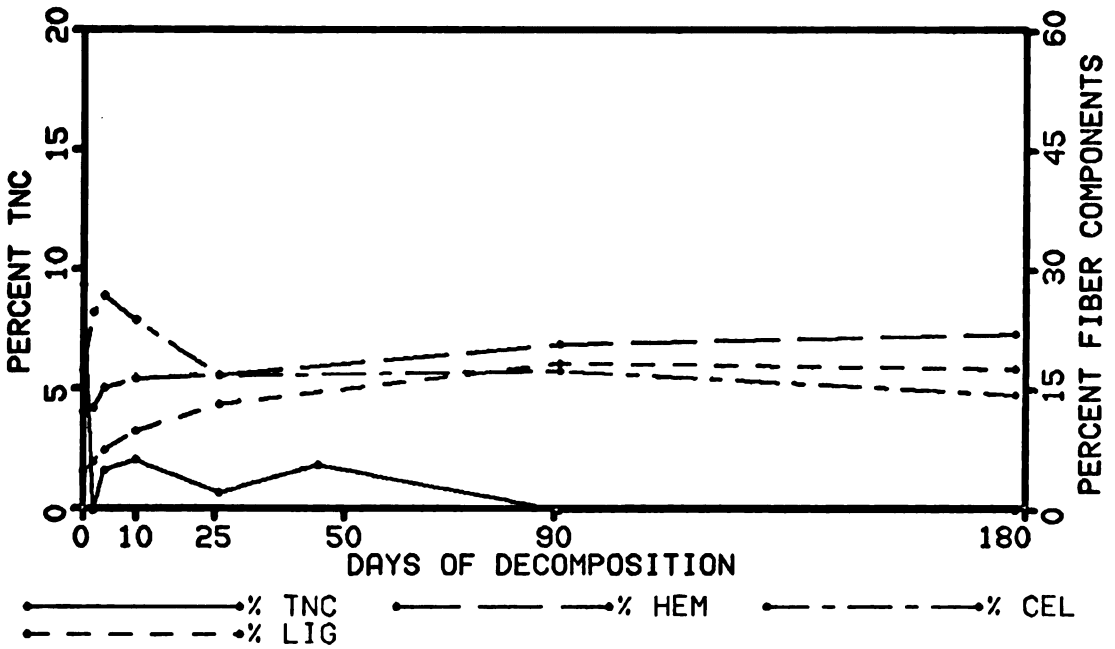
Appendix Figure 198. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



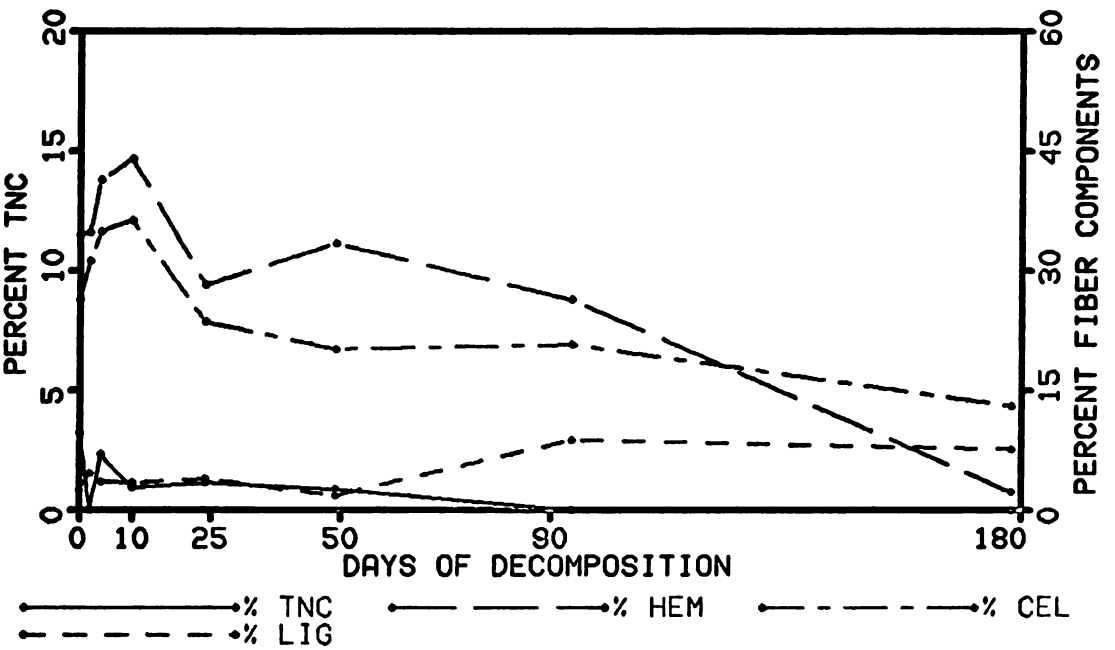
Appendix Figure 199. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



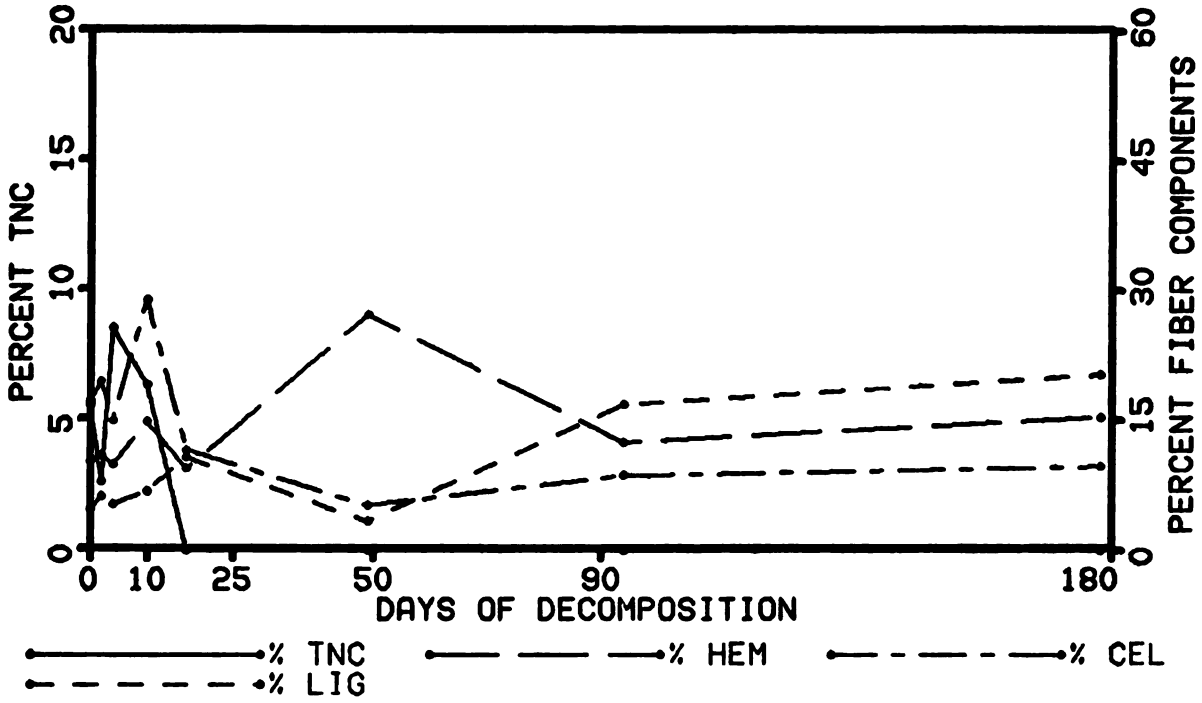
Appendix Figure 200. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



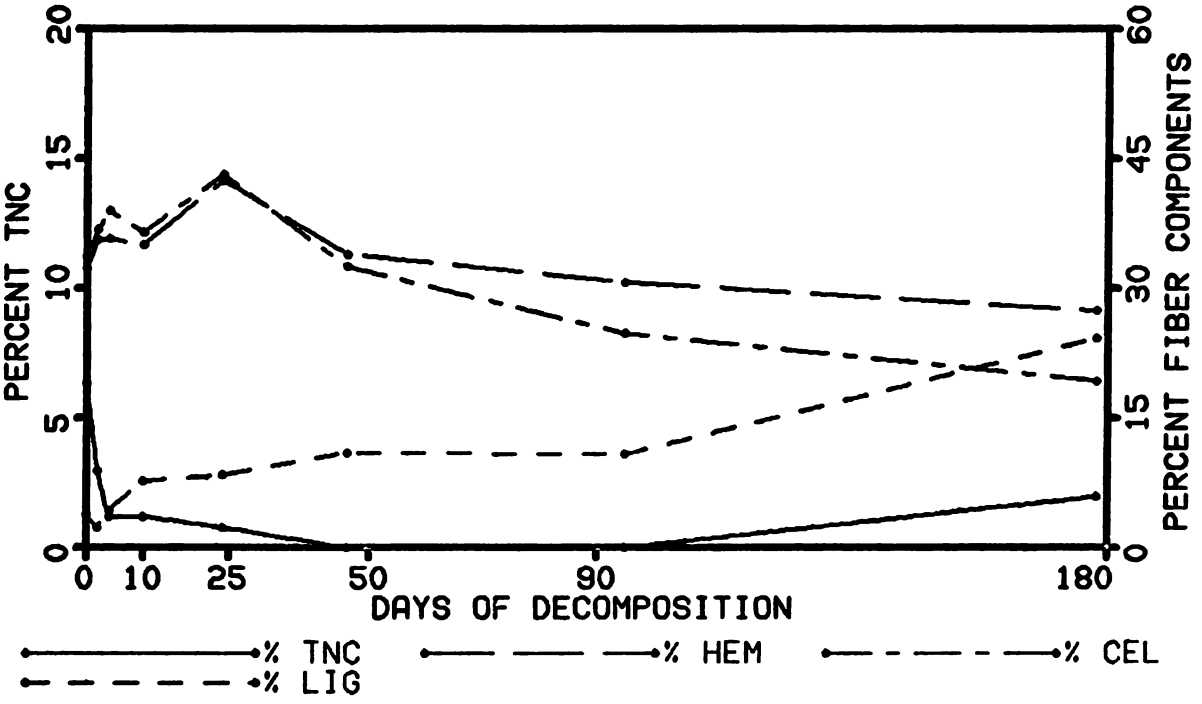
Appendix Figure 201. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



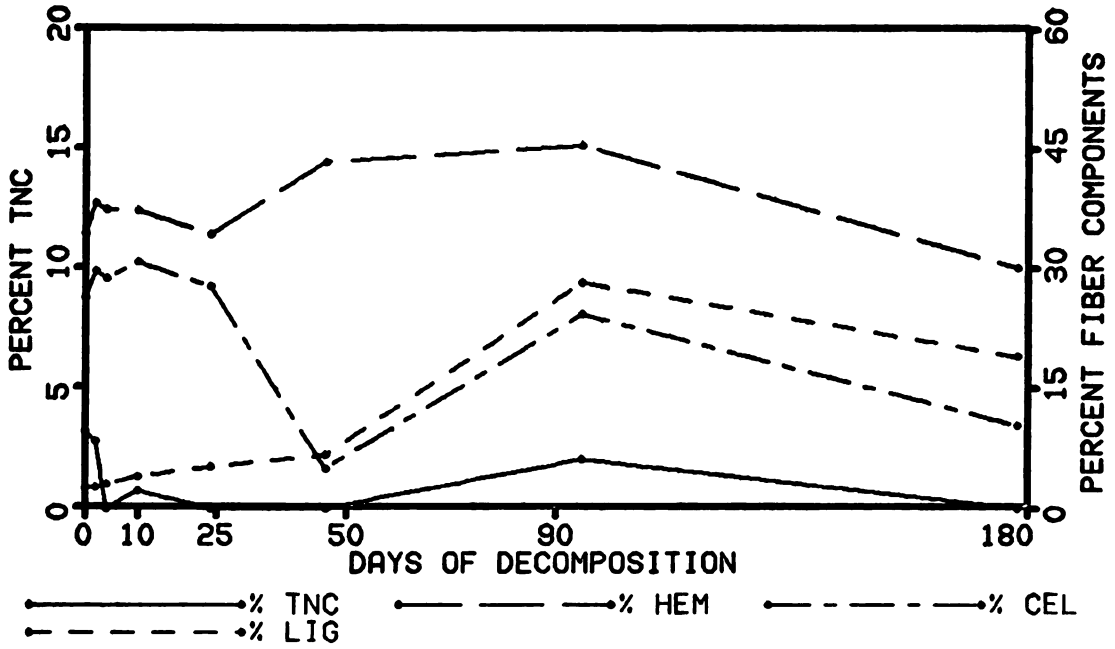
Appendix Figure 202. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



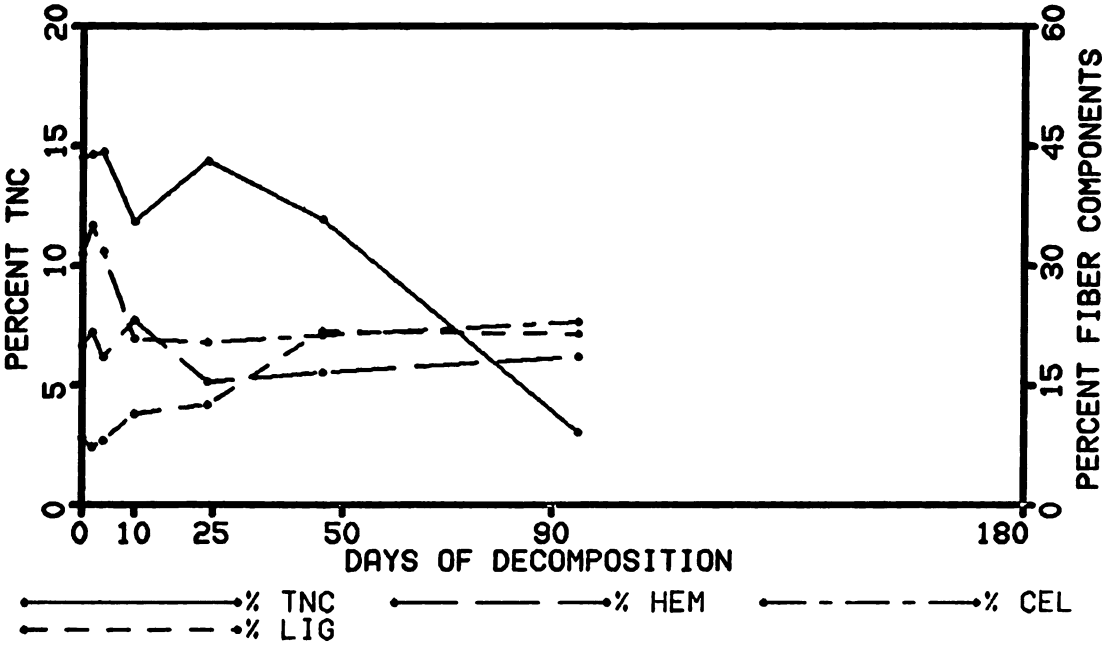
Appendix Figure 203. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



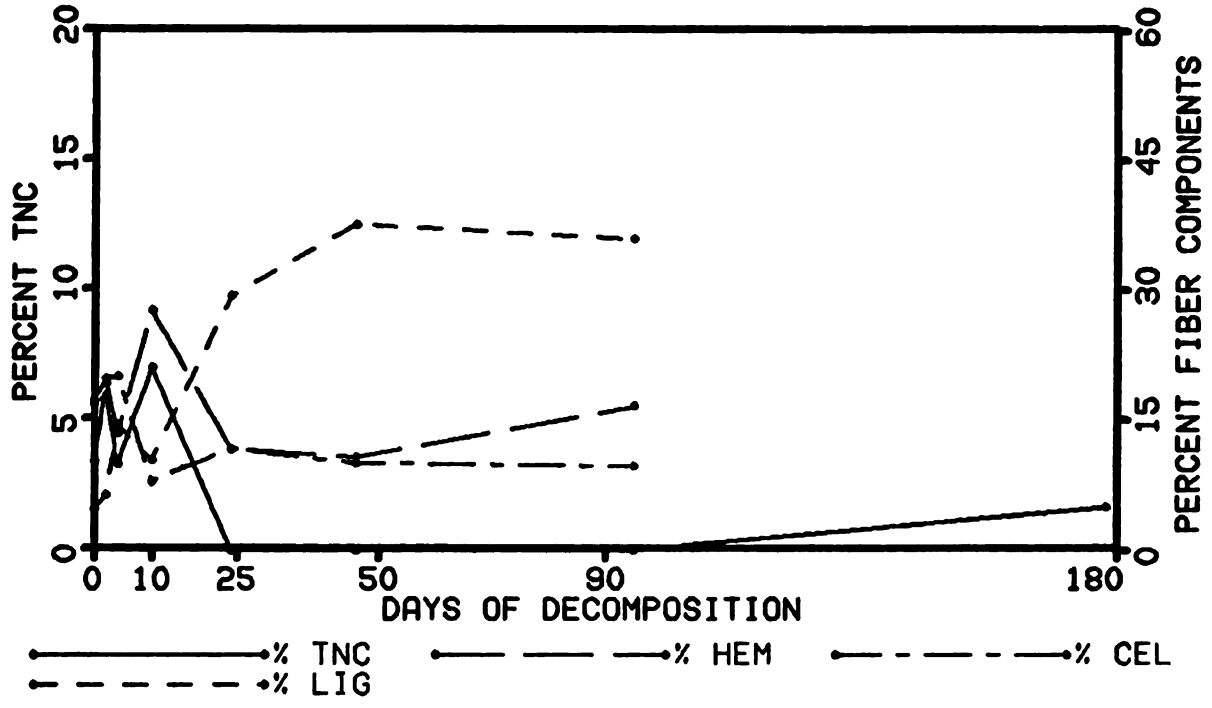
Appendix Figure 204. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



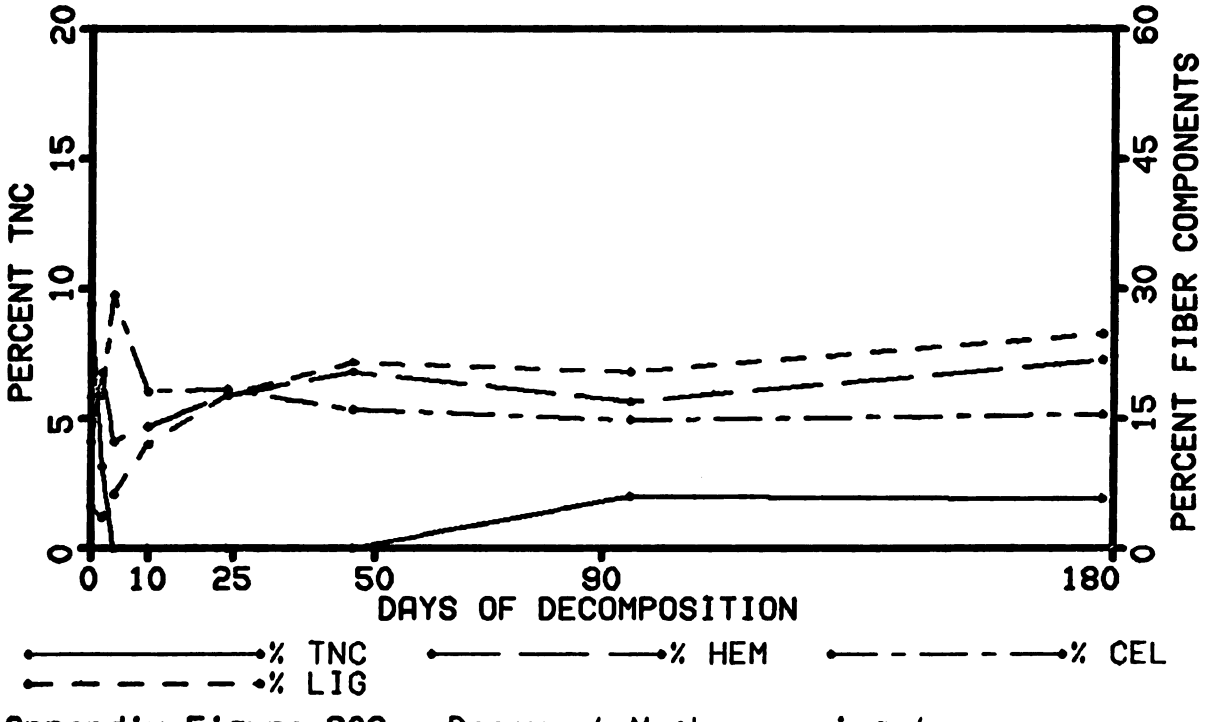
Appendix Figure 205. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



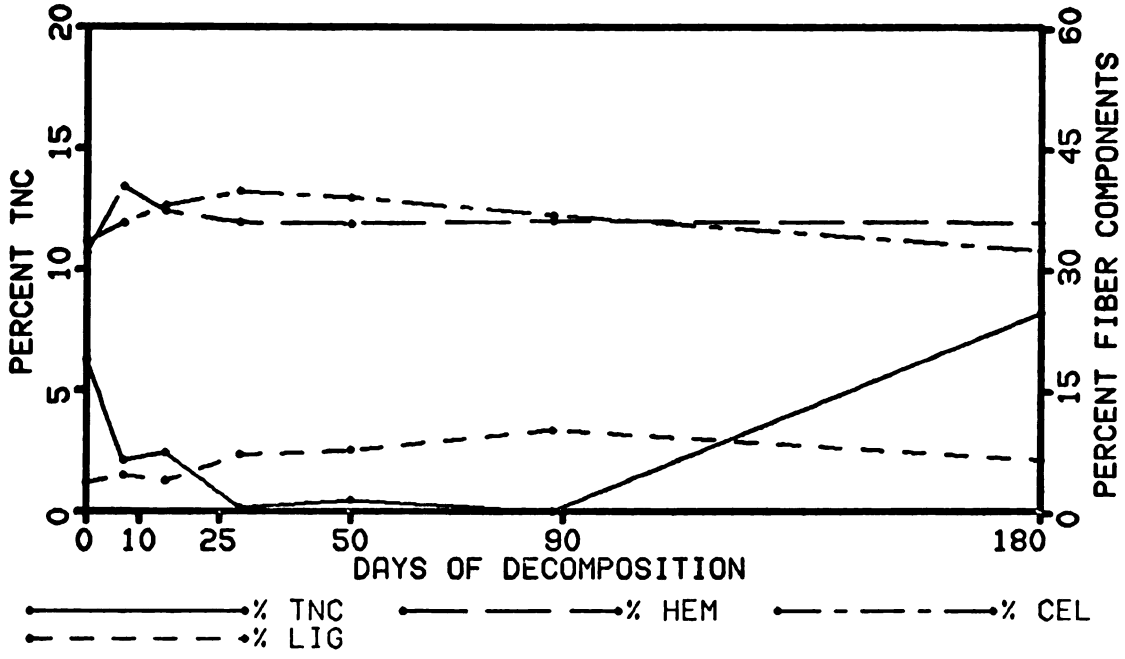
Appendix Figure 206. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



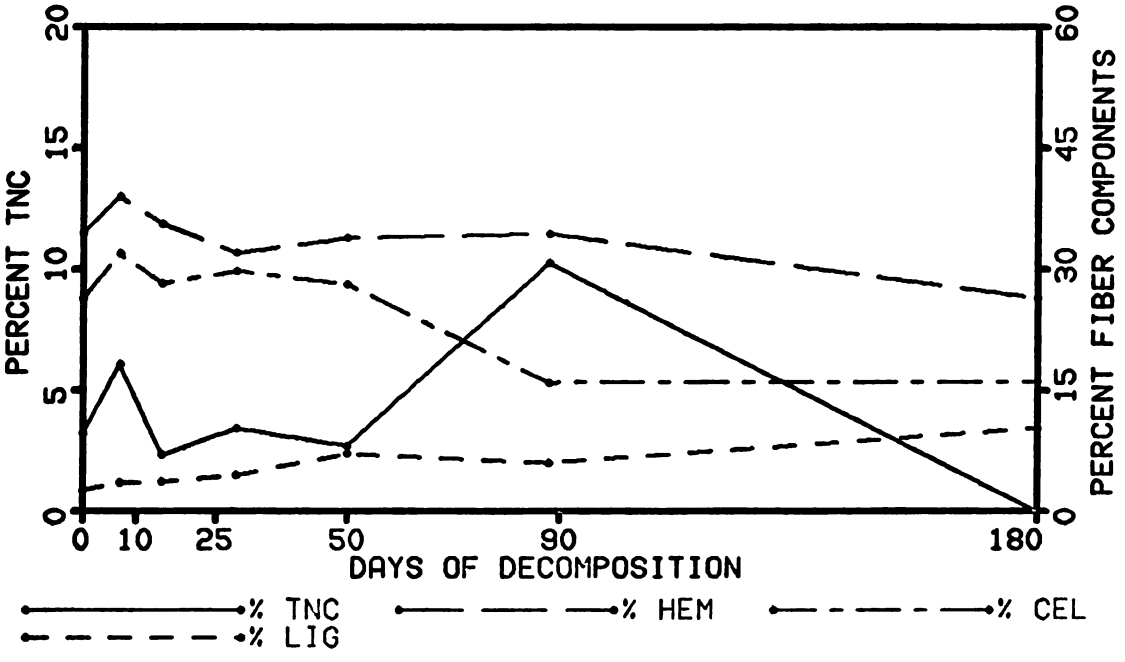
Appendix Figure 207. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



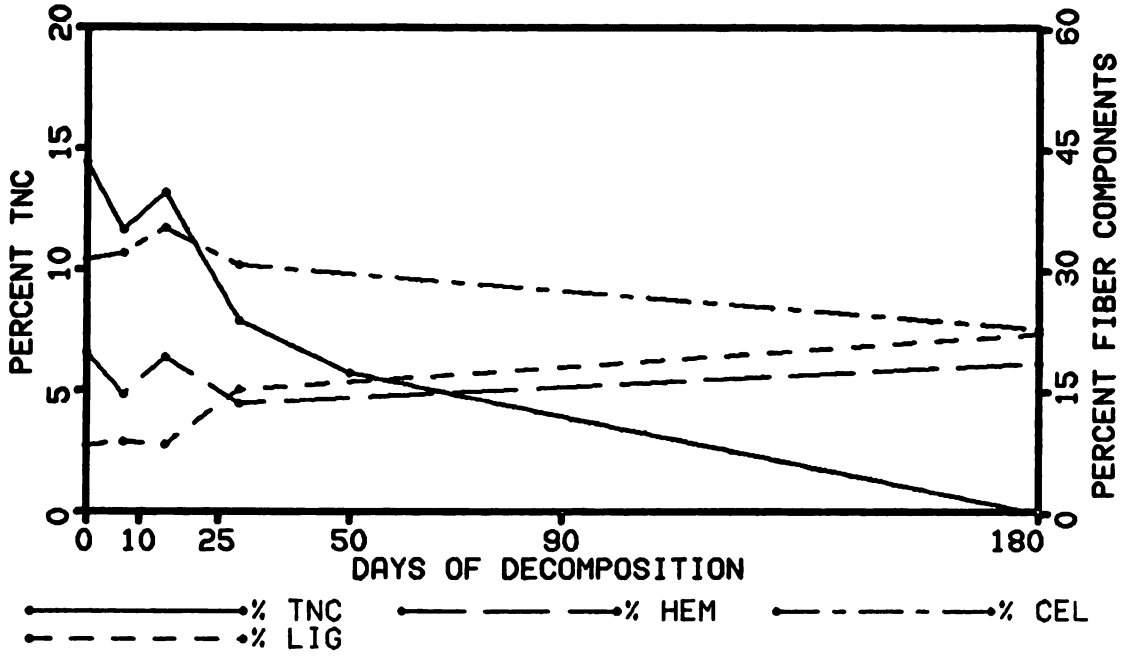
Appendix Figure 208. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



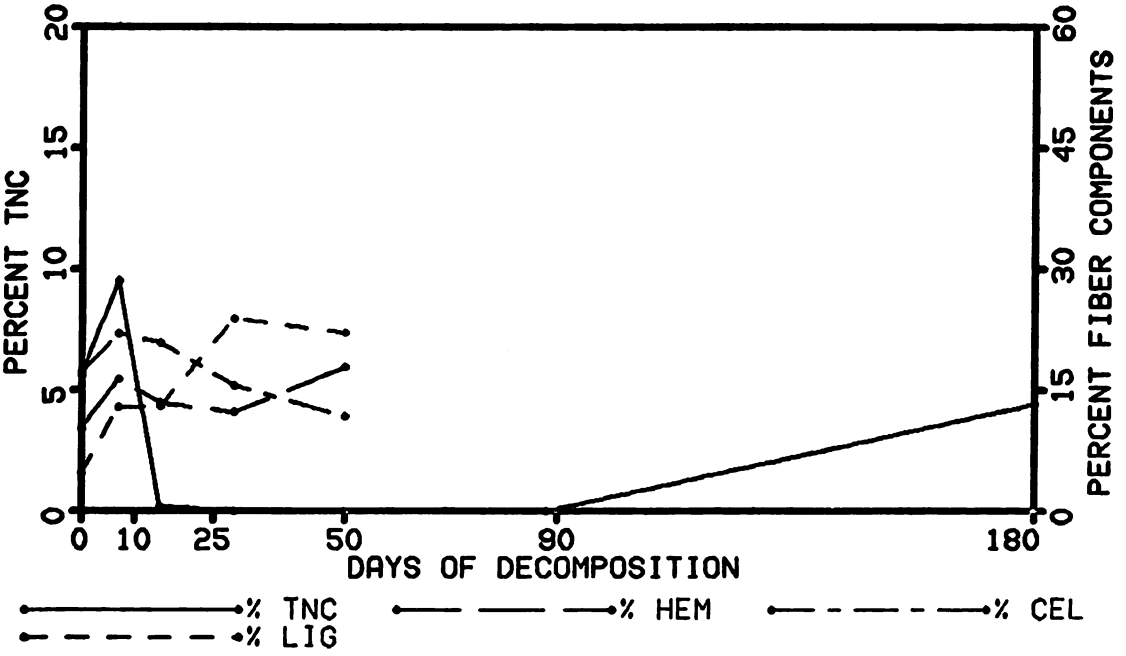
Appendix Figure 209. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during spring and summer. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



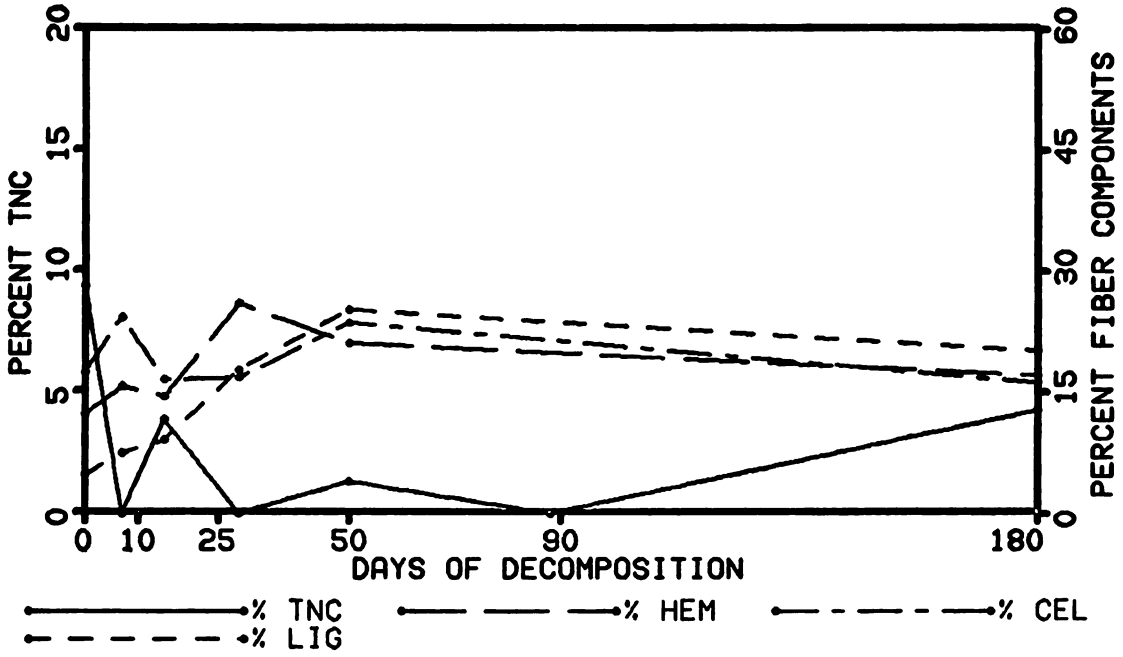
Appendix Figure 210. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during spring and summer. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



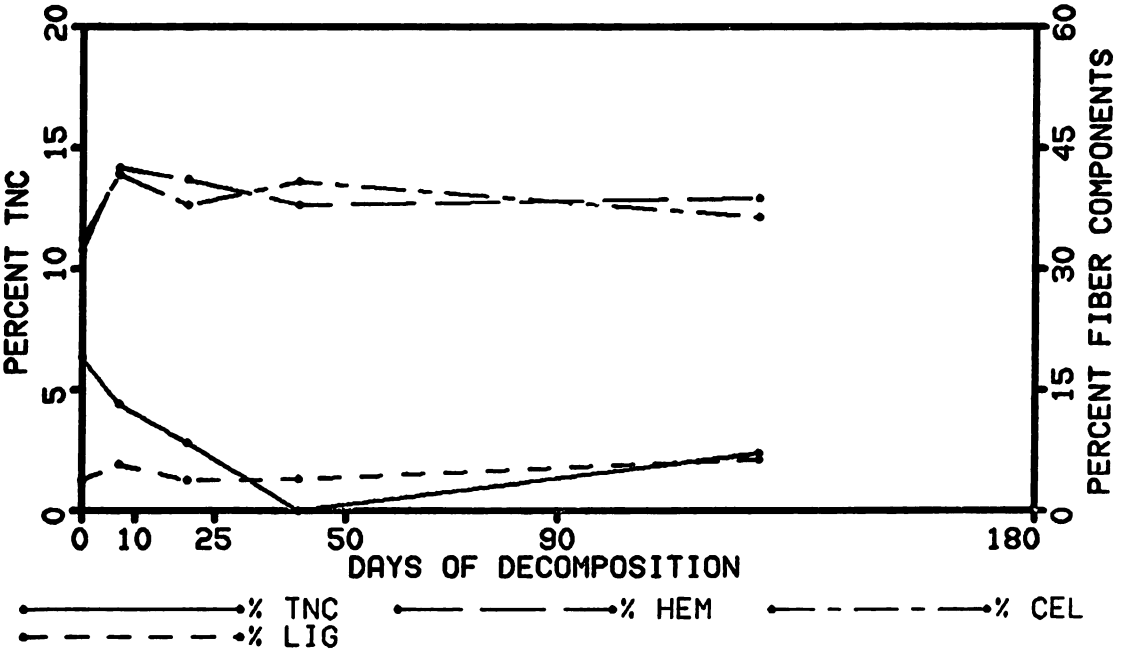
Appendix Figure 211. Decay of *Najas flexilis* in Lawrence Lake littoral zone during spring and summer. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



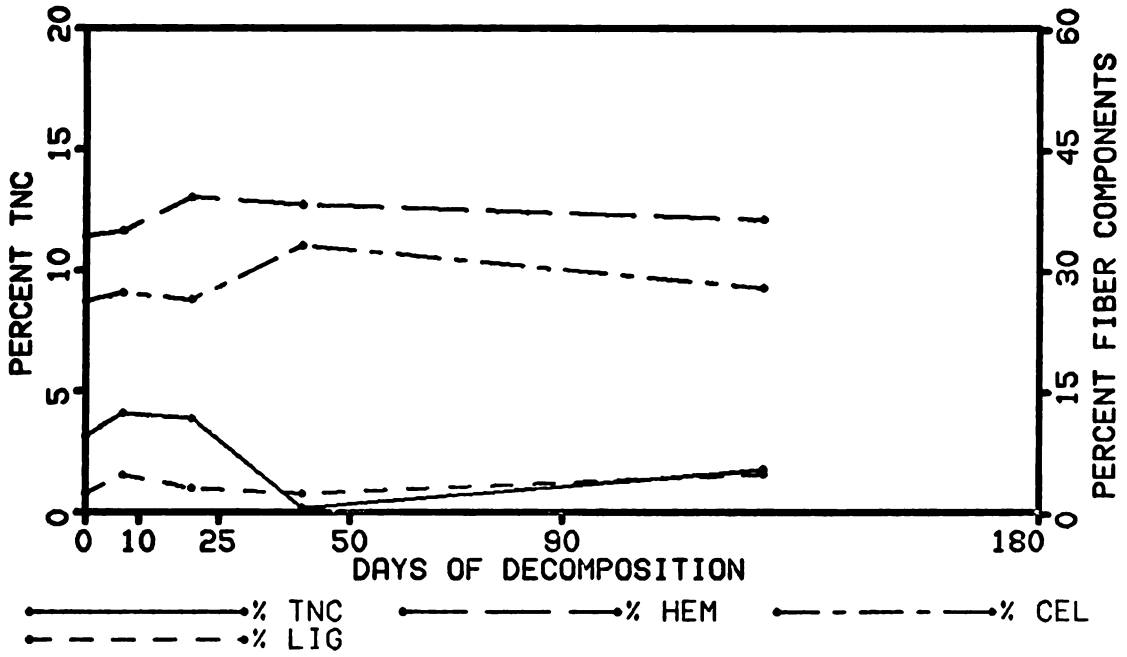
Appendix Figure 212. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during spring and summer. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



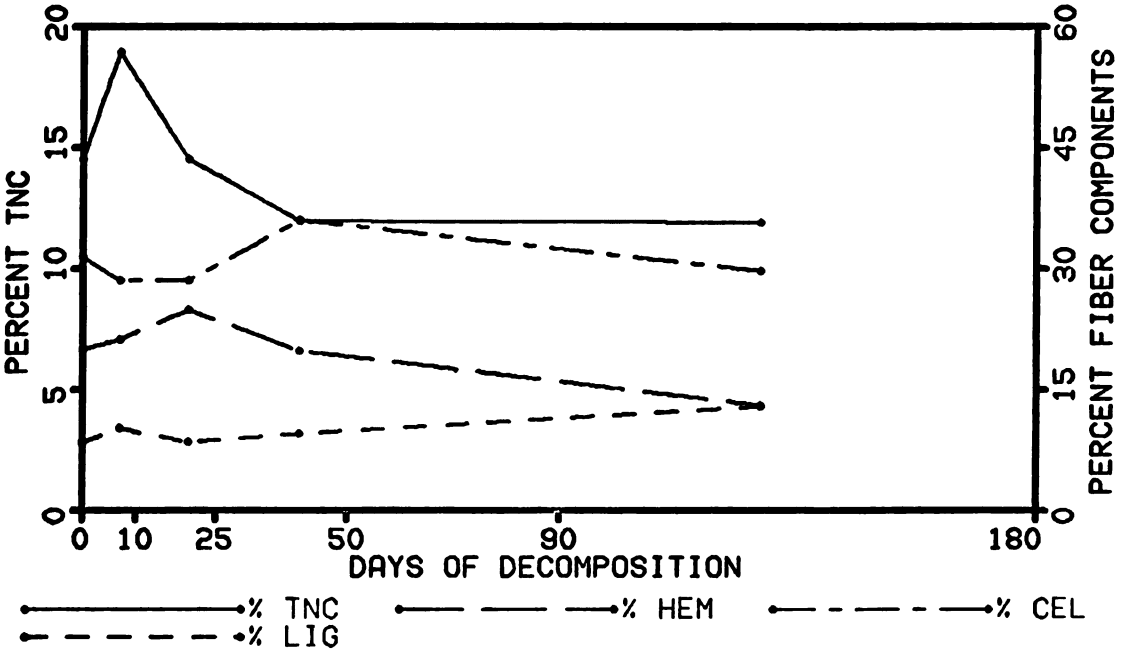
Appendix Figure 213. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during spring and summer. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



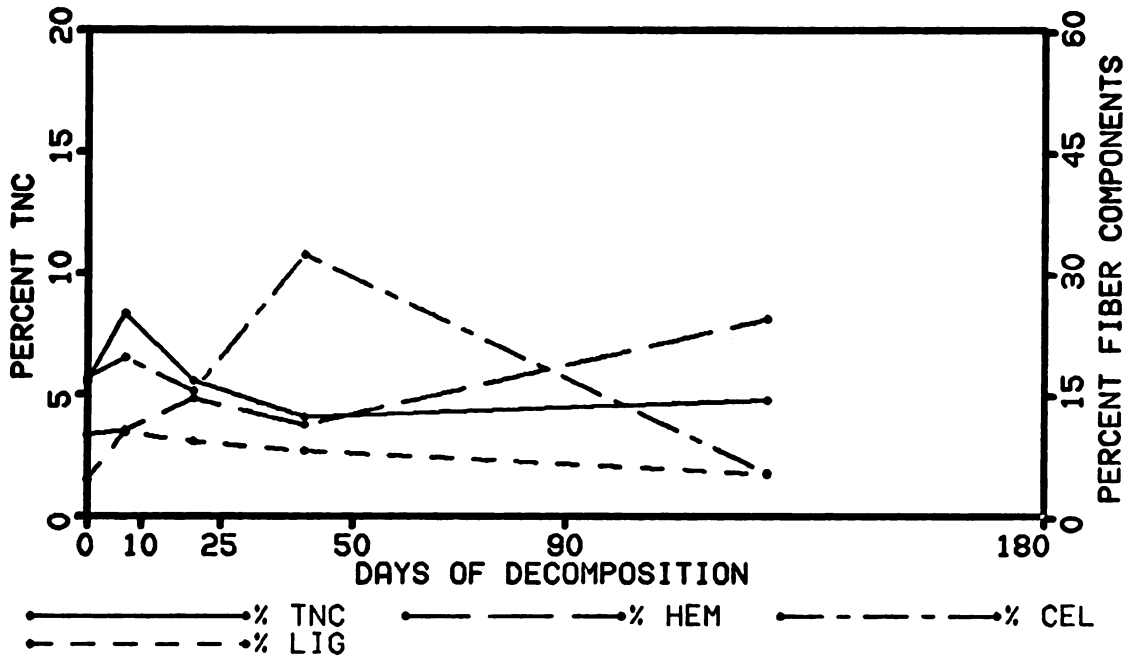
Appendix Figure 214. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



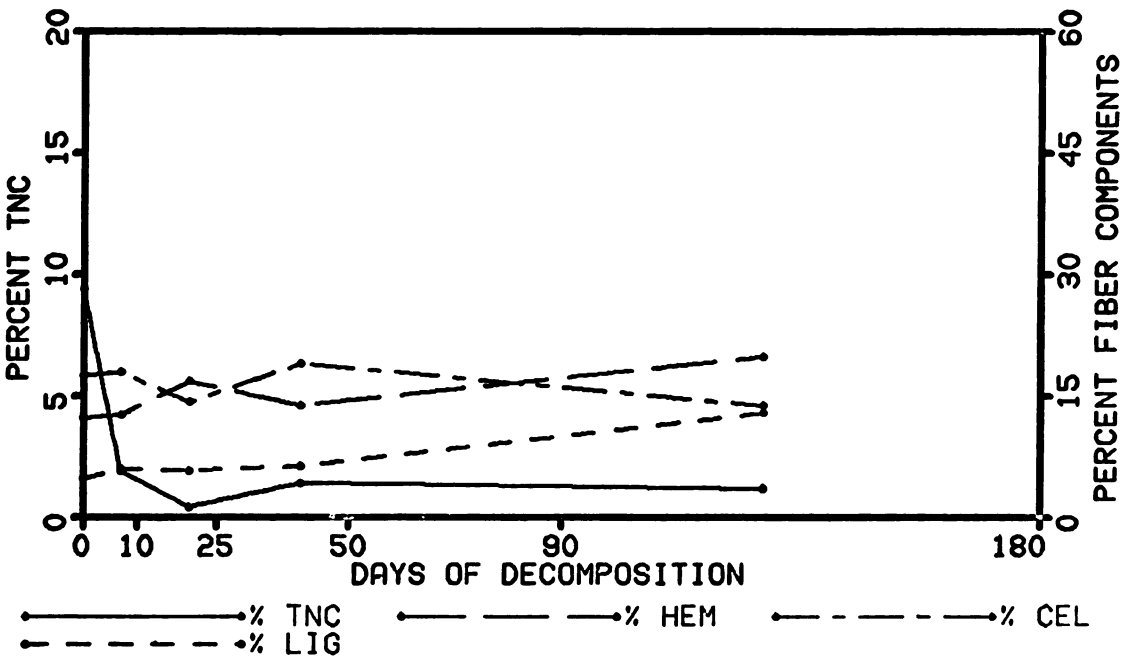
Appendix Figure 215. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



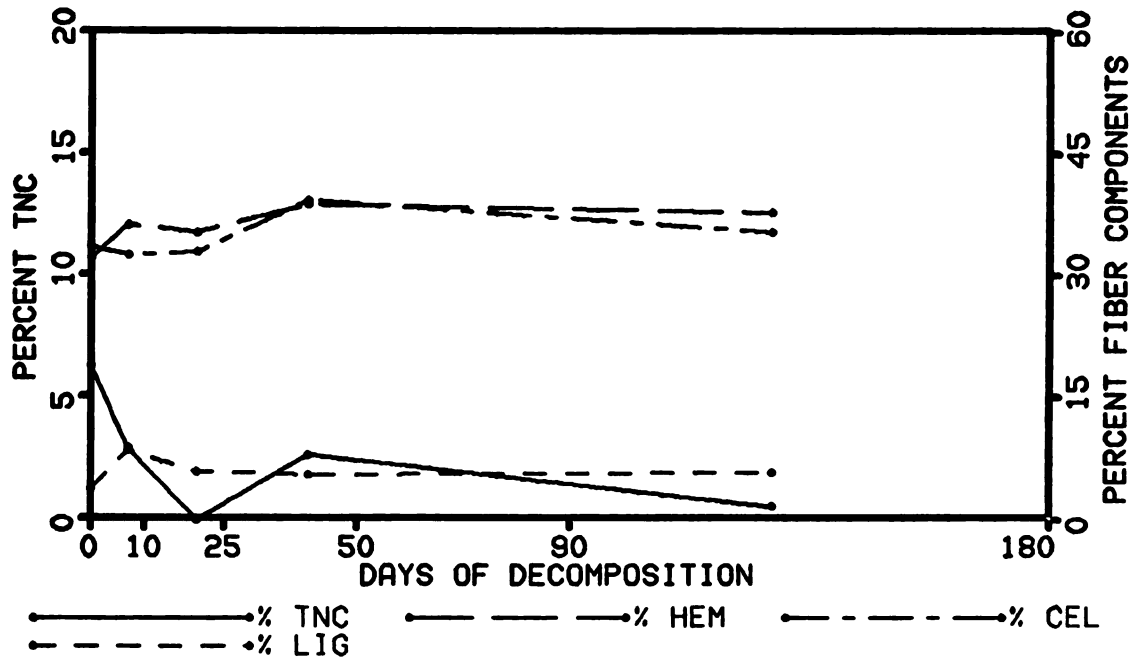
Appendix Figure 216. Decay of *Najas flexilis* in Lawrence Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



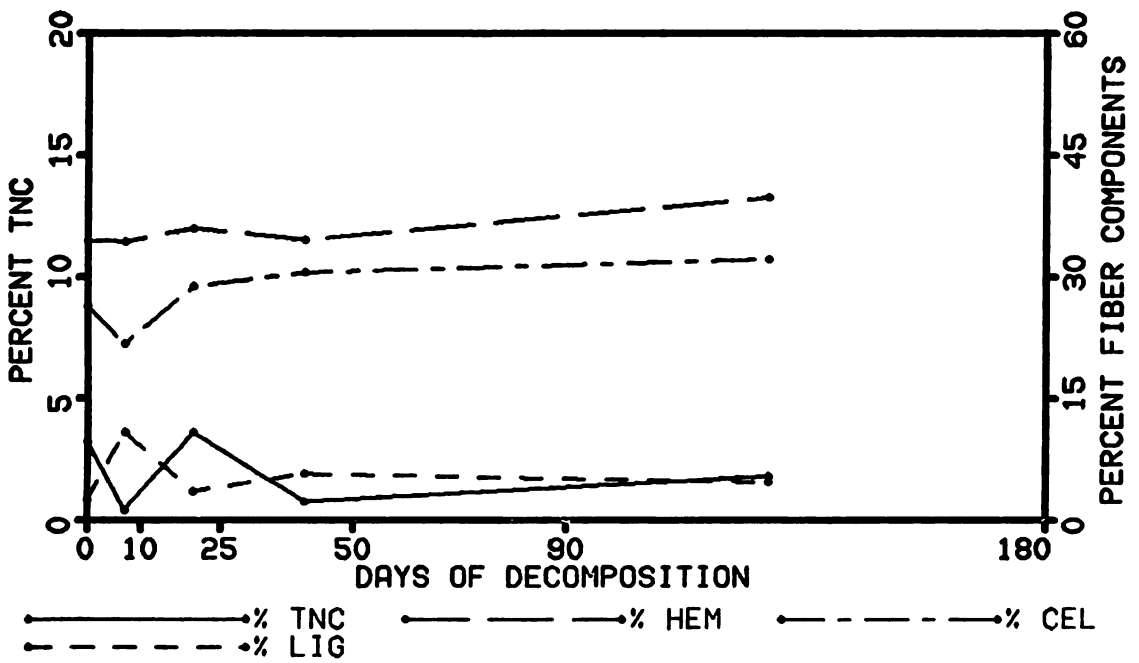
Appendix Figure 217. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



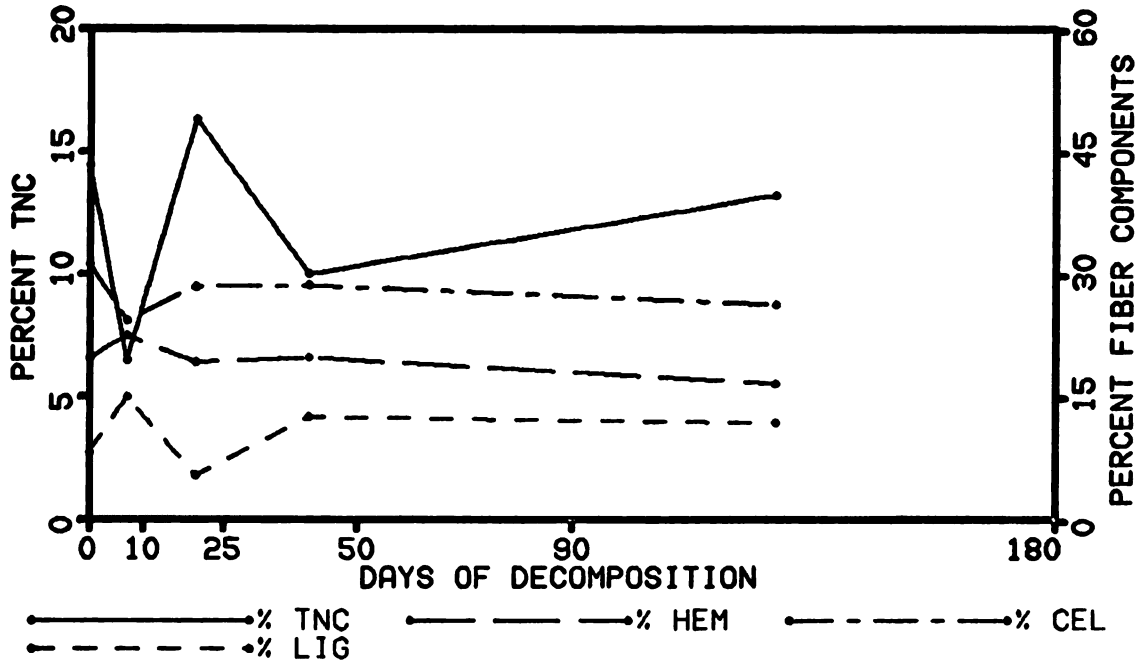
Appendix Figure 218. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



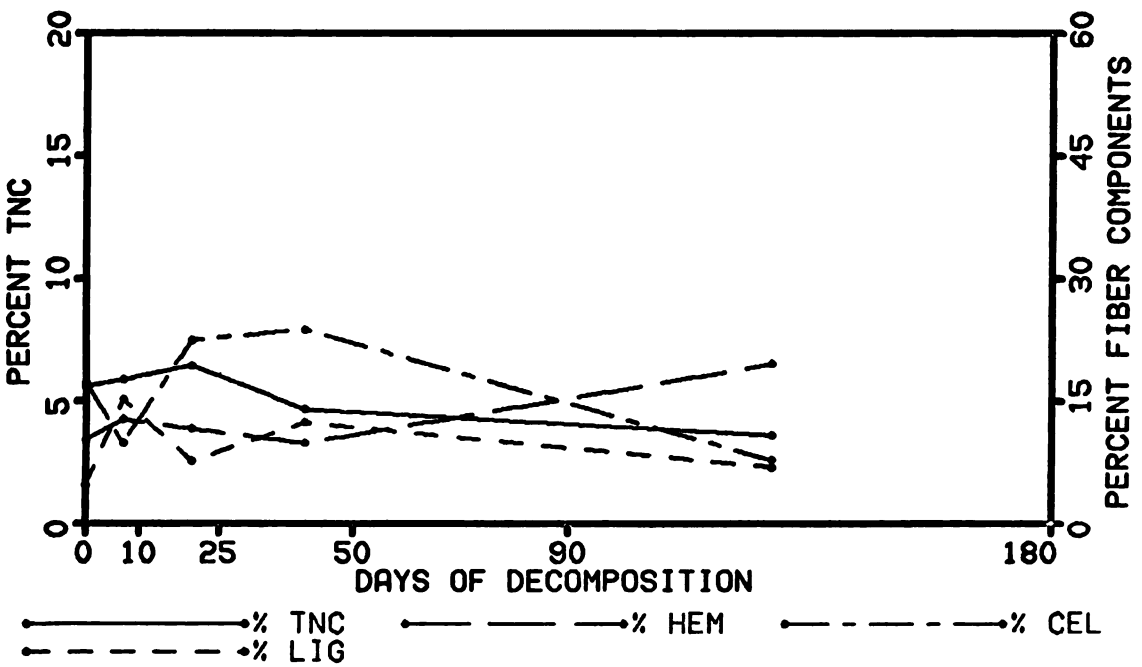
Appendix Figure 219. Decay of *Scirpus acutus* in Lawrence Lake pelagial zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



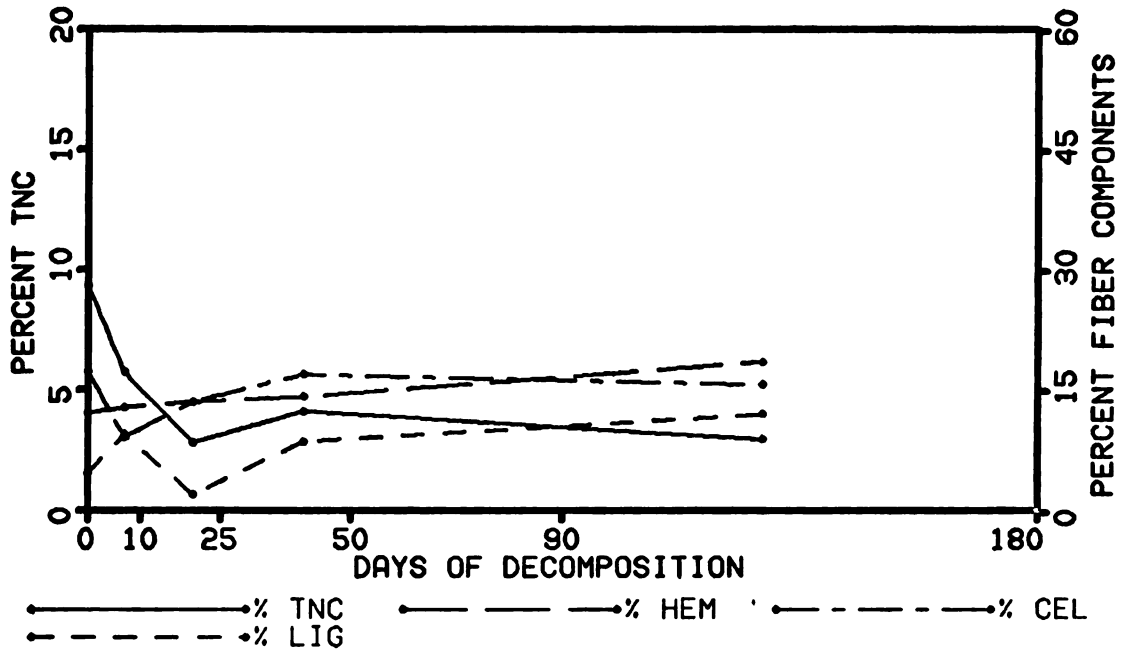
Appendix Figure 220. Decay of *Scirpus subterminalis* in Lawrence Lake pelagial zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



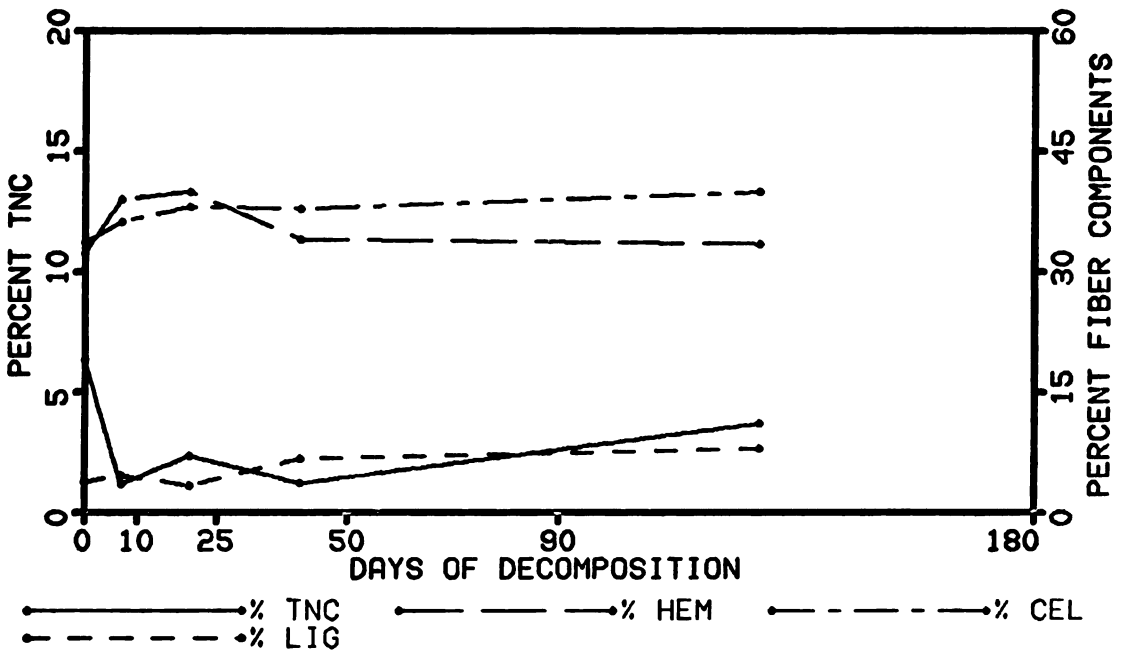
Appendix Figure 221. Decay of *Najas flexilis* in Lawrence Lake pelagial zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



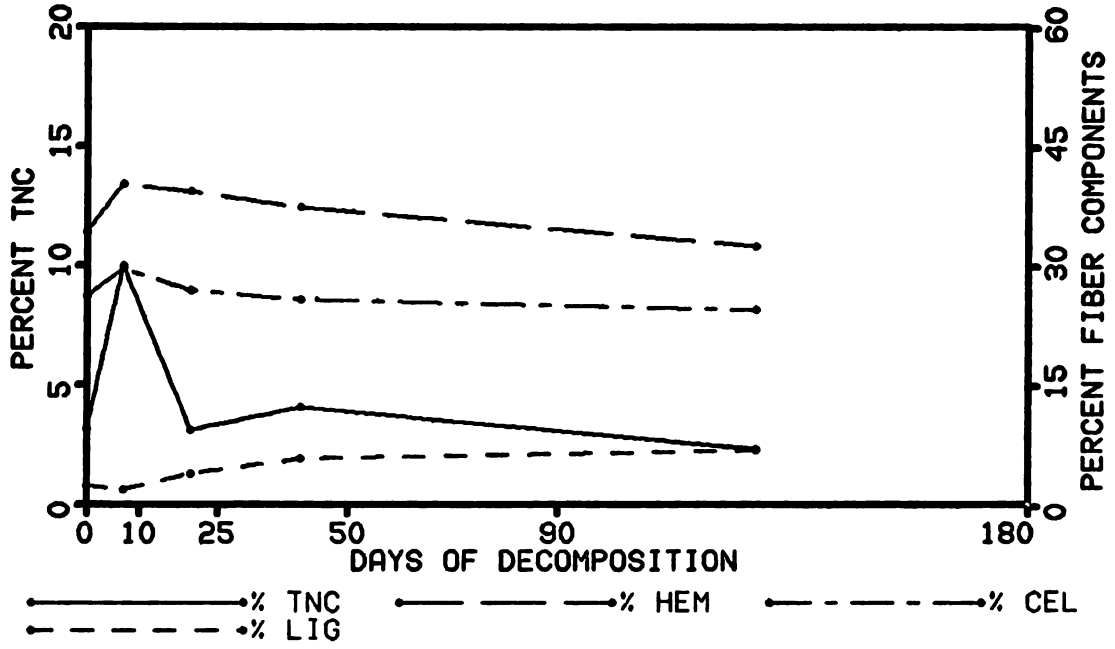
Appendix Figure 222. Decay of *Myriophyllum heterophyllum* in Lawrence Lake pelagial zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



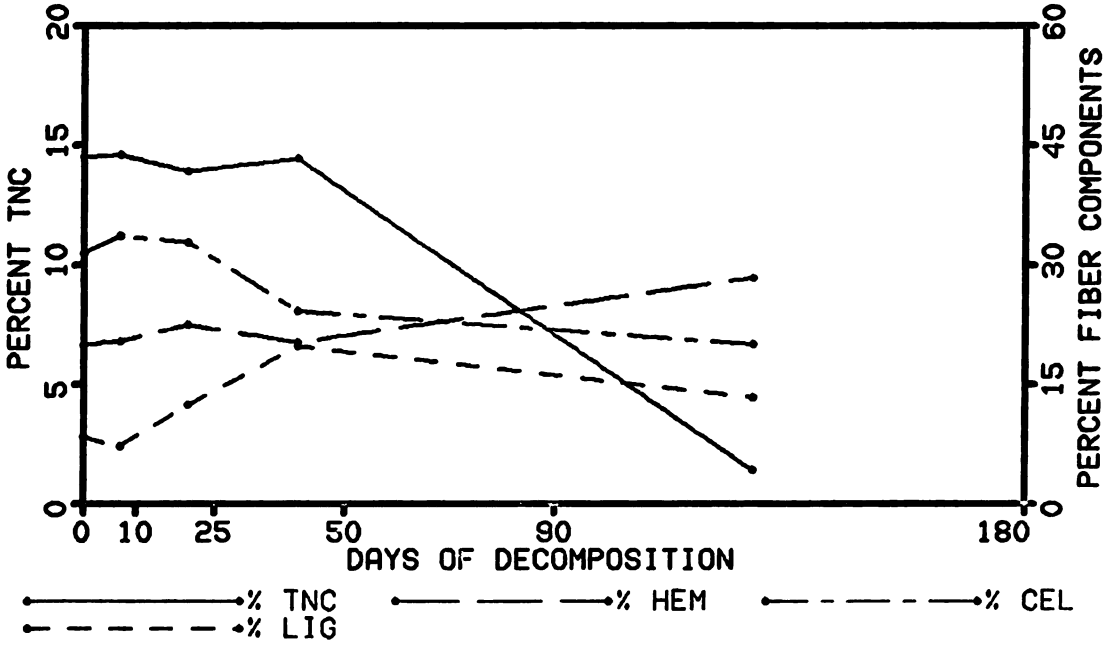
Appendix Figure 223. Decay of *Nuphar variegatum* in Lawrence Lake pelagial zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



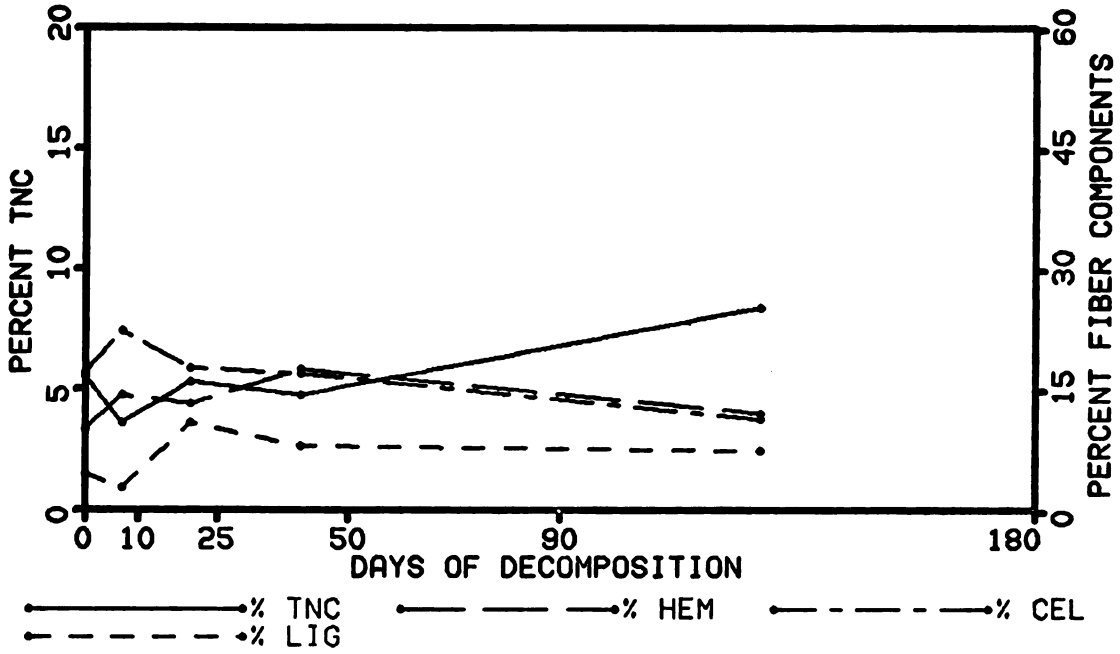
Appendix Figure 224. Decay of *Scirpus acutus* in Wintergreen Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



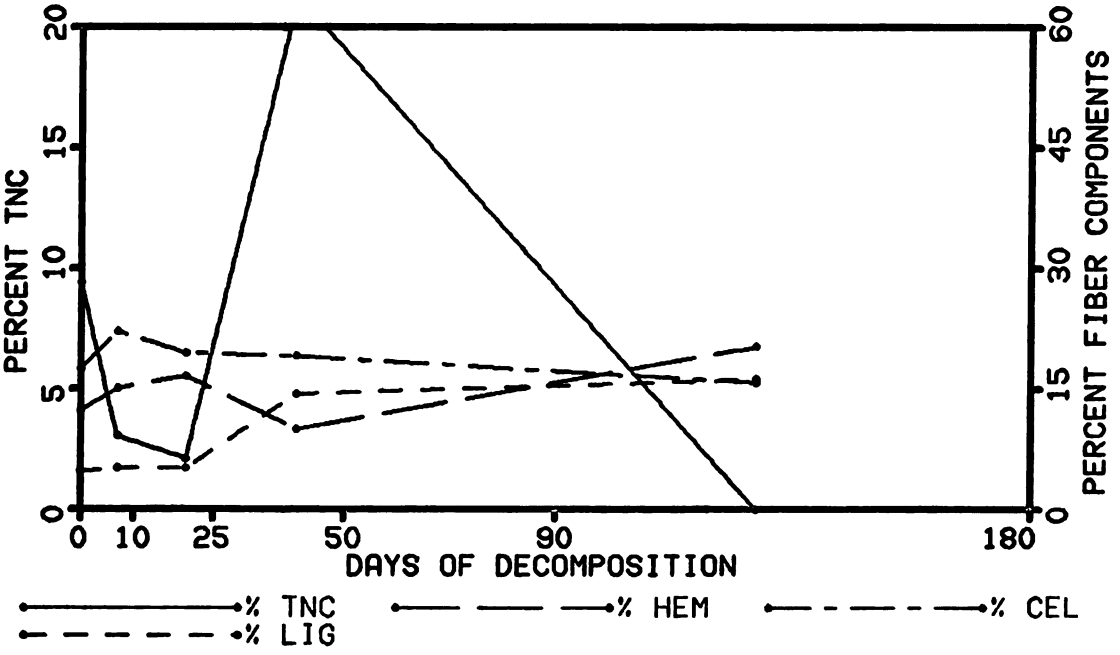
Appendix Figure 225. Decay of *Scirpus subterminalis* in Wintergreen Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



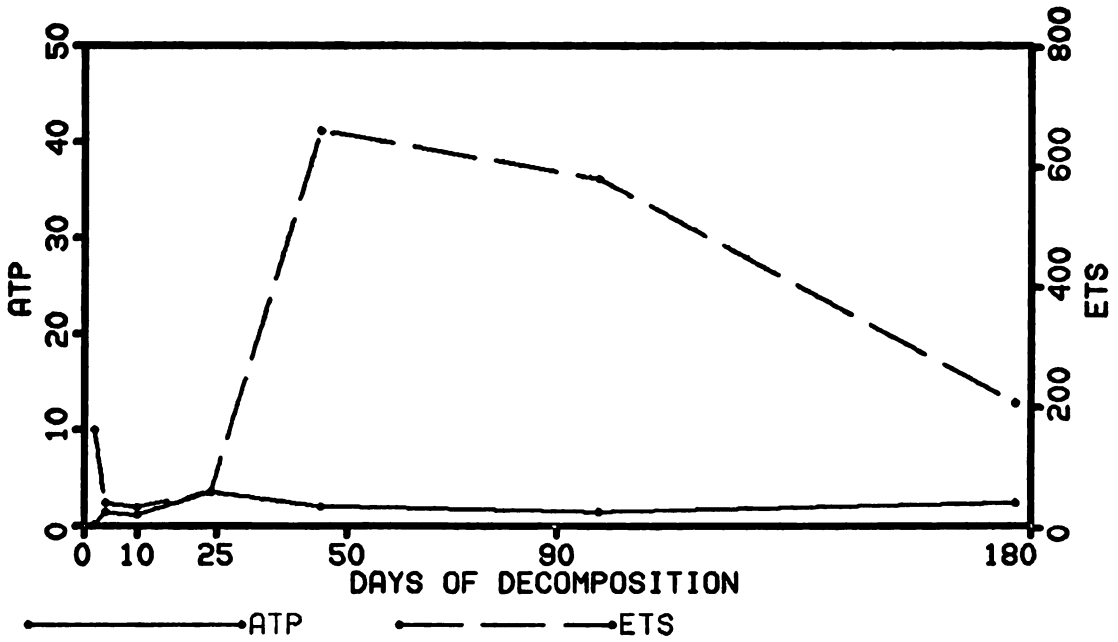
Appendix Figure 226. Decay of *Najas flexilis* in Wintergreen Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



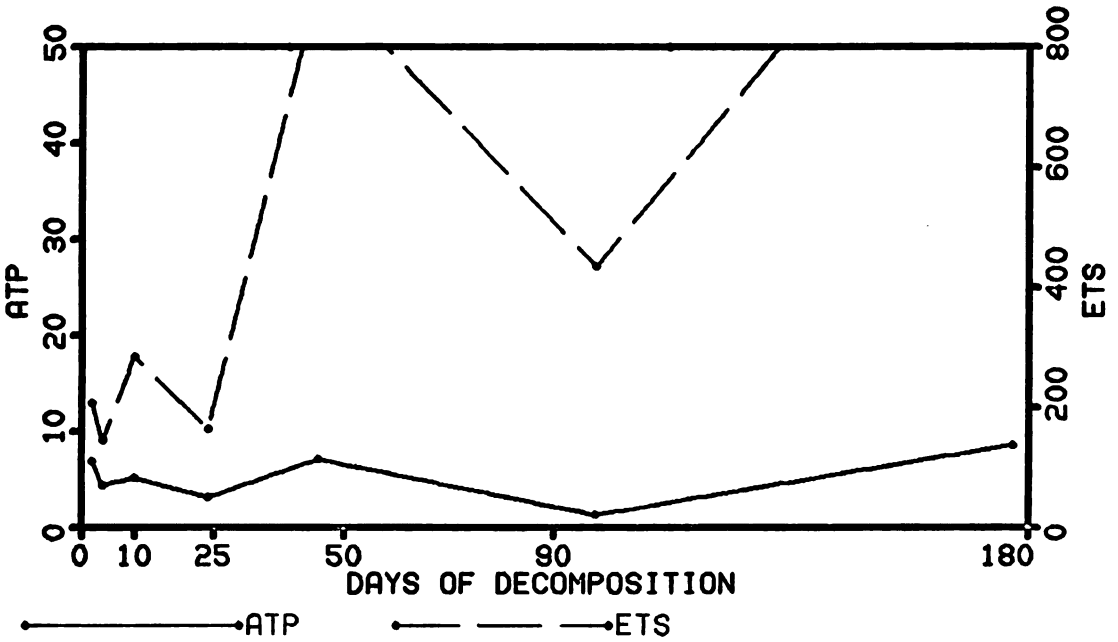
Appendix Figure 227. Decay of *Myriophyllum heterophyllum* in Wintergreen Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



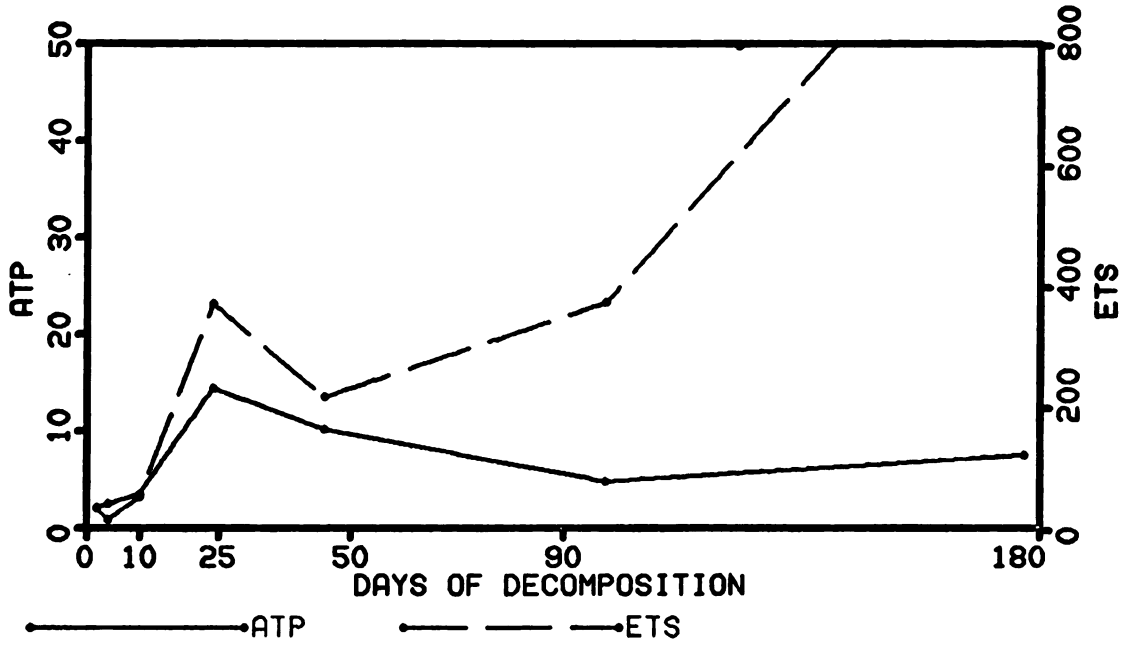
Appendix Figure 228. Decay of *Nuphar variegatum* in Wintergreen Lake littoral zone during fall and winter. Percent of ash-free dry weight of plant material as total nonstructural carbohydrate (TNC), hemicellulose (HEM), cellulose (CEL), and lignin (LIG).



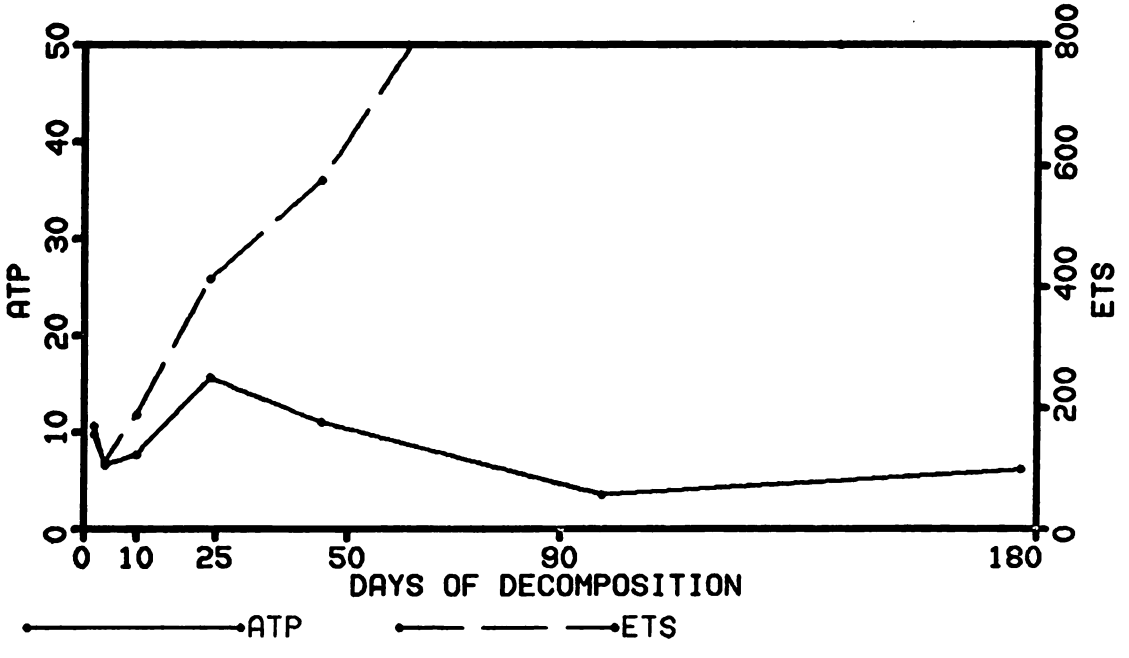
Appendix Figure 229. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



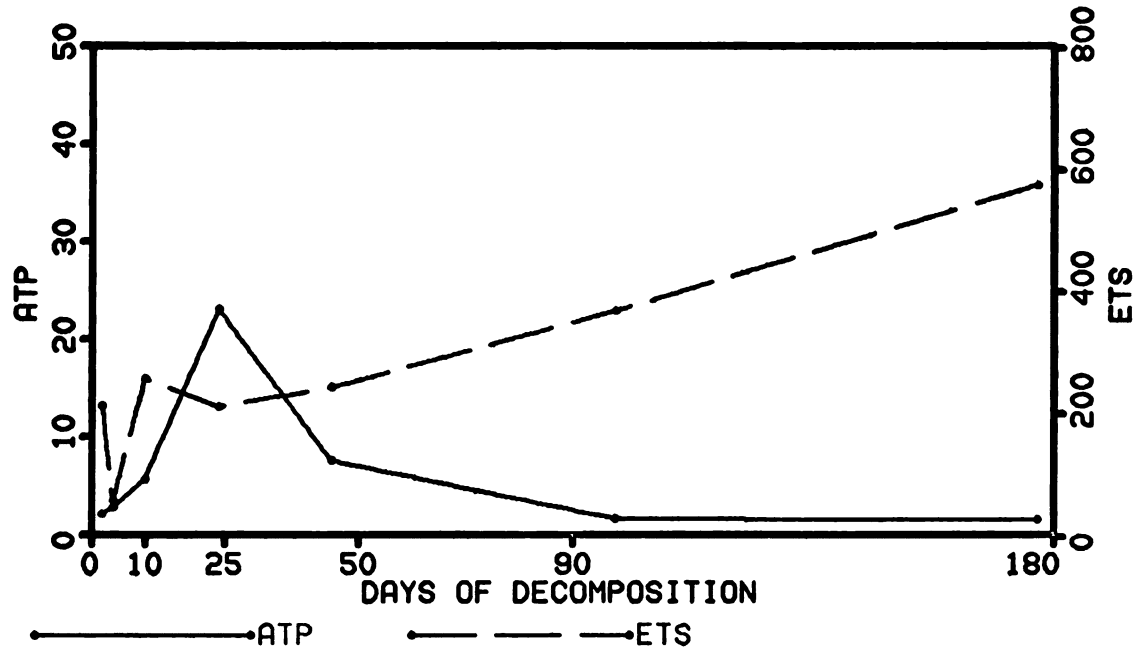
Appendix Figure 230. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



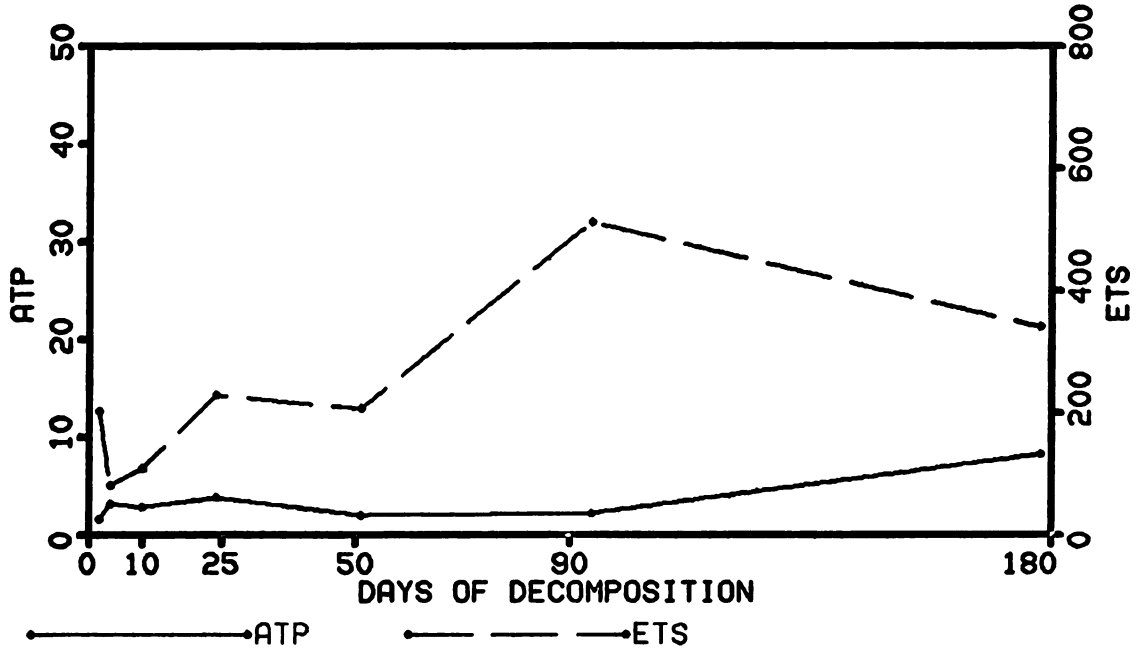
Appendix Figure 231. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



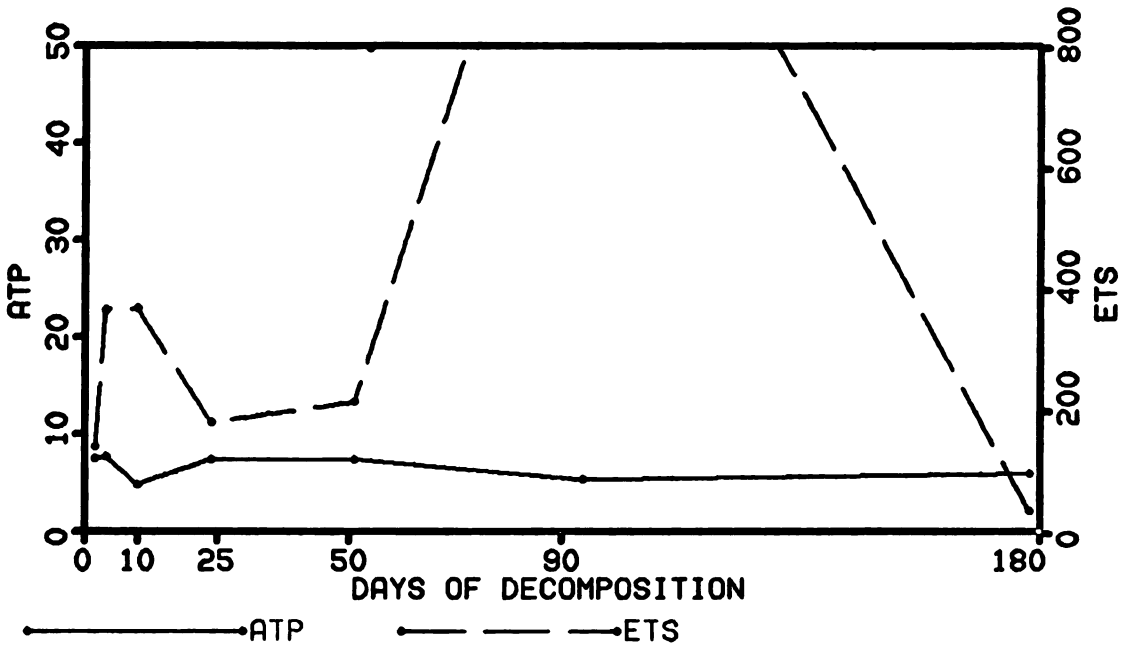
Appendix Figure 232. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



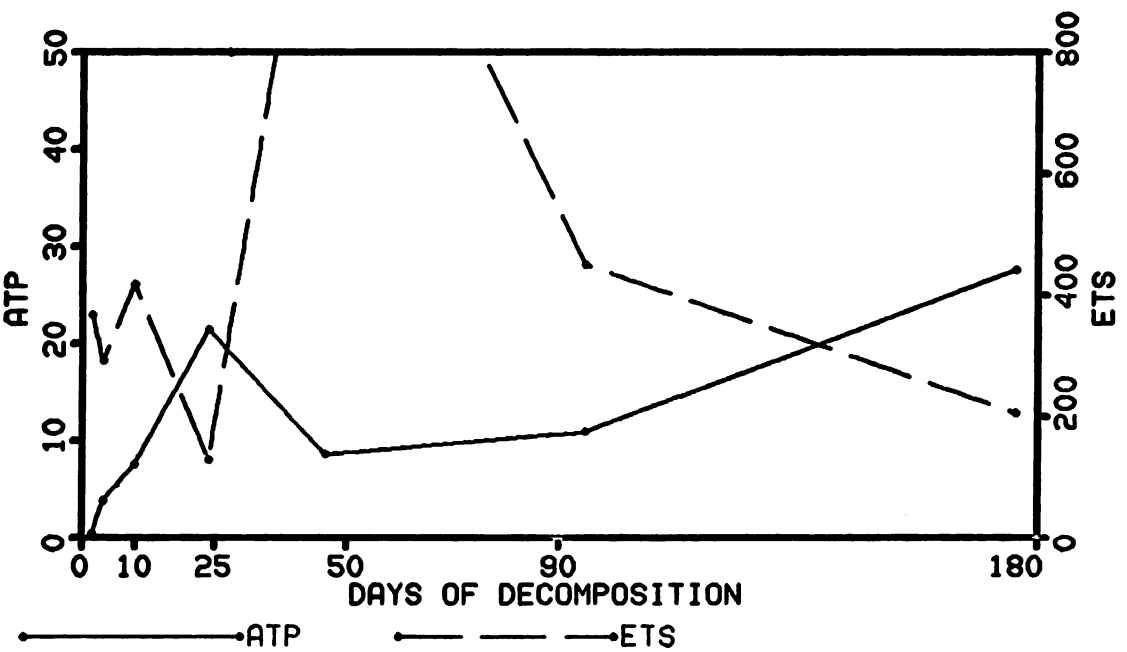
Appendix Figure 233. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



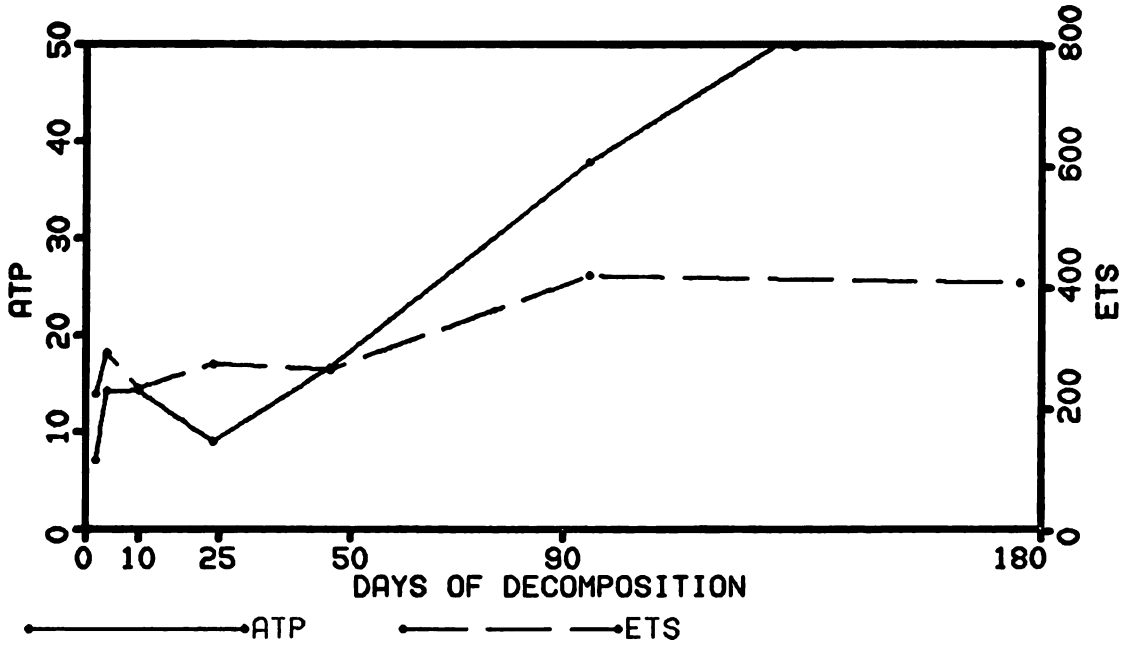
Appendix Figure 234. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



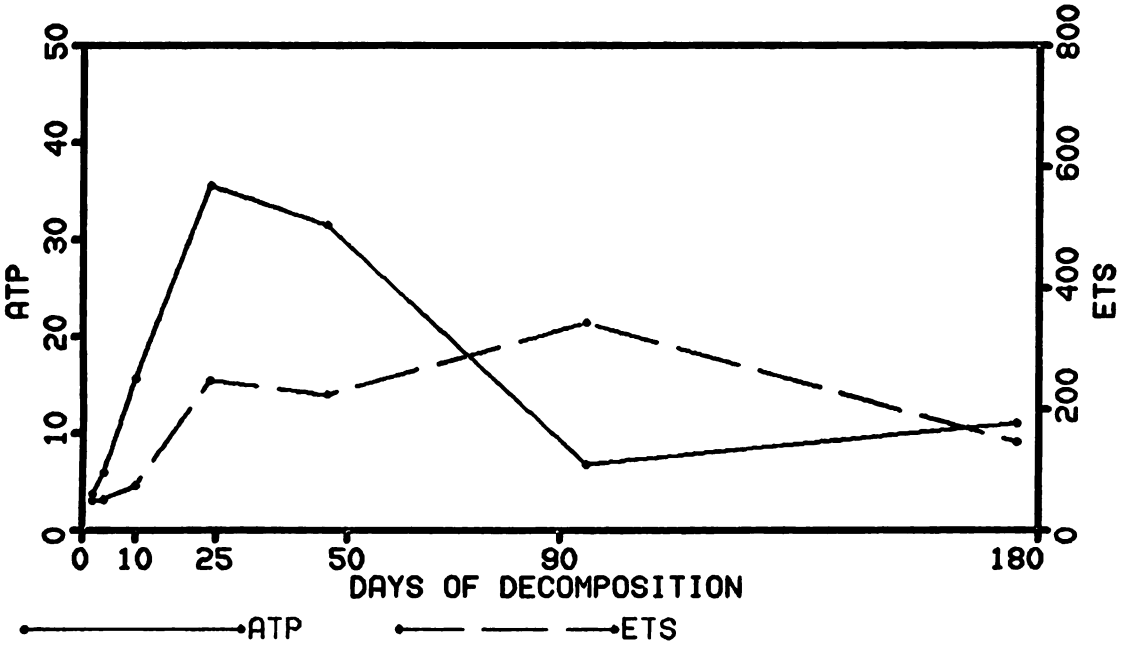
Appendix Figure 235. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



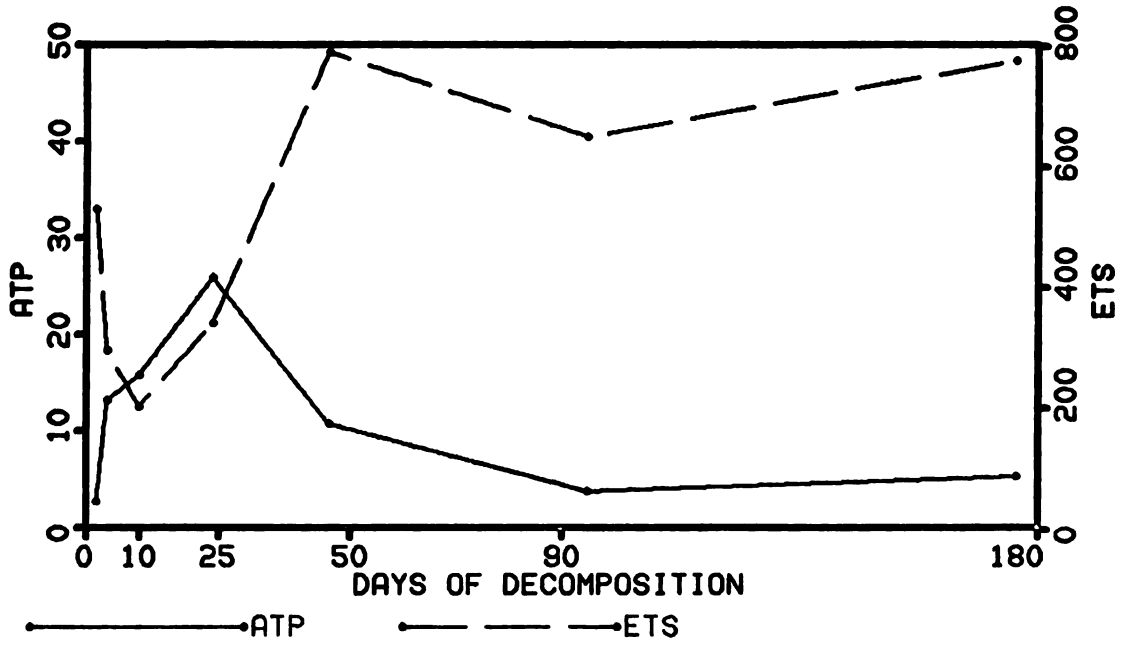
Appendix Figure 236. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



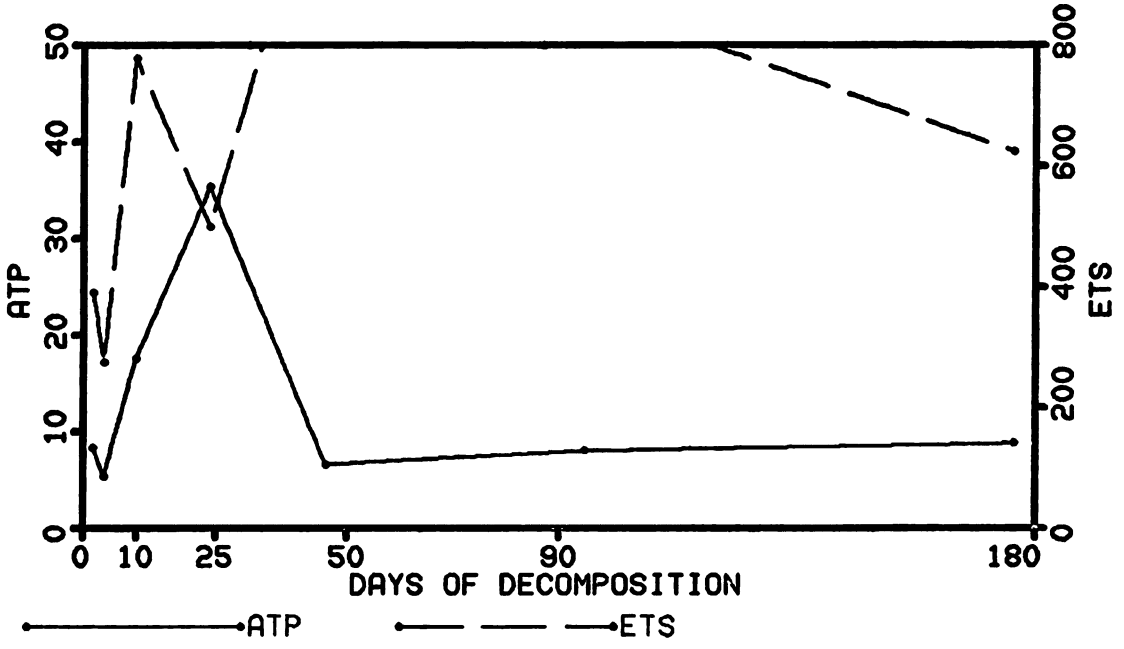
Appendix Figure 237. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



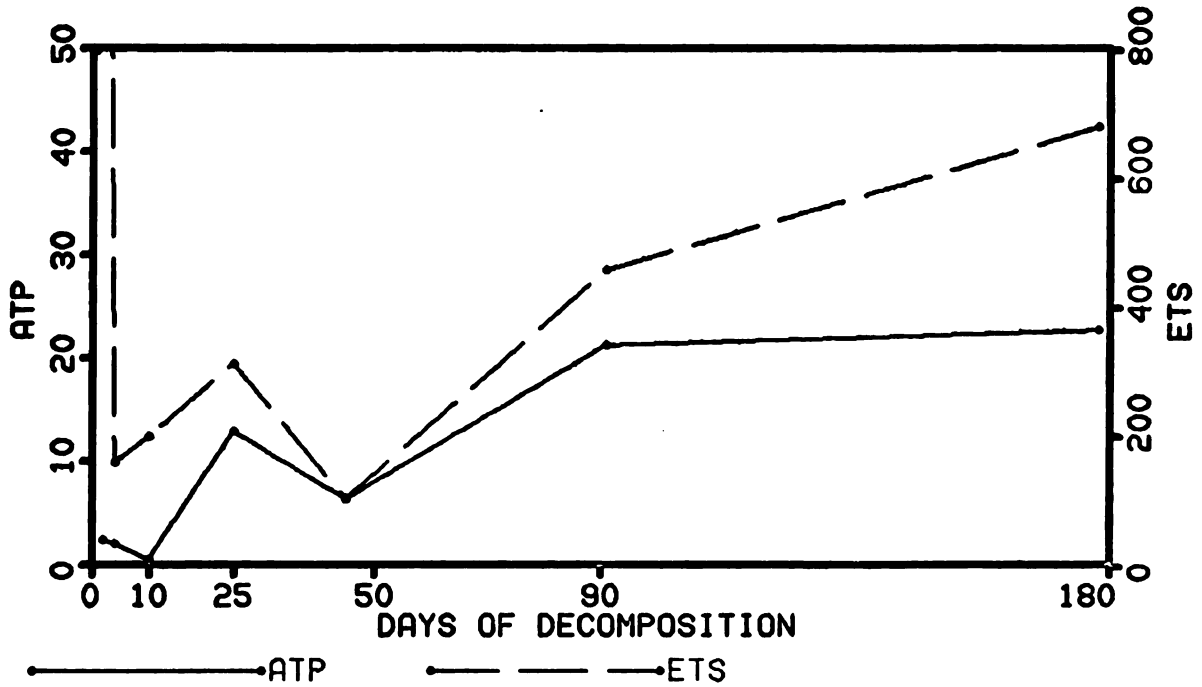
Appendix Figure 238. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



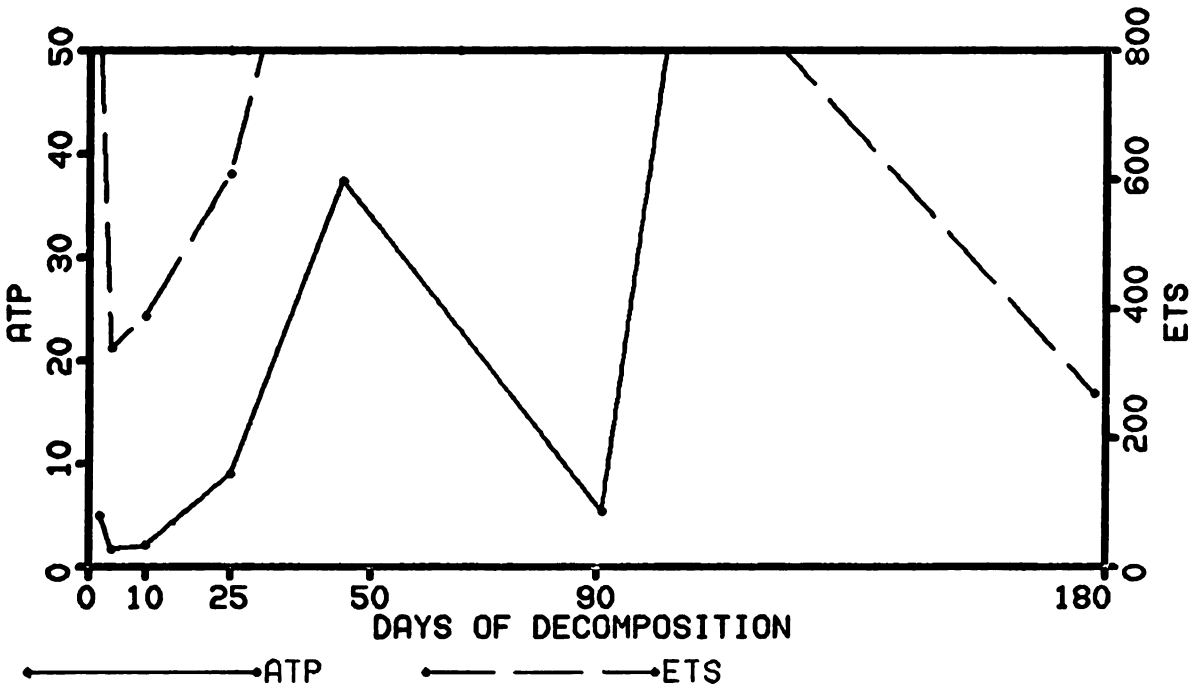
Appendix Figure 239. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



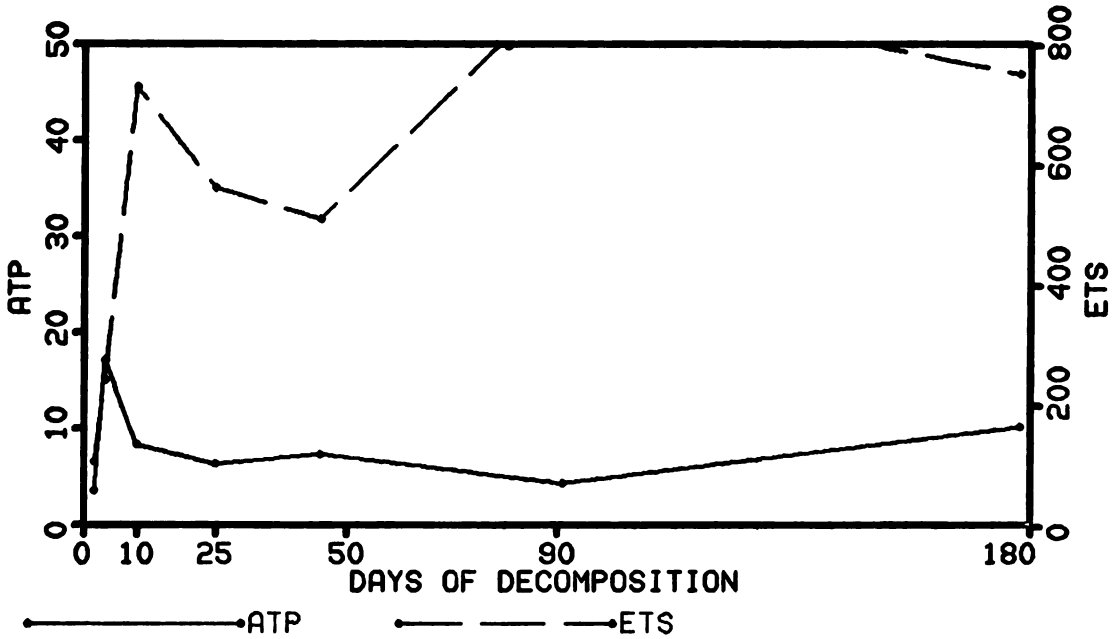
Appendix Figure 240. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



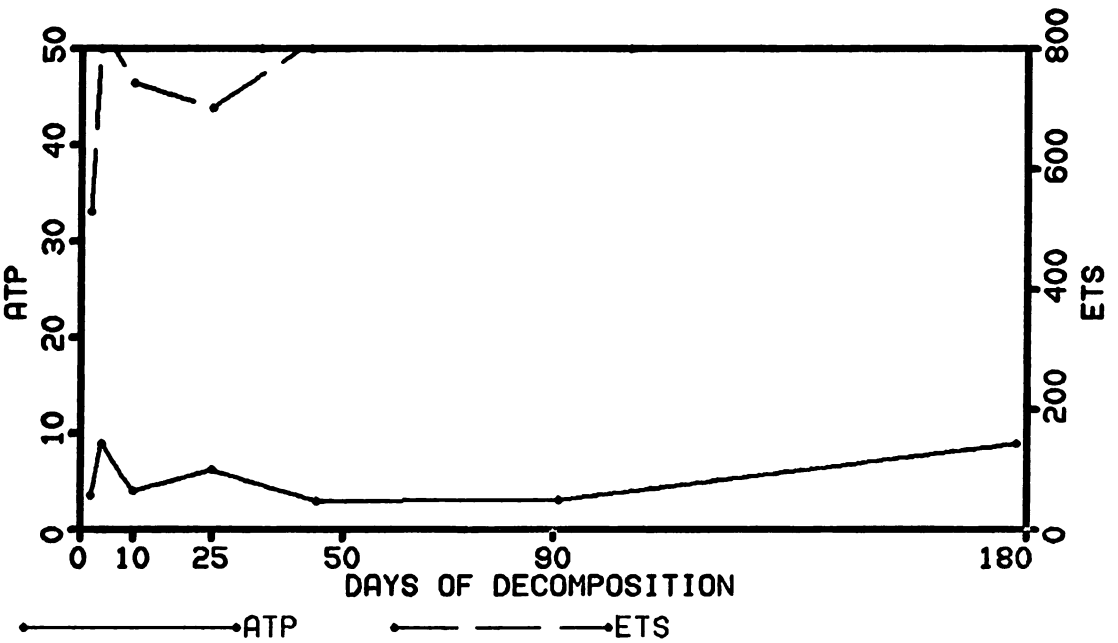
Appendix Figure 241. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



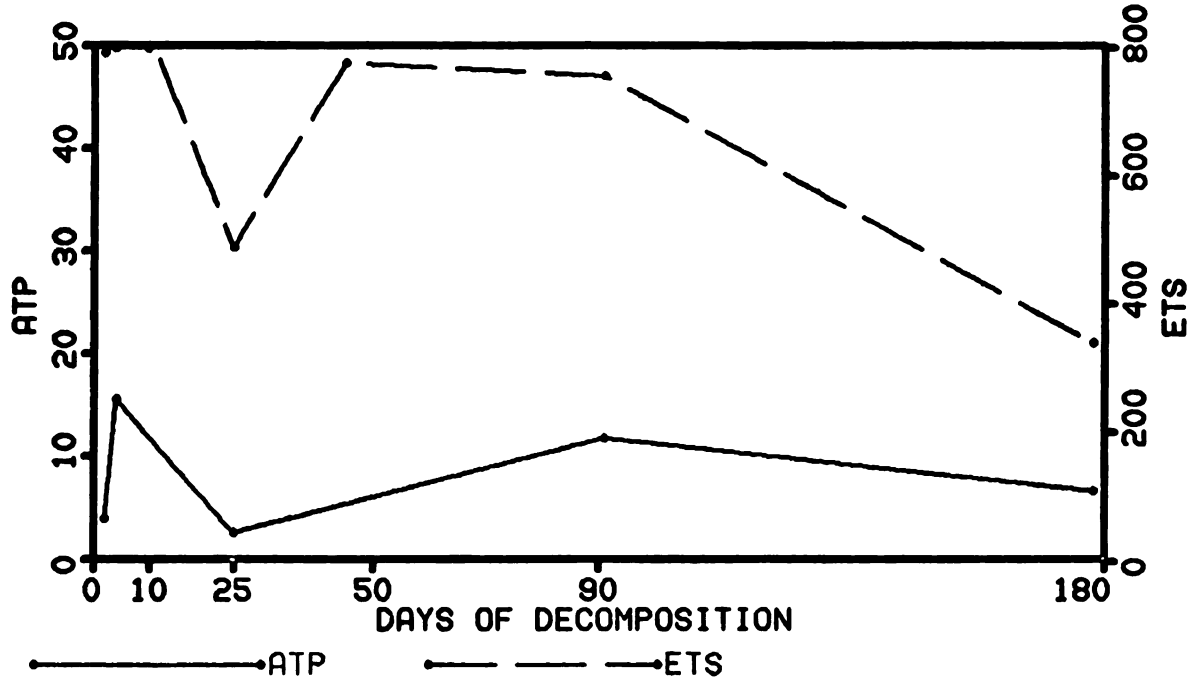
Appendix Figure 242. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



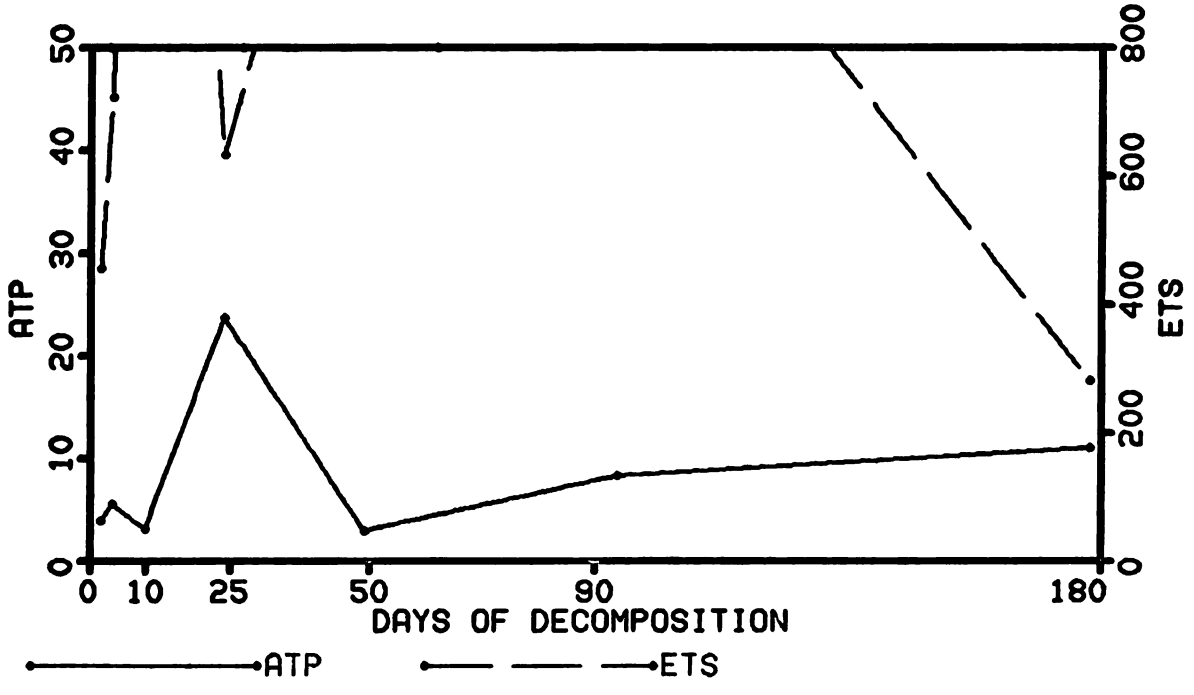
Appendix Figure 243. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



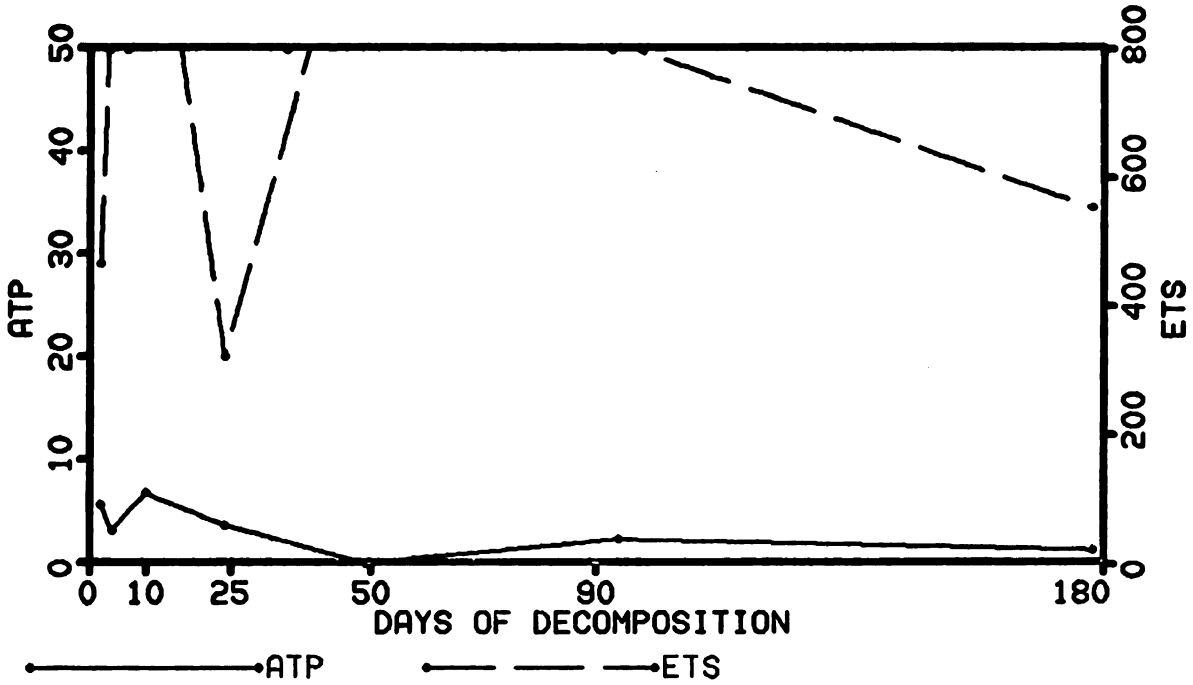
Appendix Figure 244. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



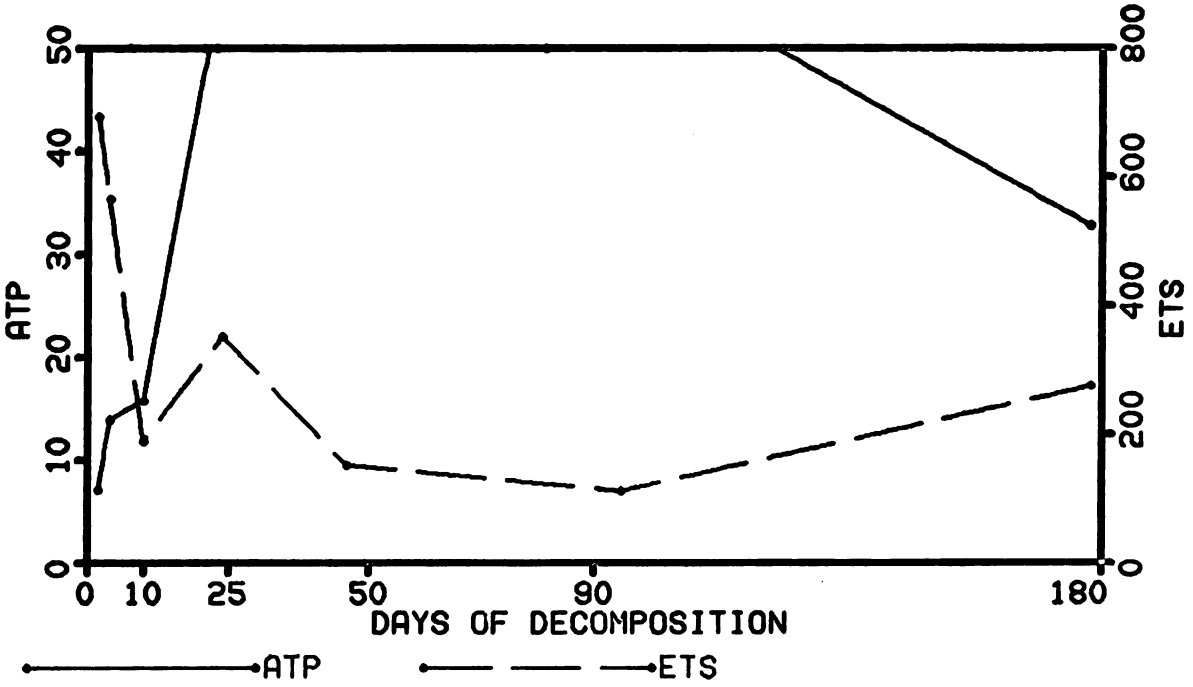
Appendix Figure 245. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



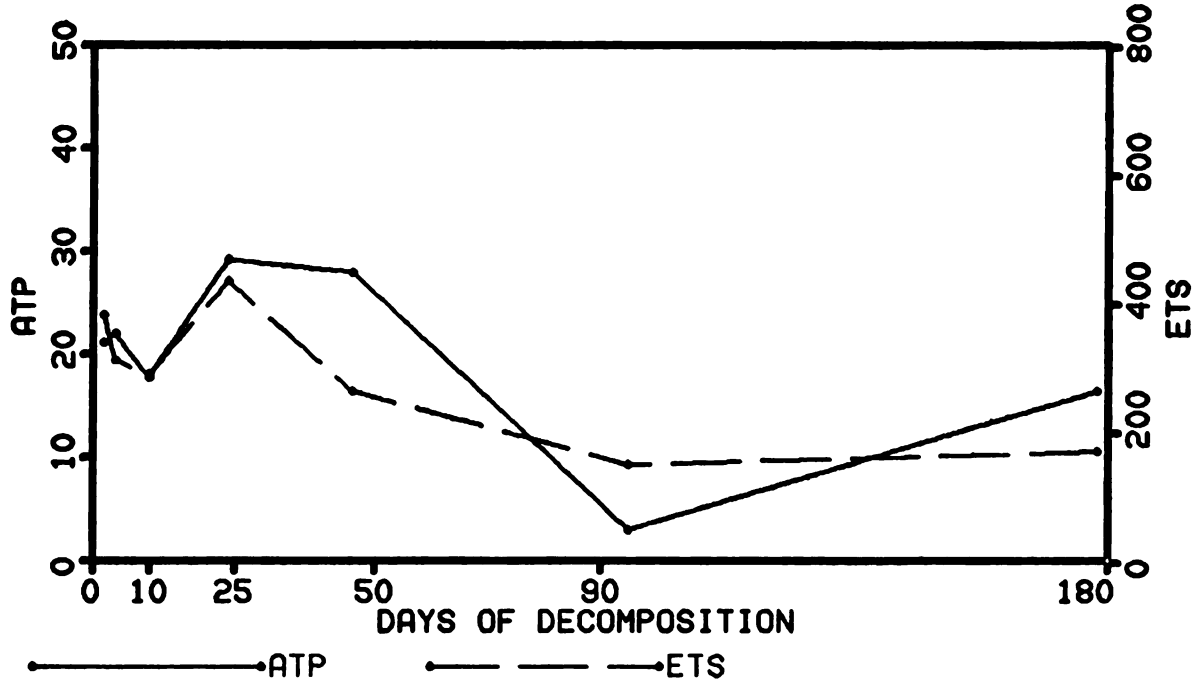
Appendix Figure 246. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



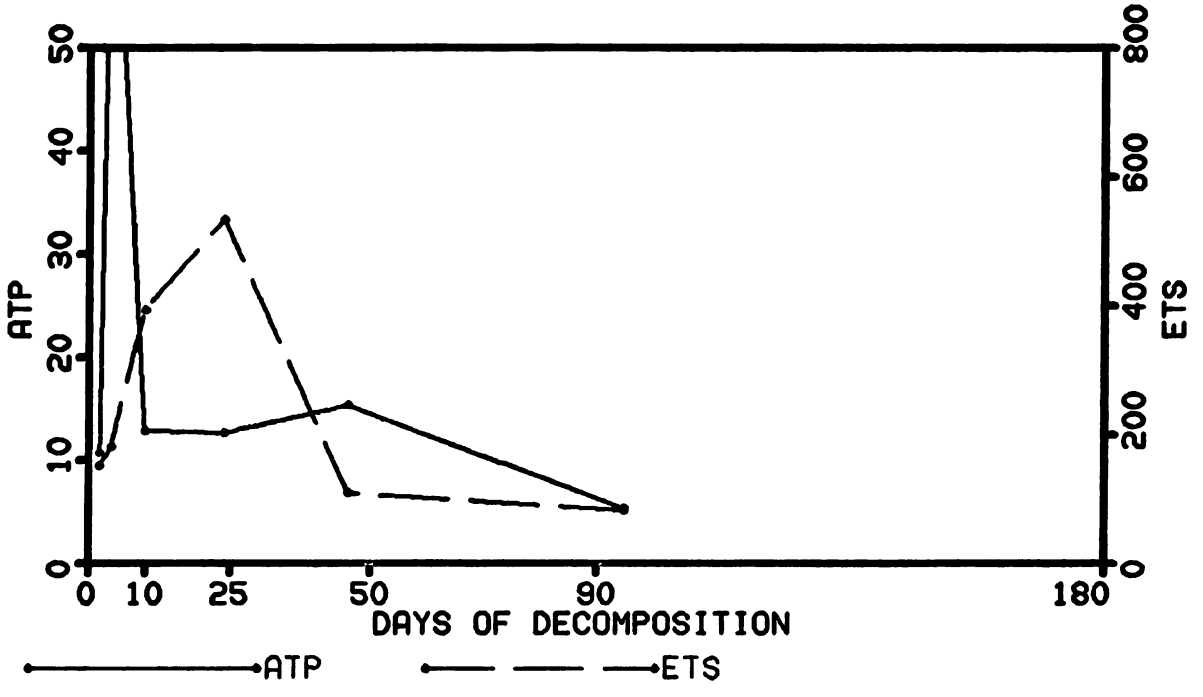
Appendix Figure 247. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



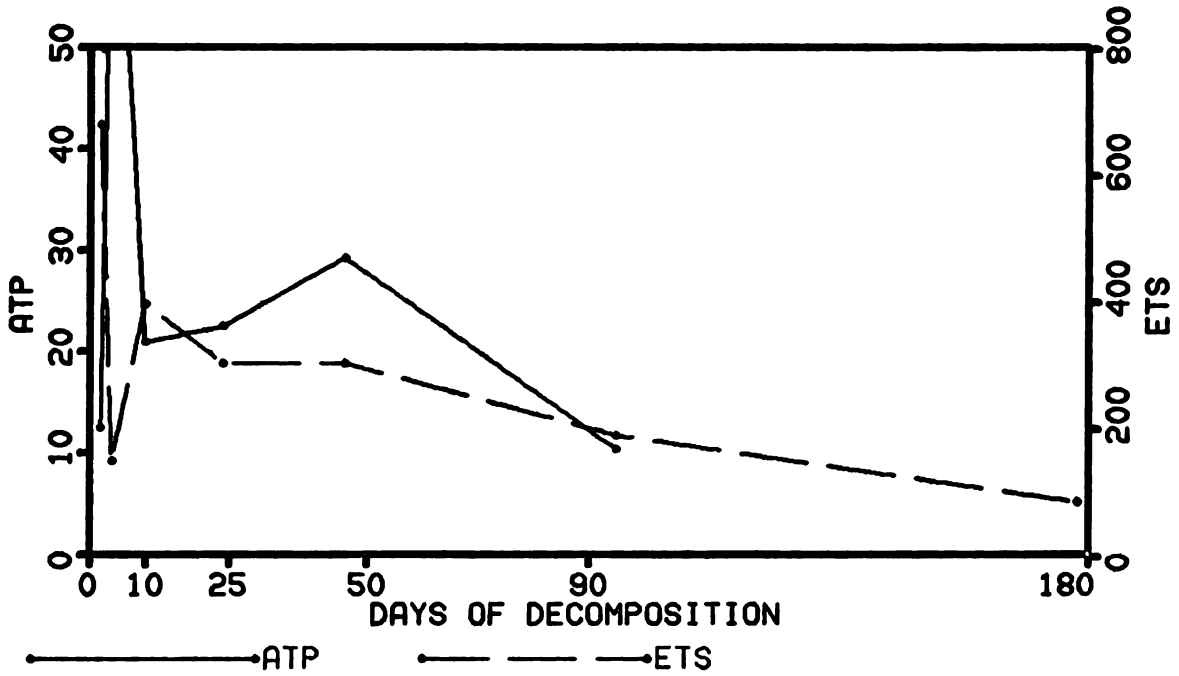
Appendix Figure 248. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



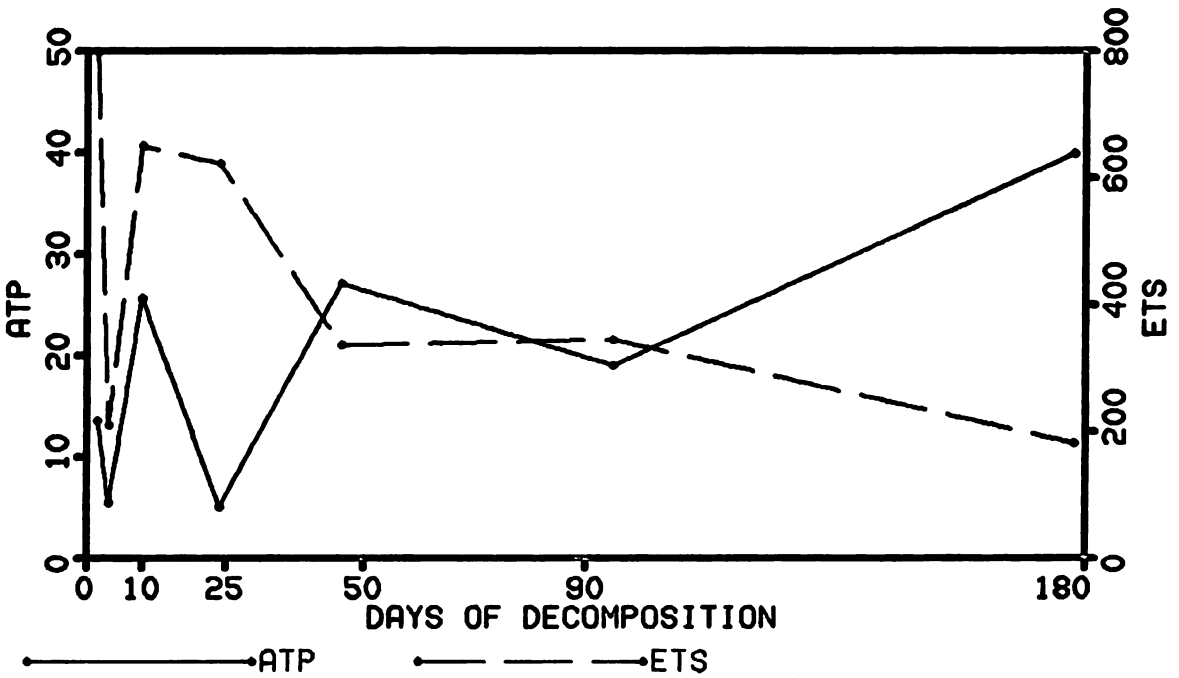
Appendix Figure 249. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



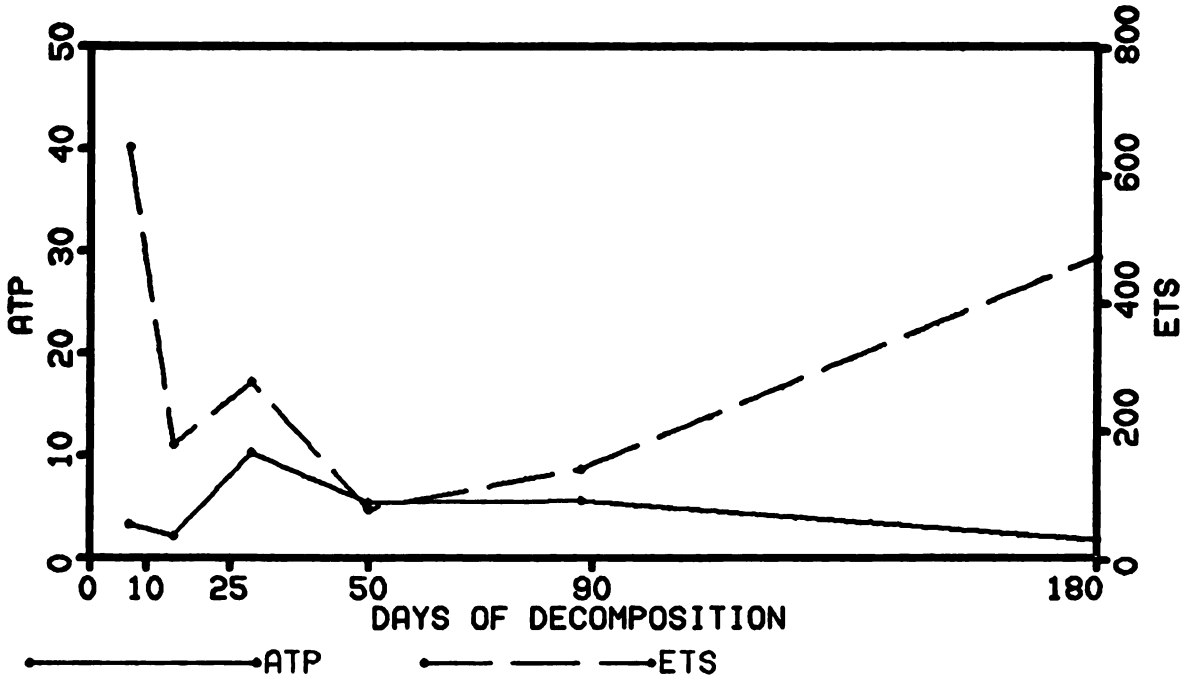
Appendix Figure 250. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



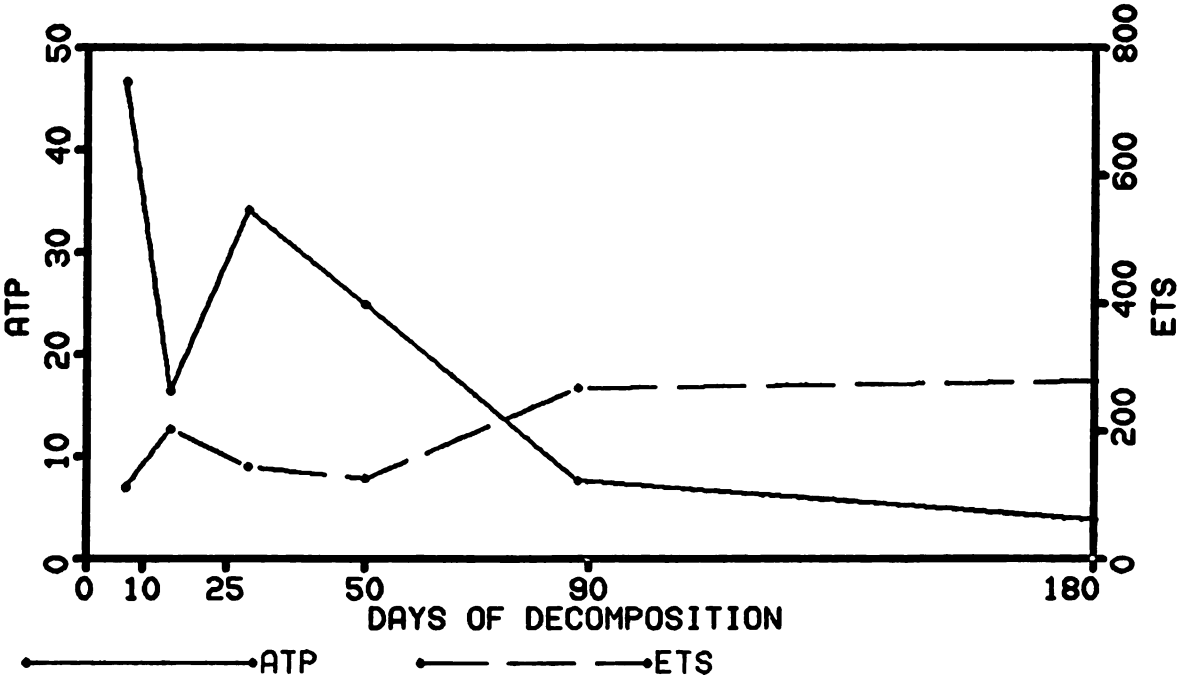
Appendix Figure 251. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



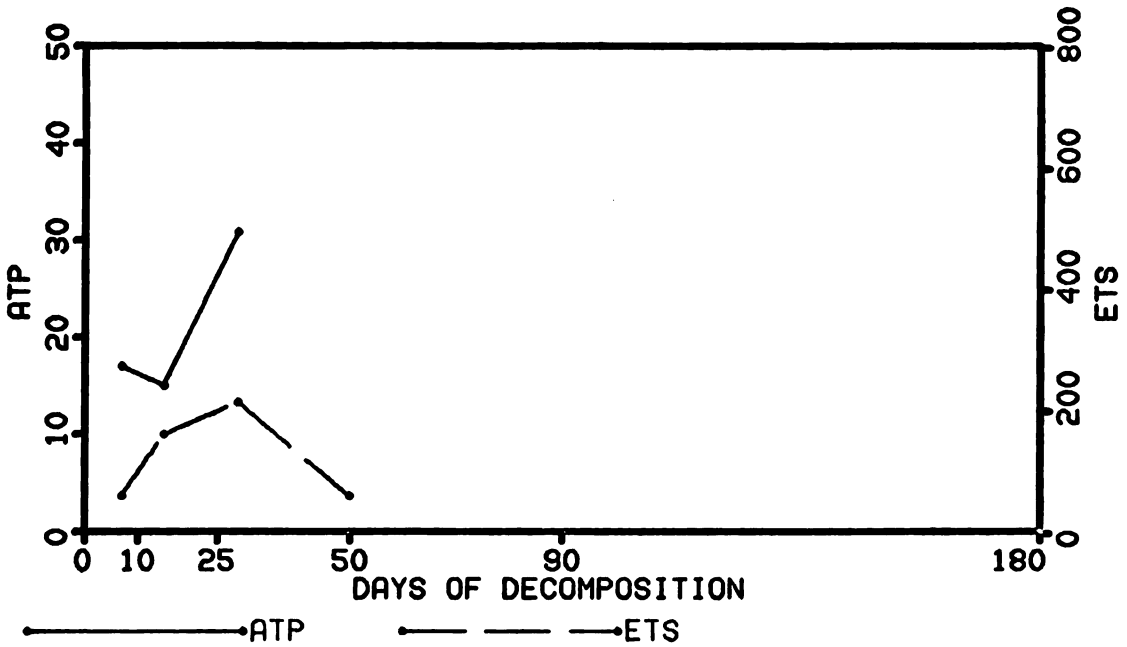
Appendix Figure 252. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



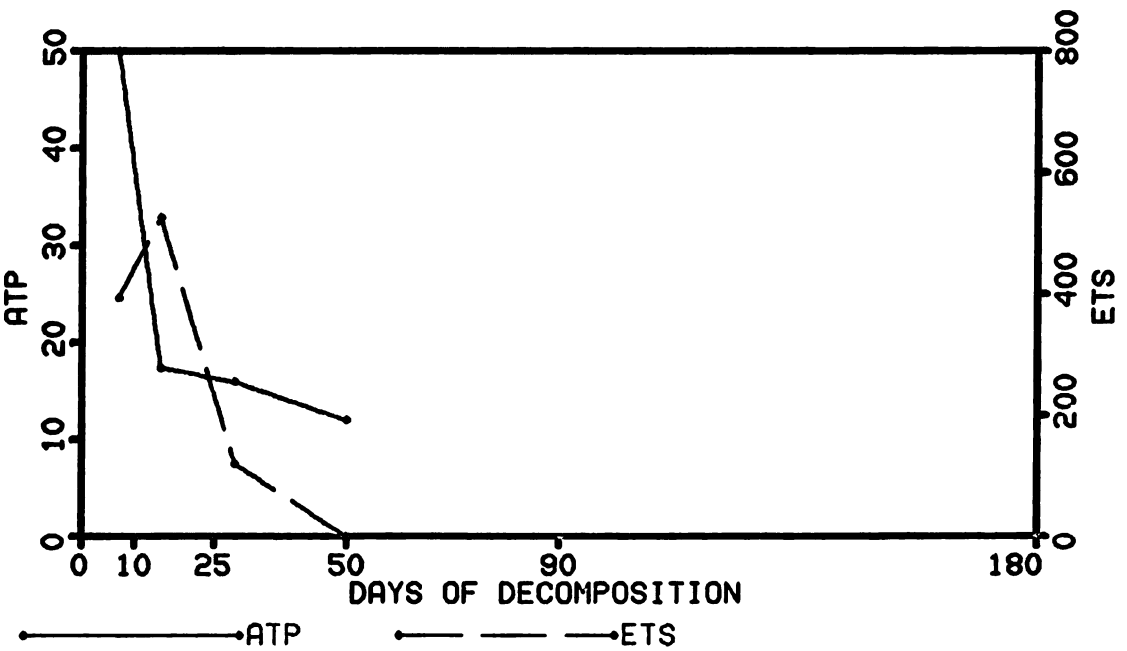
Appendix Figure 253. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during spring and summer. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



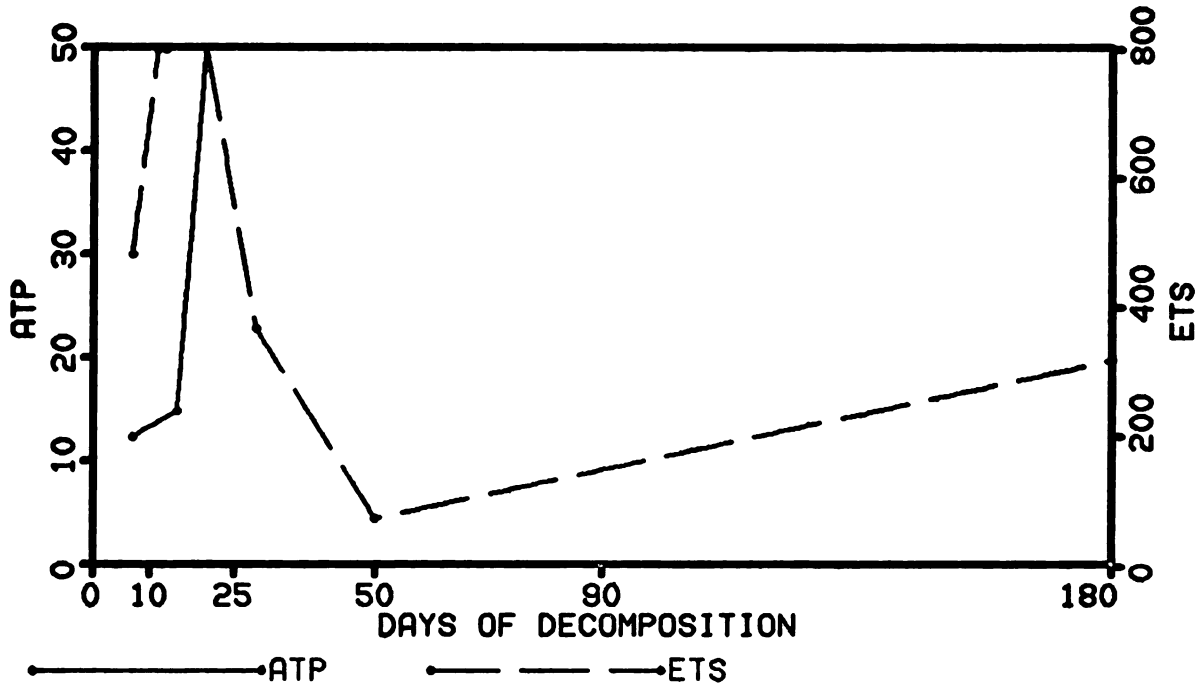
Appendix Figure 254. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during spring and summer. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



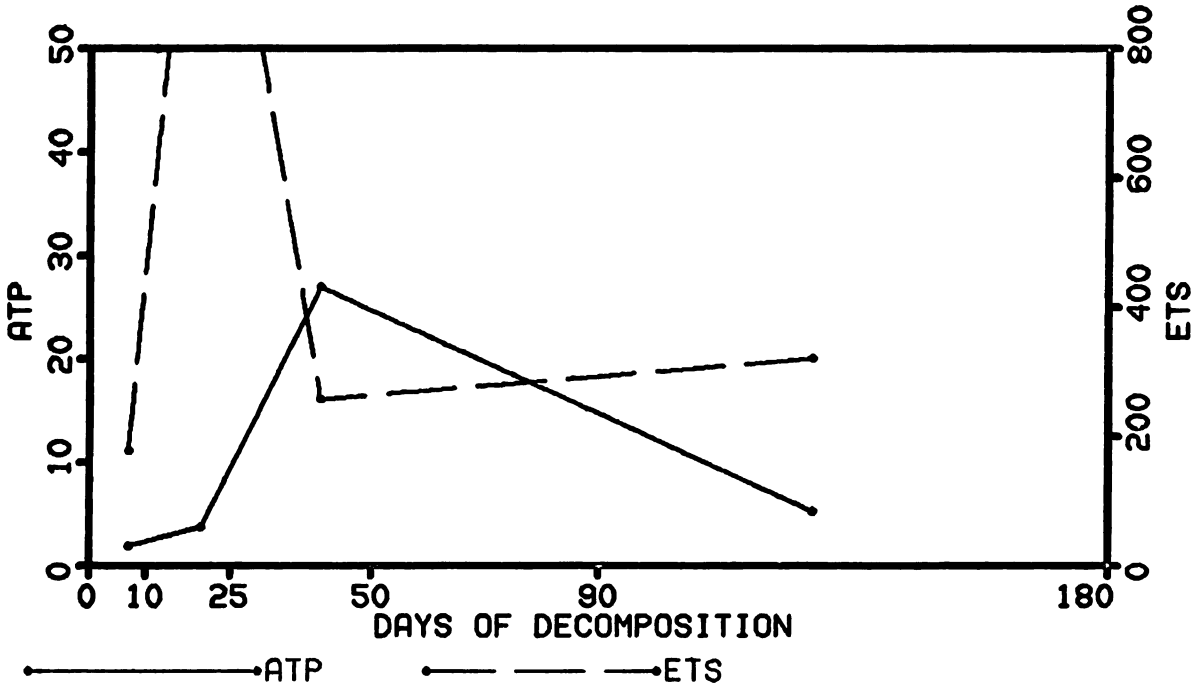
Appendix Figure 255. Decay of *Najas flexilis* in Lawrence Lake littoral zone during spring and summer. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



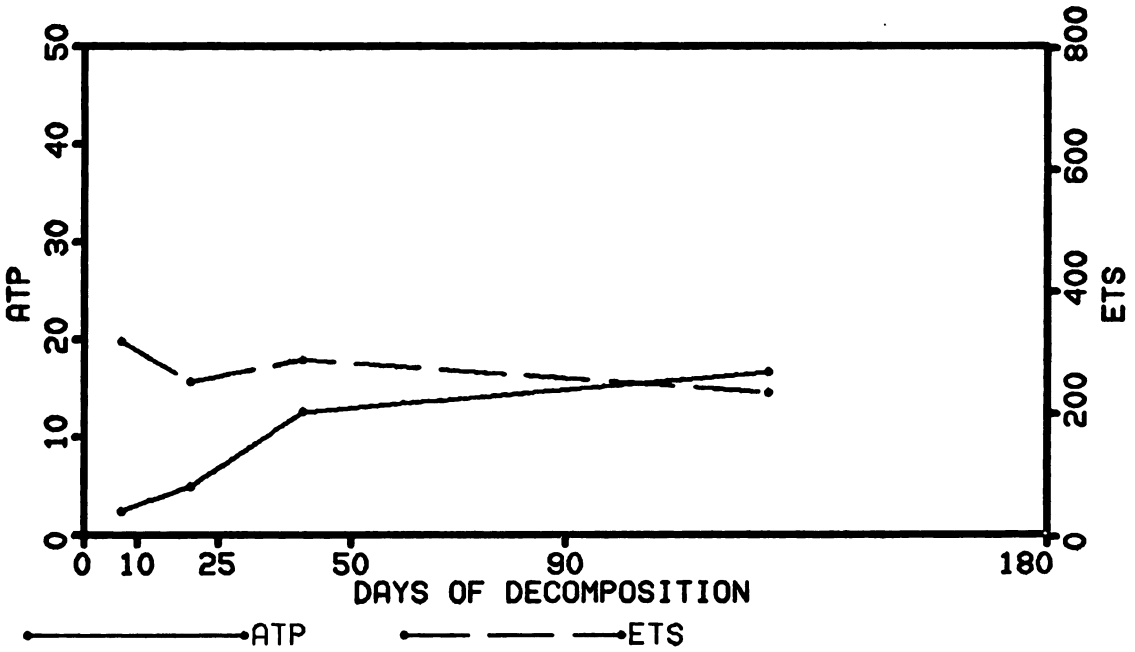
Appendix Figure 256. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during spring and summer. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



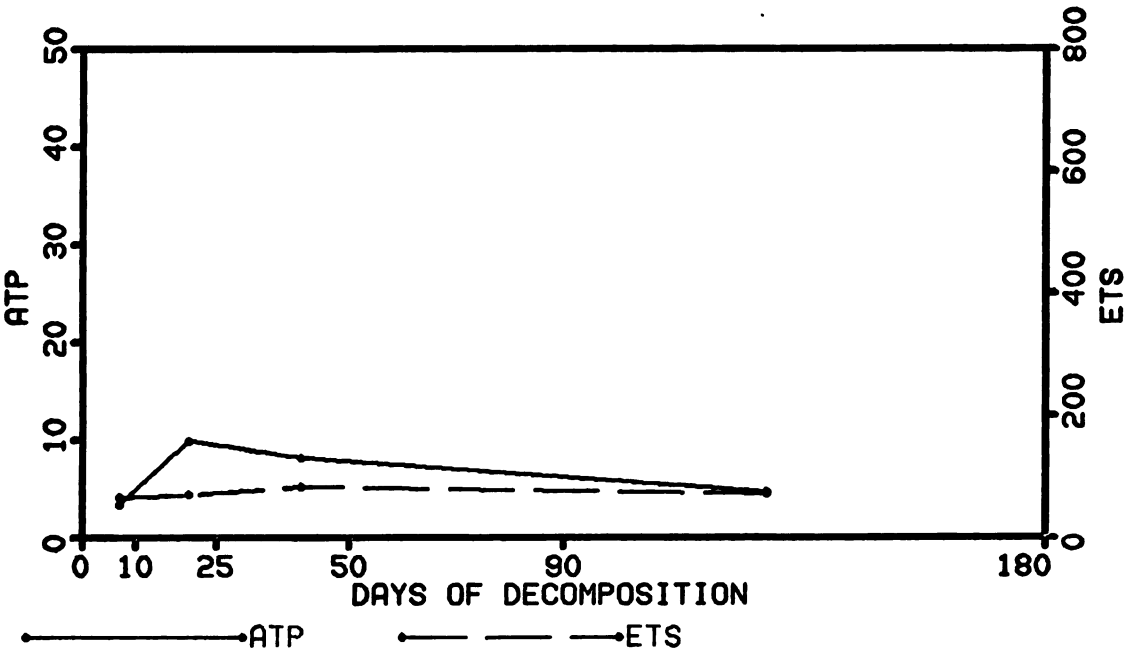
Appendix Figure 257. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during spring and summer. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



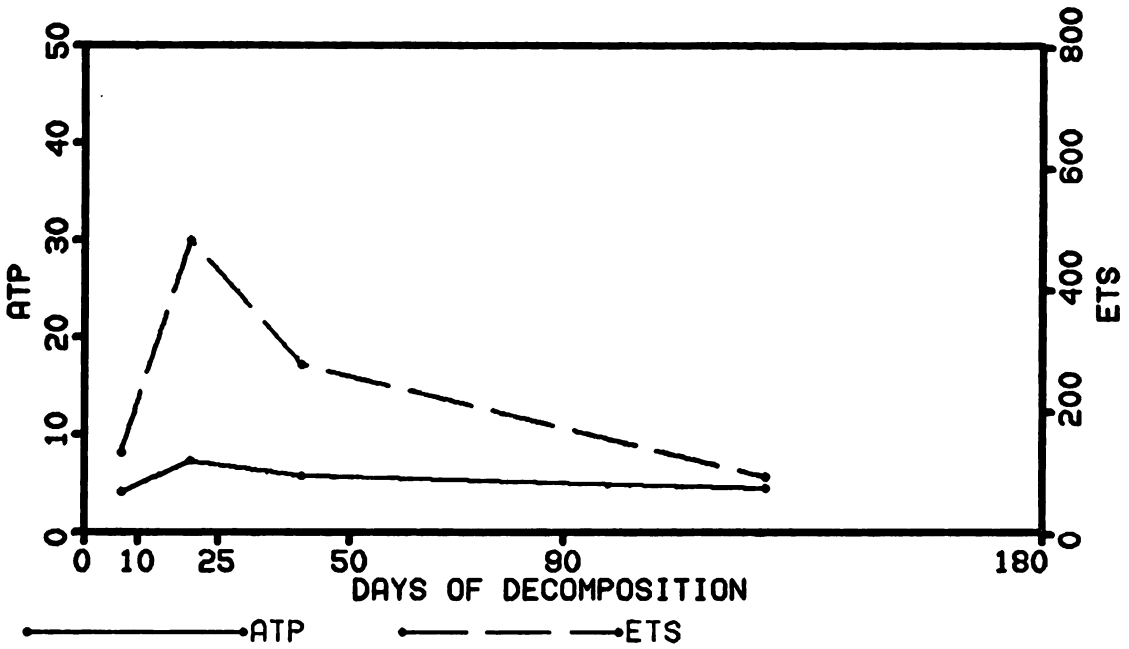
Appendix Figure 258. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



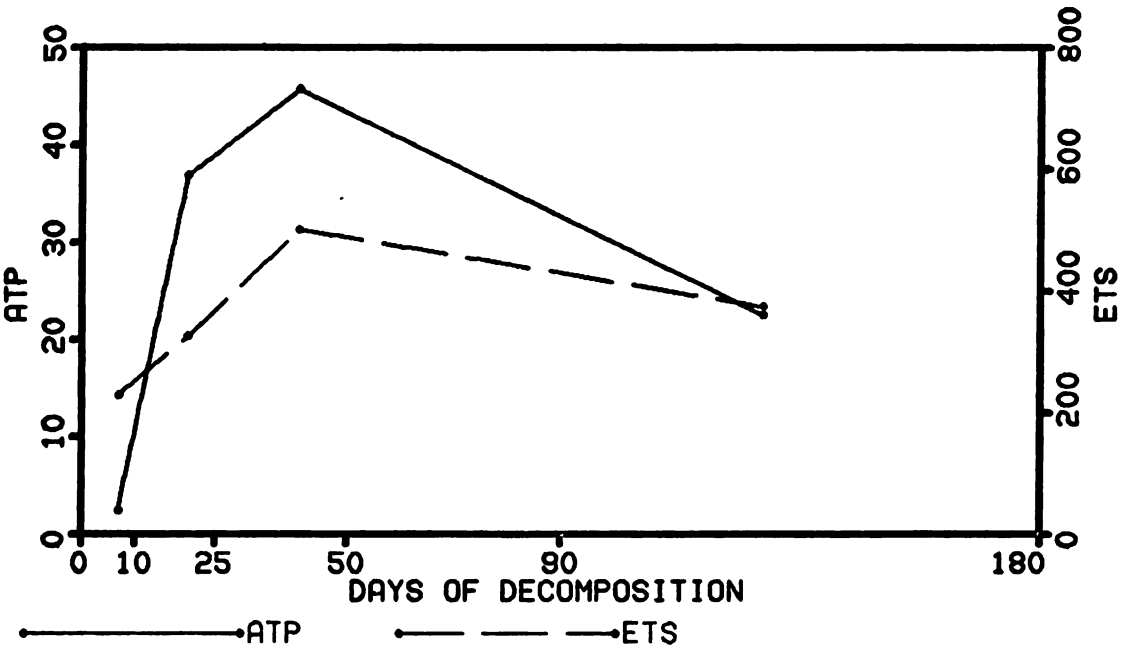
Appendix Figure 259. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



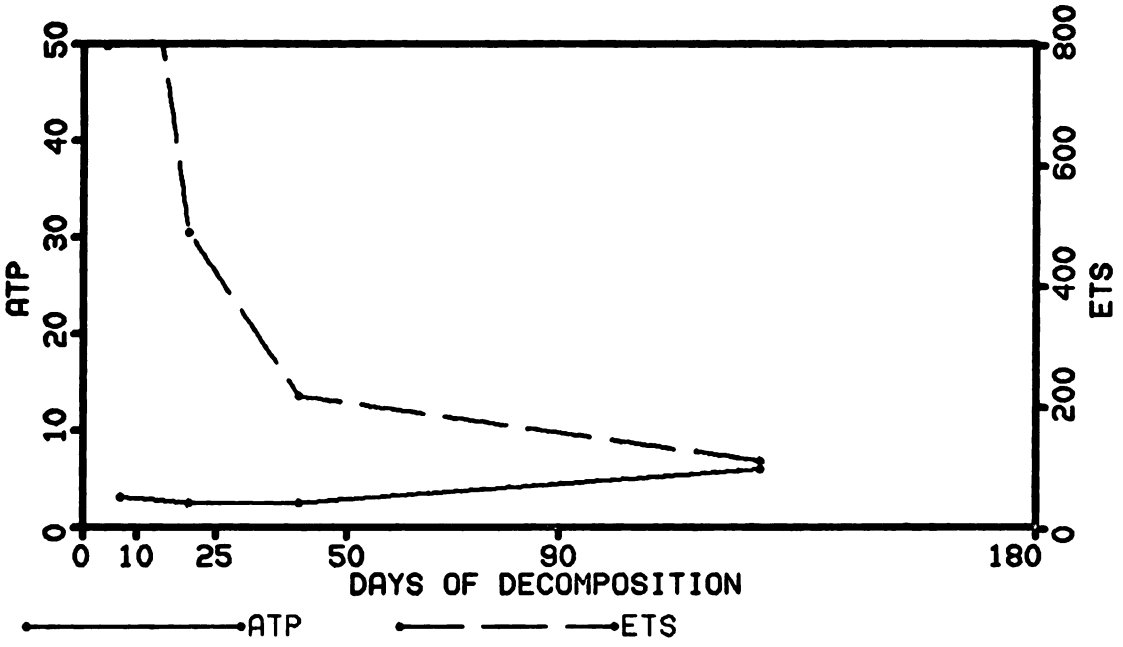
Appendix Figure 260. Decay of *Najas flexilis* in Lawrence Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



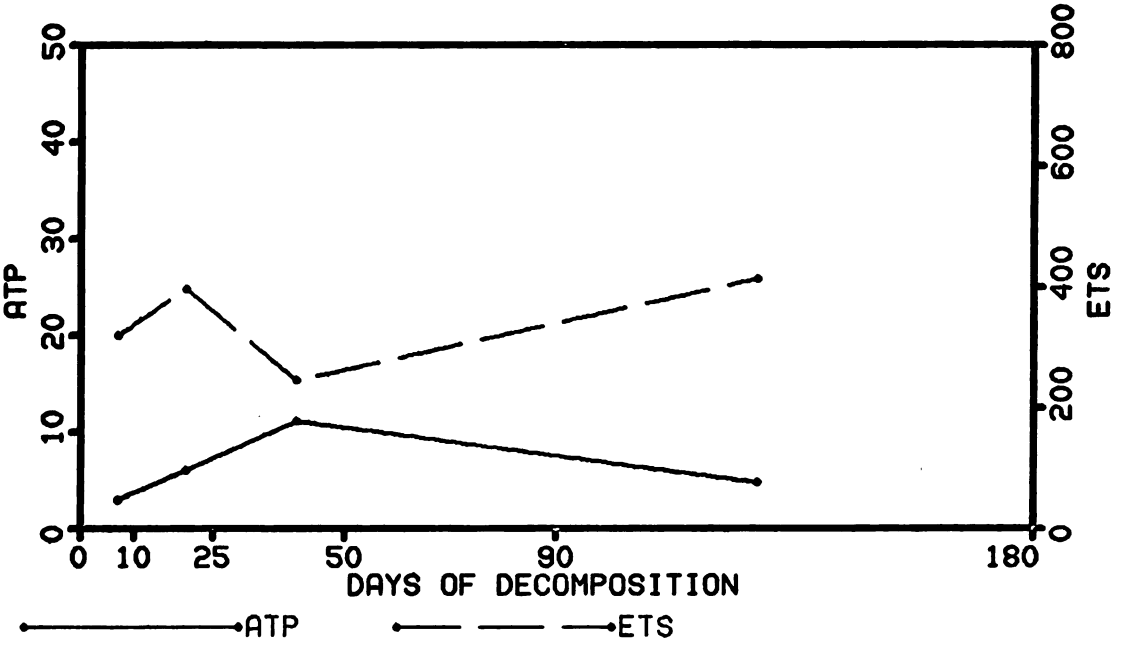
Appendix Figure 261. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



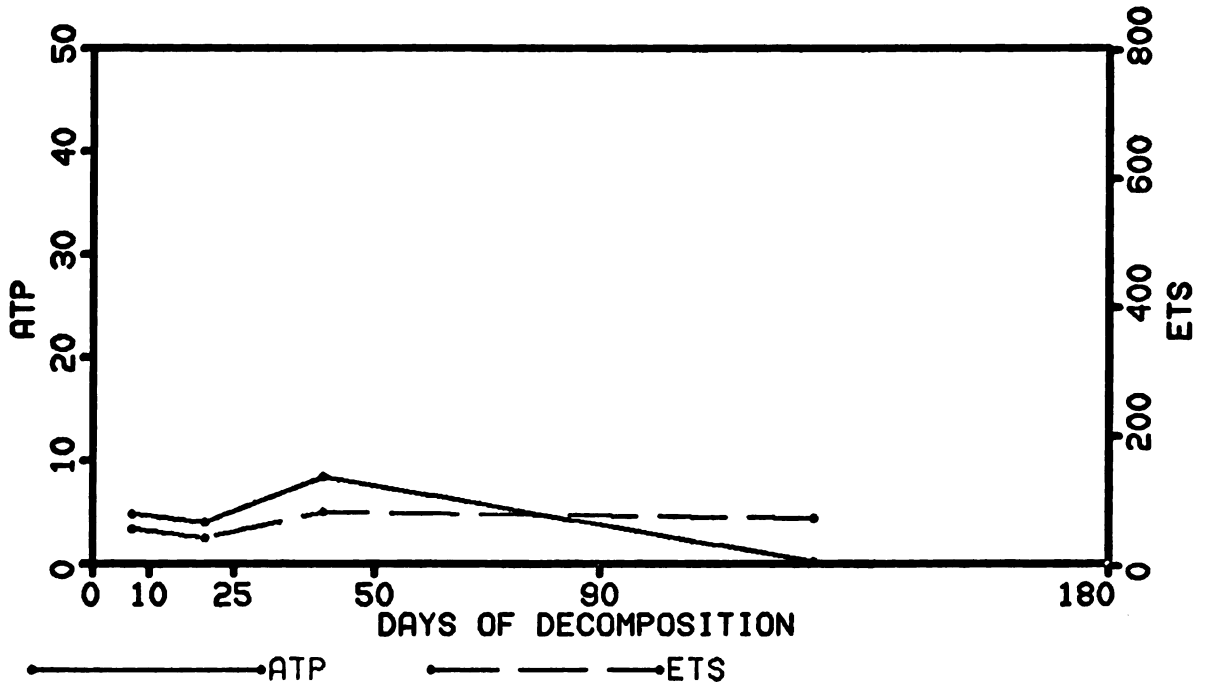
Appendix Figure 262. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



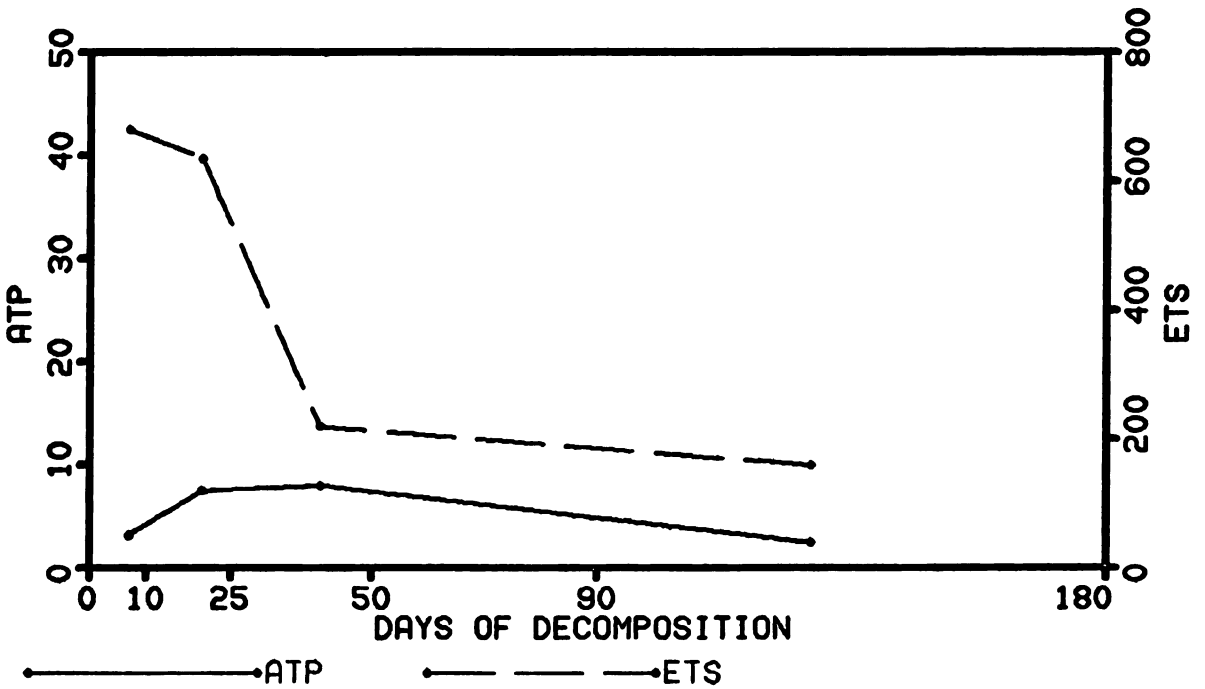
Appendix Figure 263. Decay of *Scirpus acutus* in Lawrence Lake pelagial zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



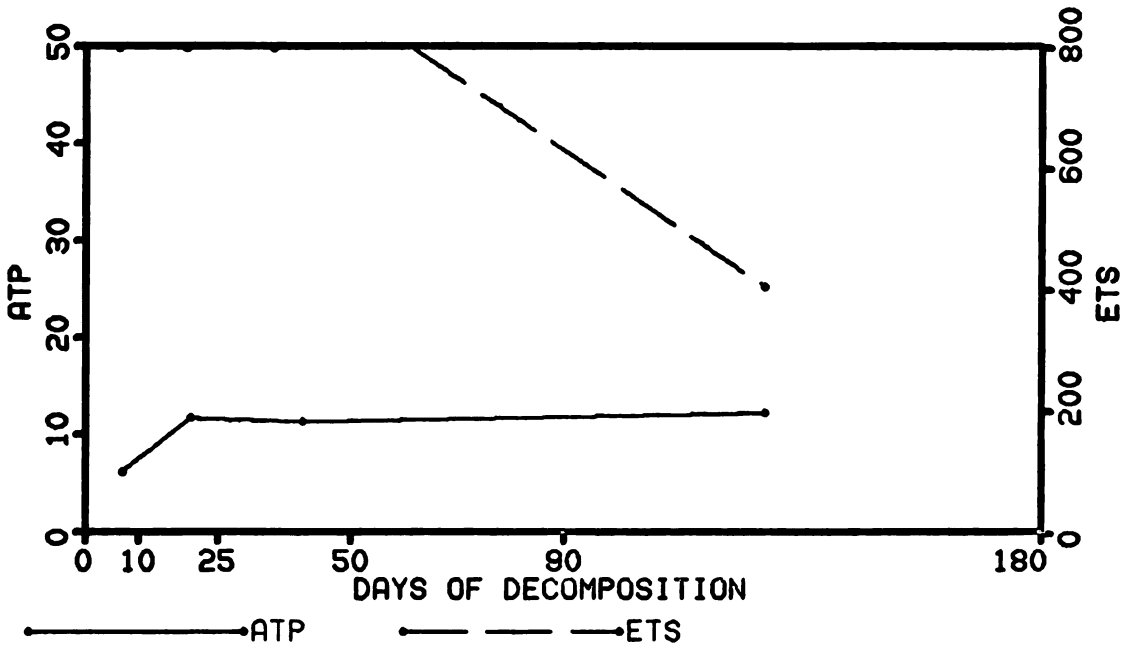
Appendix Figure 264. Decay of *Scirpus subterminalis* in Lawrence Lake pelagial zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



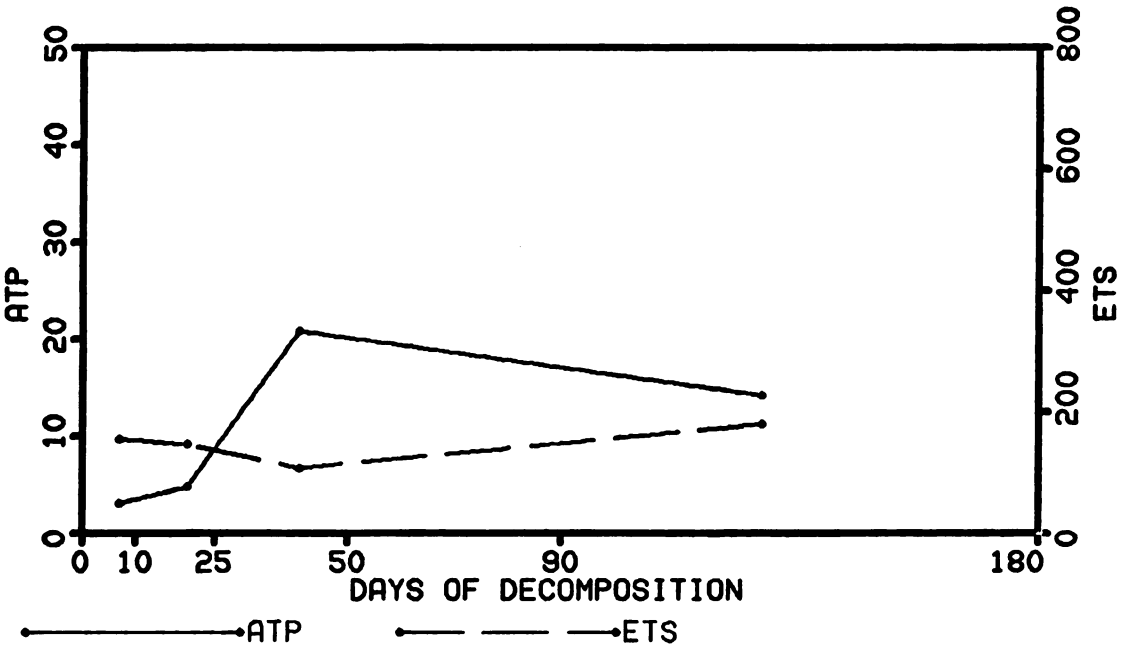
Appendix Figure 265. Decay of *Najas flexilis* in Lawrence Lake pelagial zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



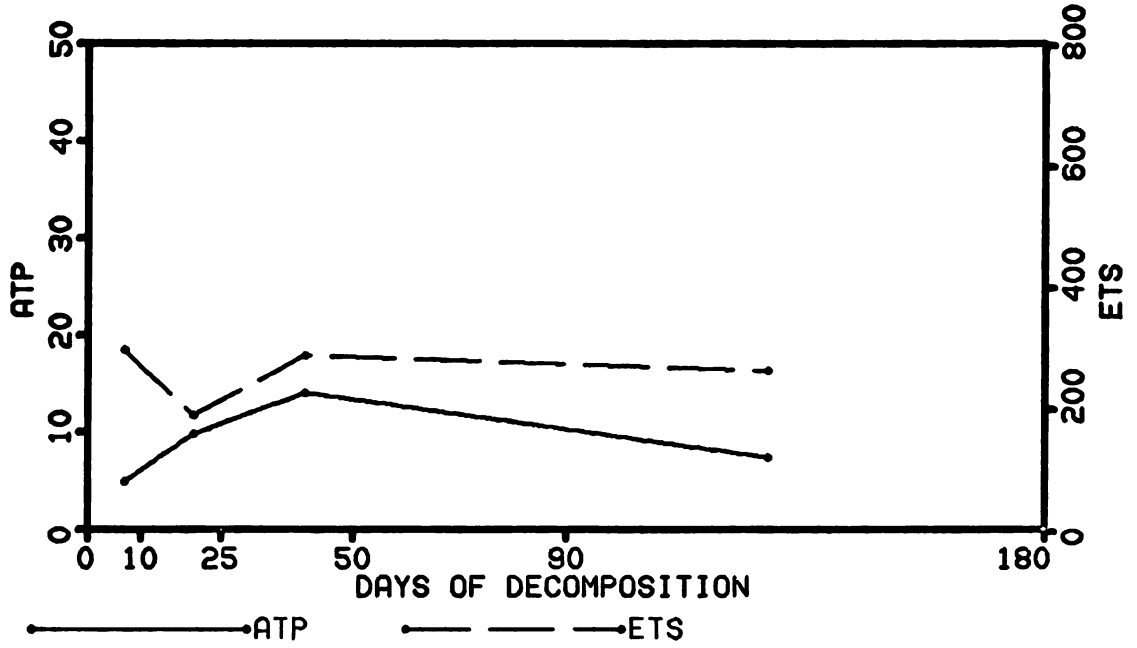
Appendix Figure 266. Decay of *Myriophyllum heterophyllum* in Lawrence Lake pelagial zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



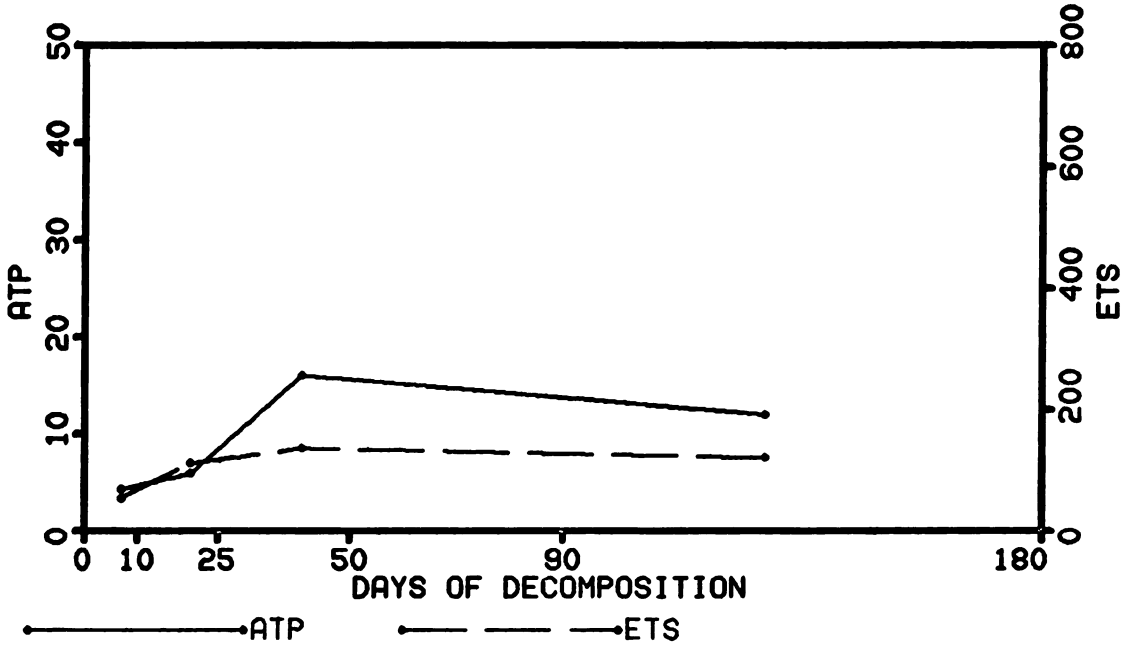
Appendix Figure 267. Decay of *Nuphar variegatum* in Lawrence Lake pelagial zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



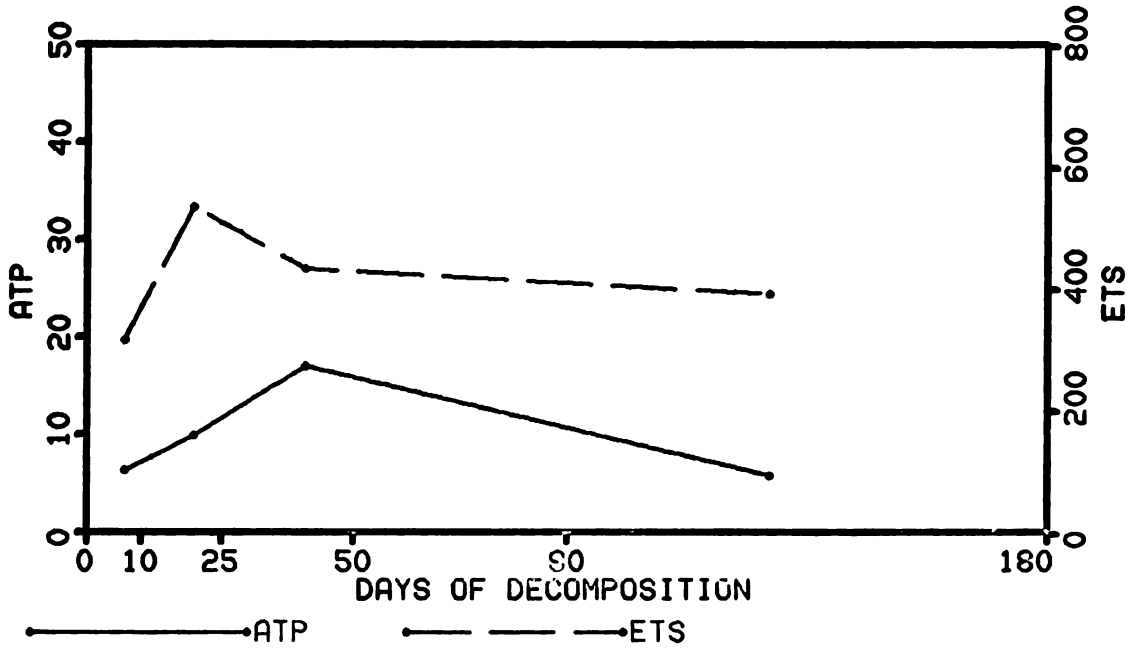
Appendix Figure 268. Decay of *Scirpus acutus* in Wintergreen Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



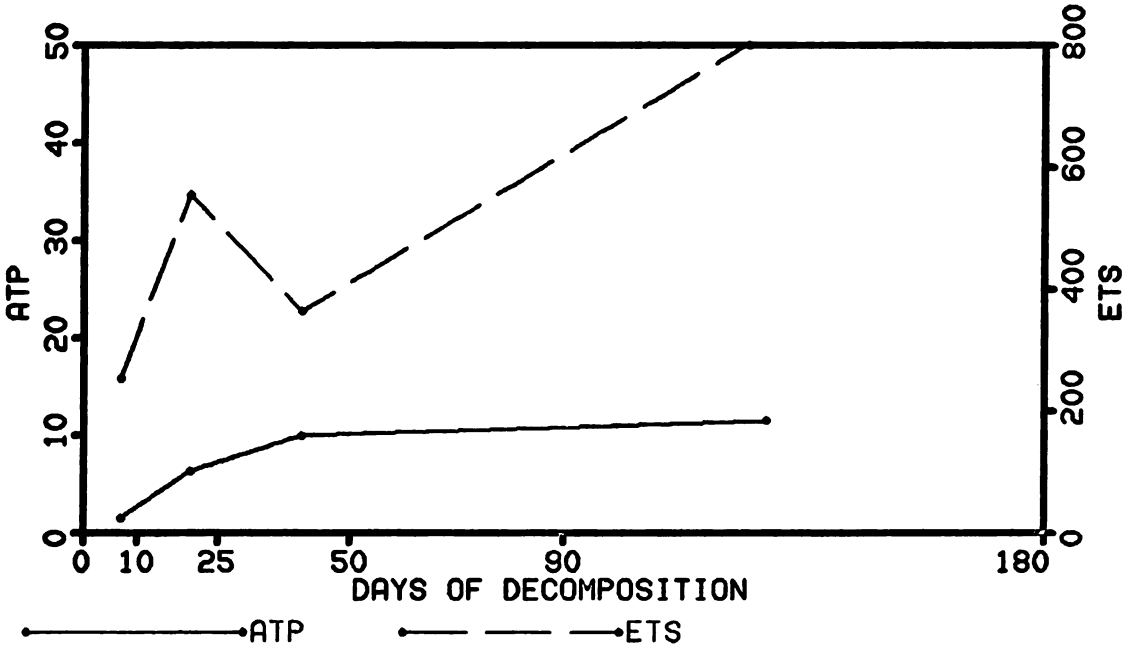
Appendix Figure 269. Decay of *Scirpus subterminalis* in Wintergreen Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



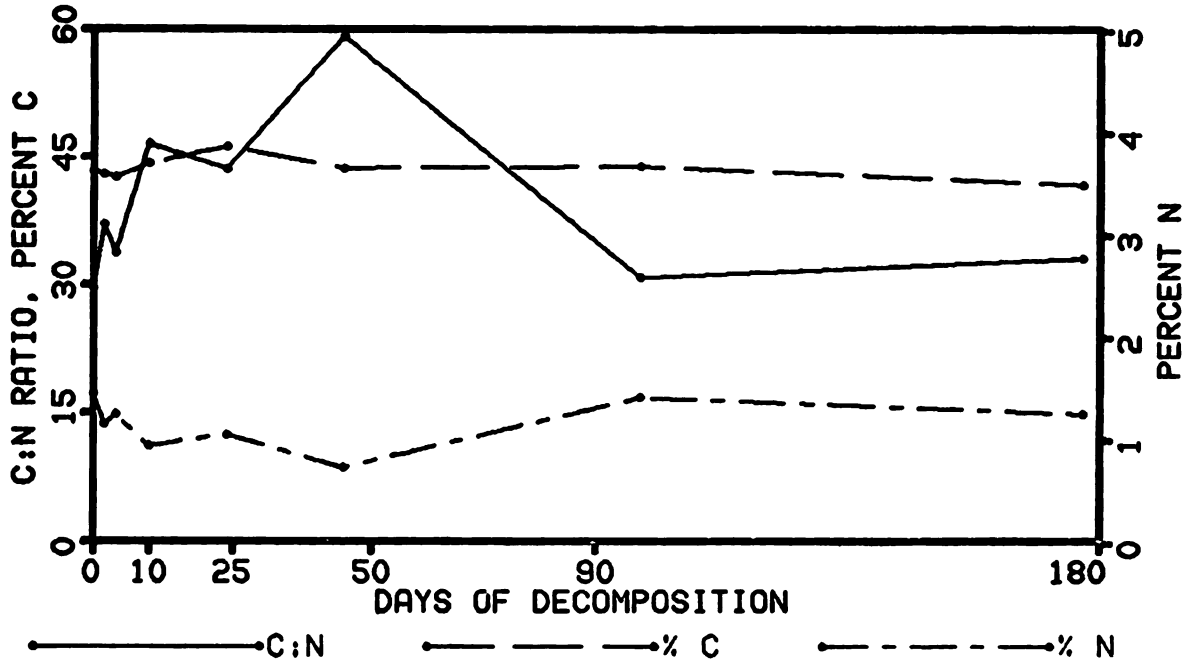
Appendix Figure 270. Decay of *Najas flexilis* in Wintergreen Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



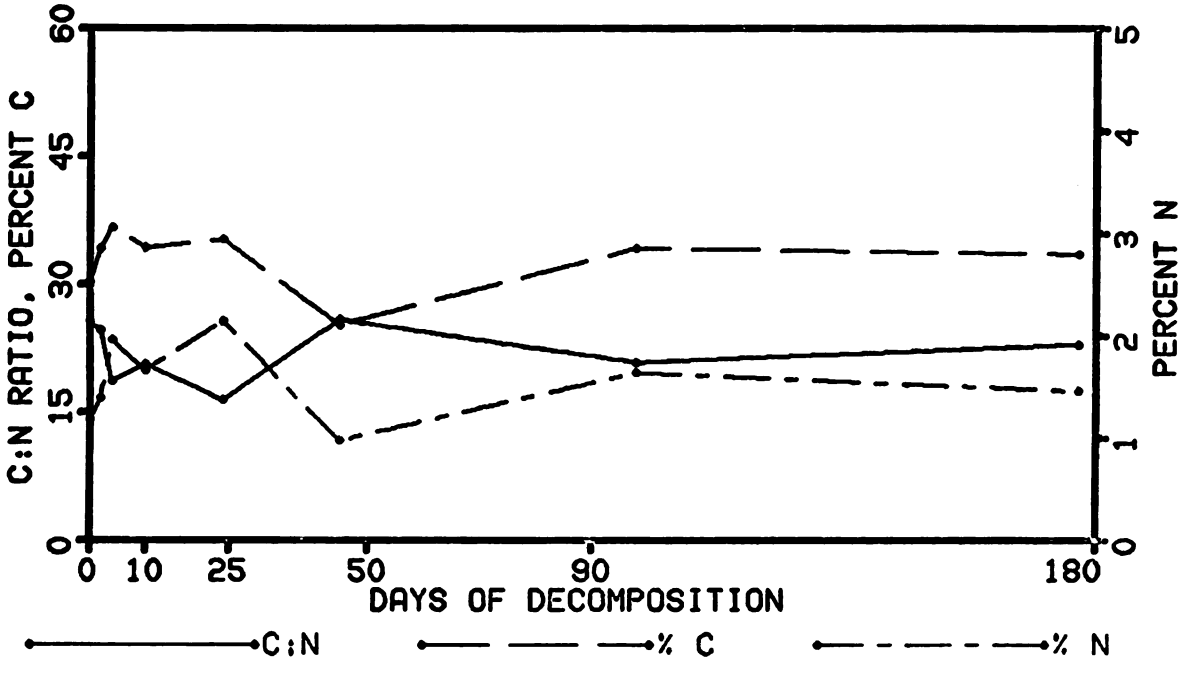
Appendix Figure 271. Decay of *Myriophyllum heterophyllum* in Wintergreen Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



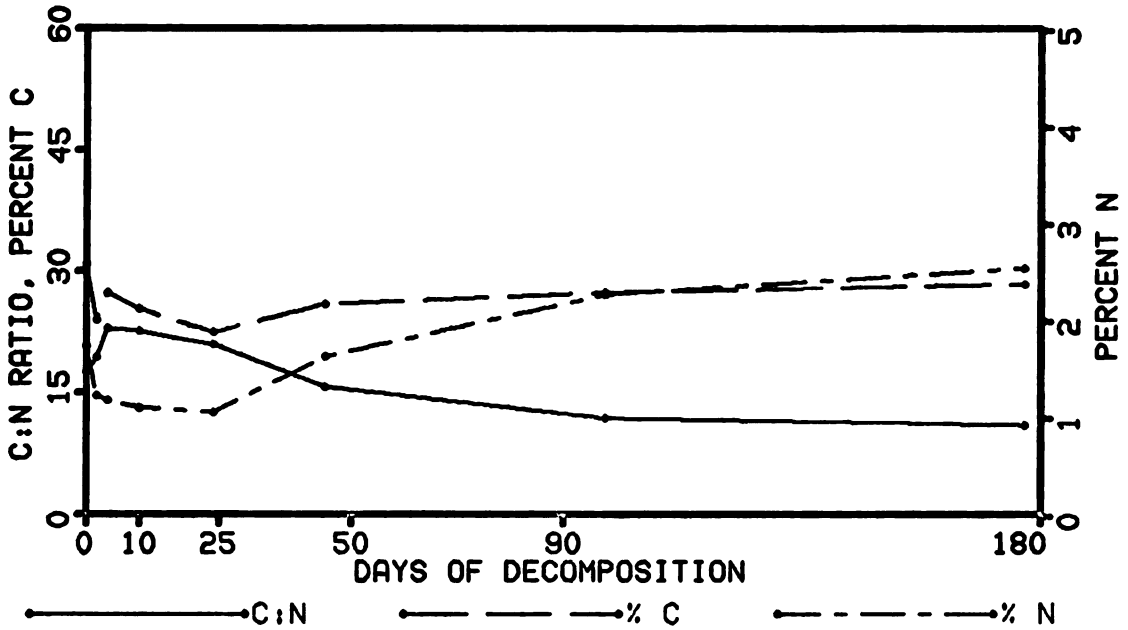
Appendix Figure 272. Decay of *Nuphar variegatum* in Wintergreen Lake littoral zone during fall and winter. ATP content (µg ATP) and ETS activity (relative absorbance units) per g ash-free dry weight of plant tissue.



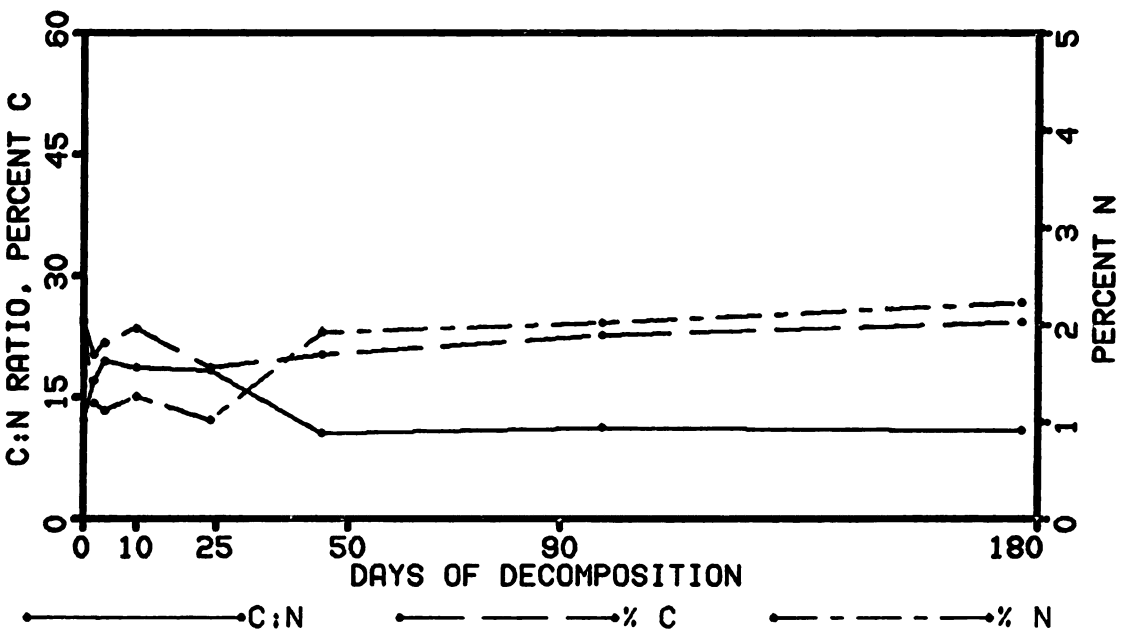
Appendix Figure 273. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



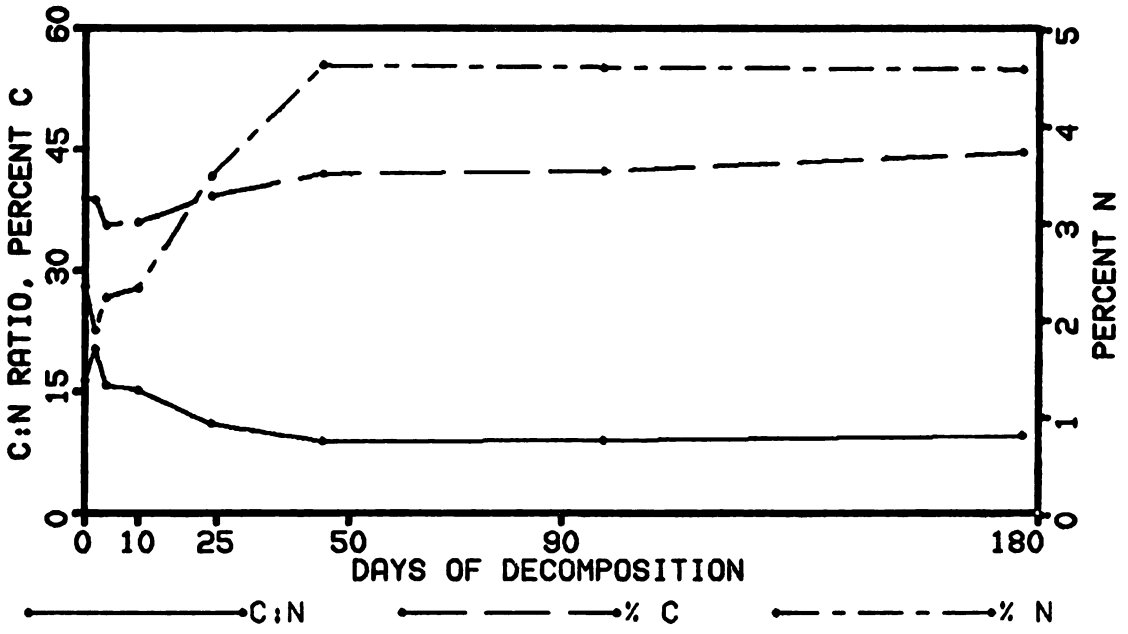
Appendix Figure 274. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



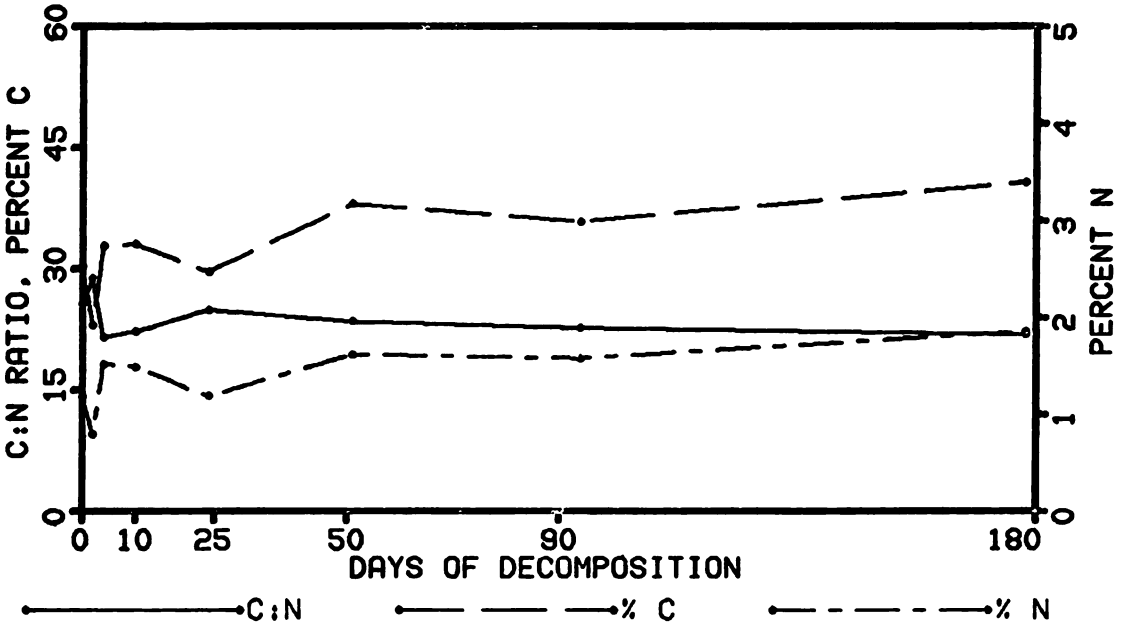
Appendix Figure 275. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



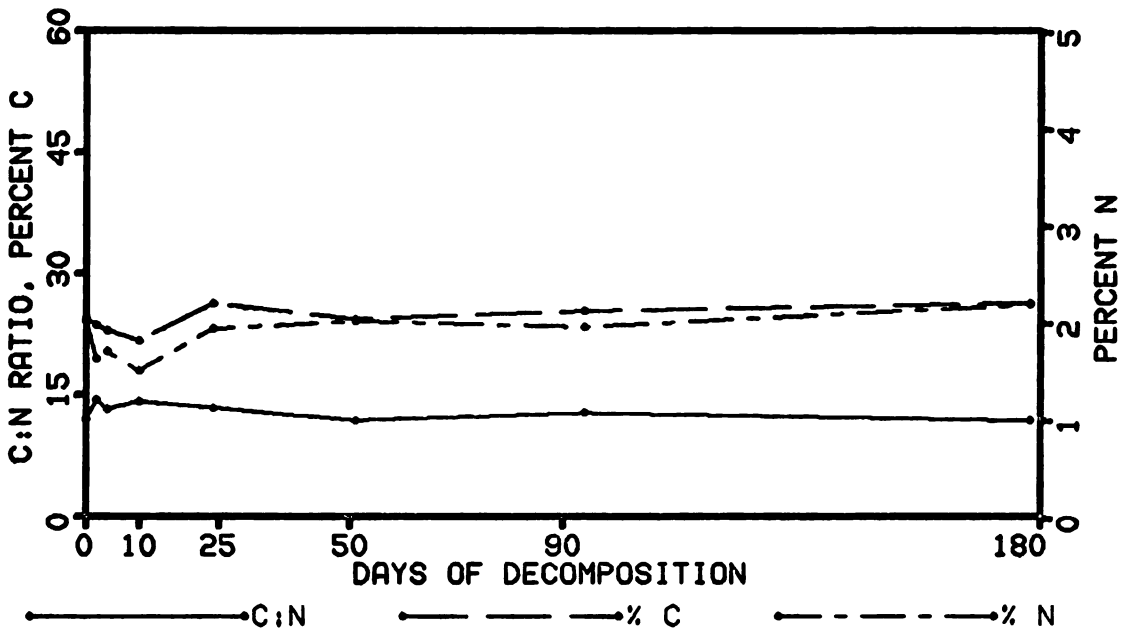
Appendix Figure 276. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



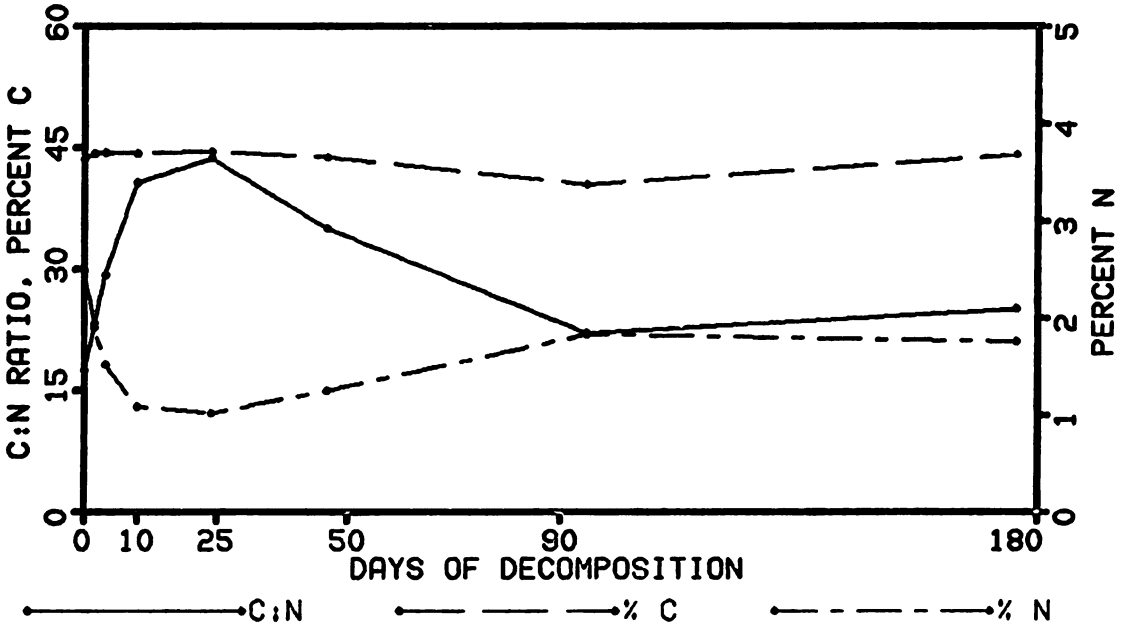
Appendix Figure 277. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



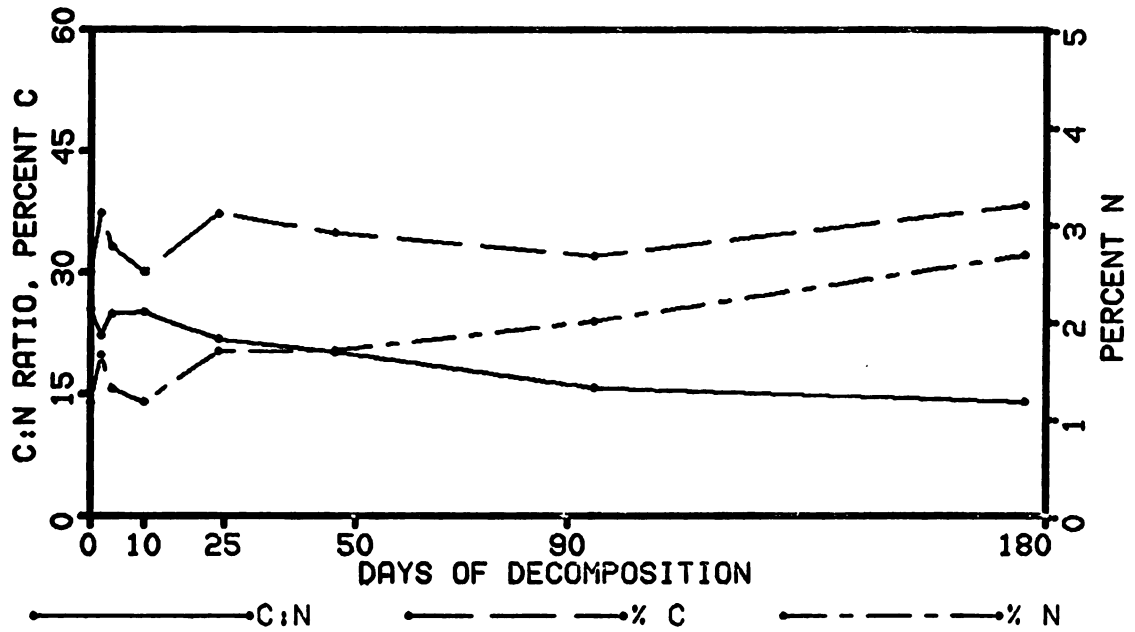
Appendix Figure 278. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



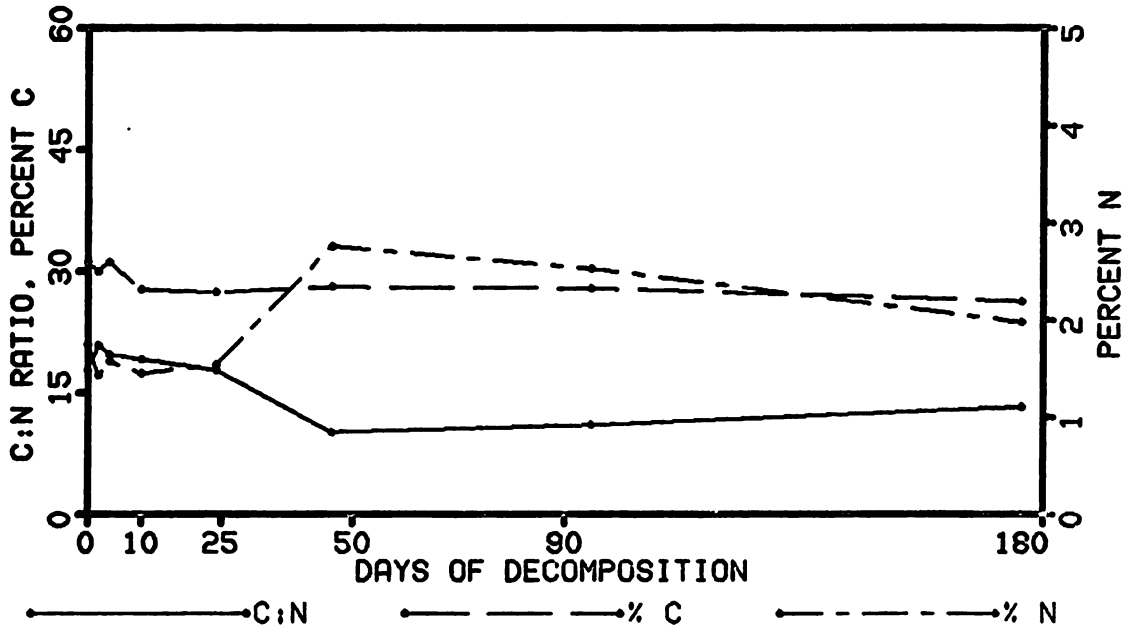
Appendix Figure 279. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



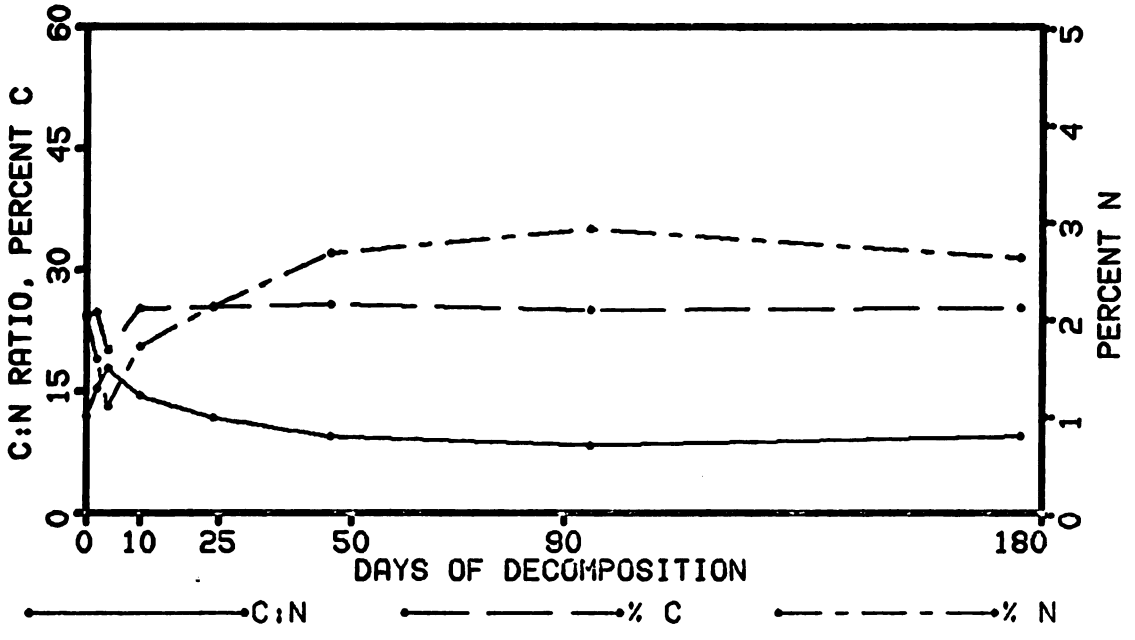
Appendix Figure 280. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



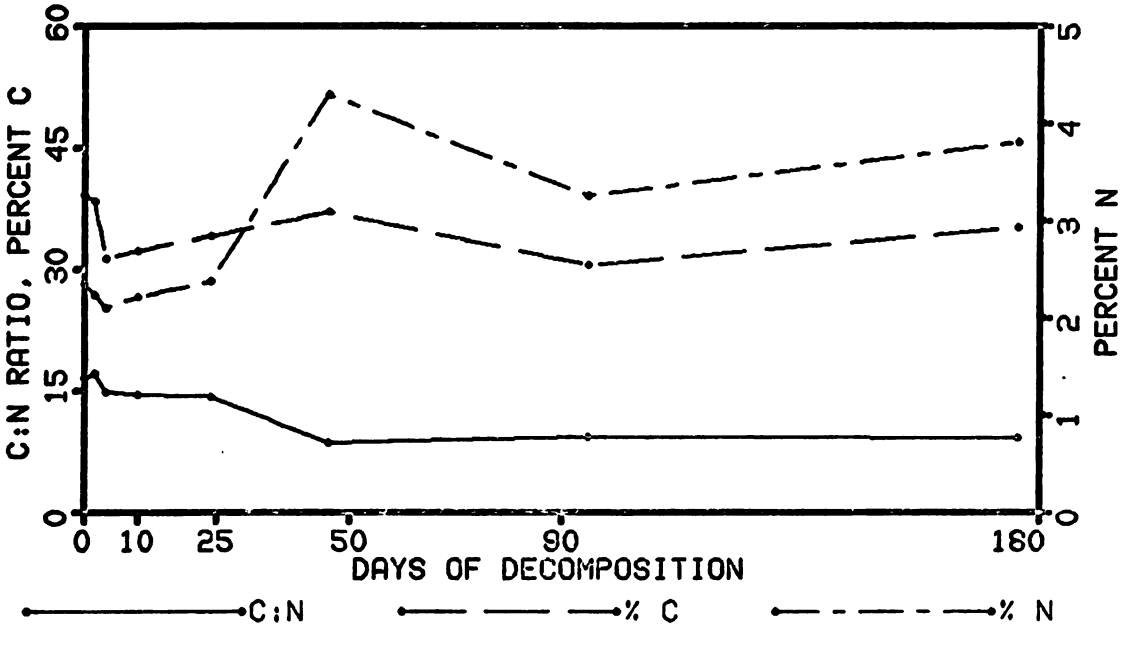
Appendix Figure 281. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



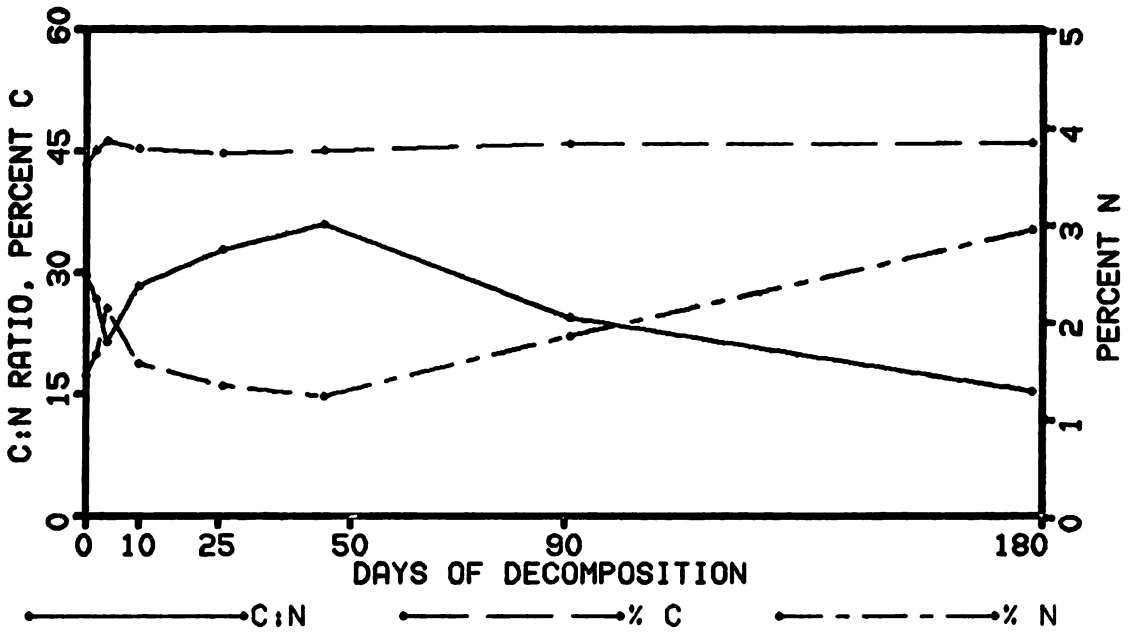
Appendix Figure 282. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



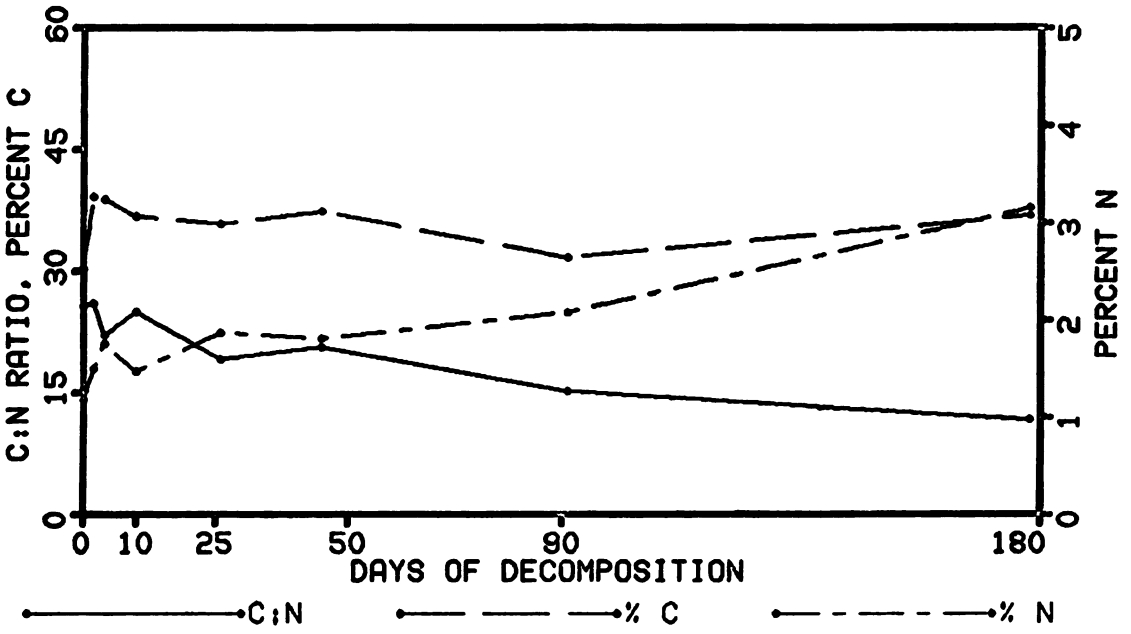
Appendix Figure 283. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



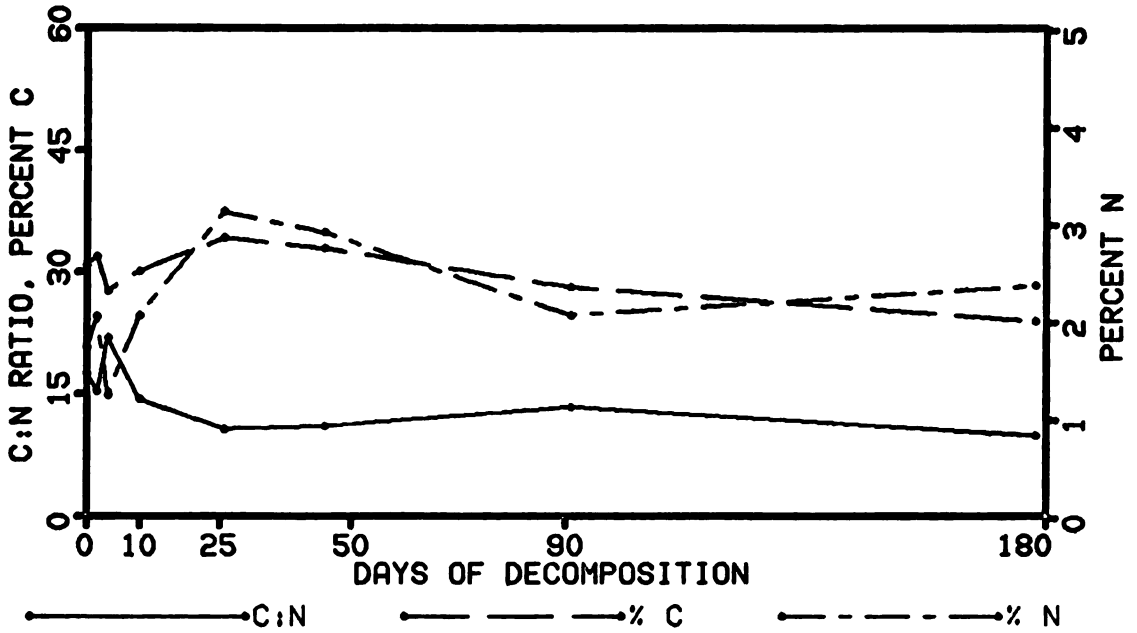
Appendix Figure 284. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



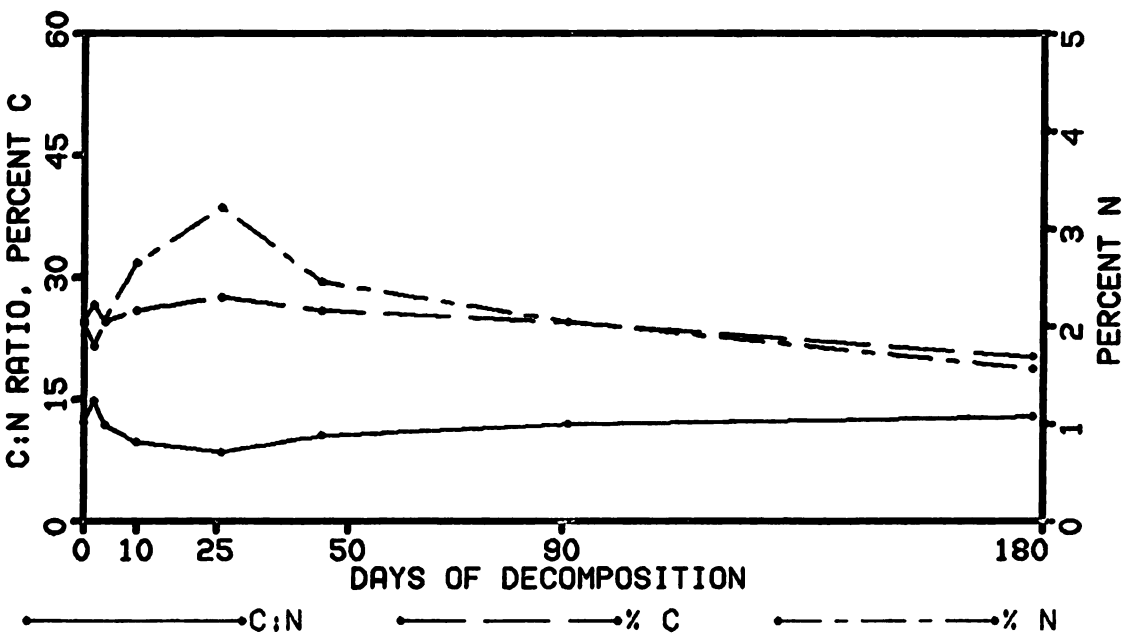
Appendix Figure 285. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



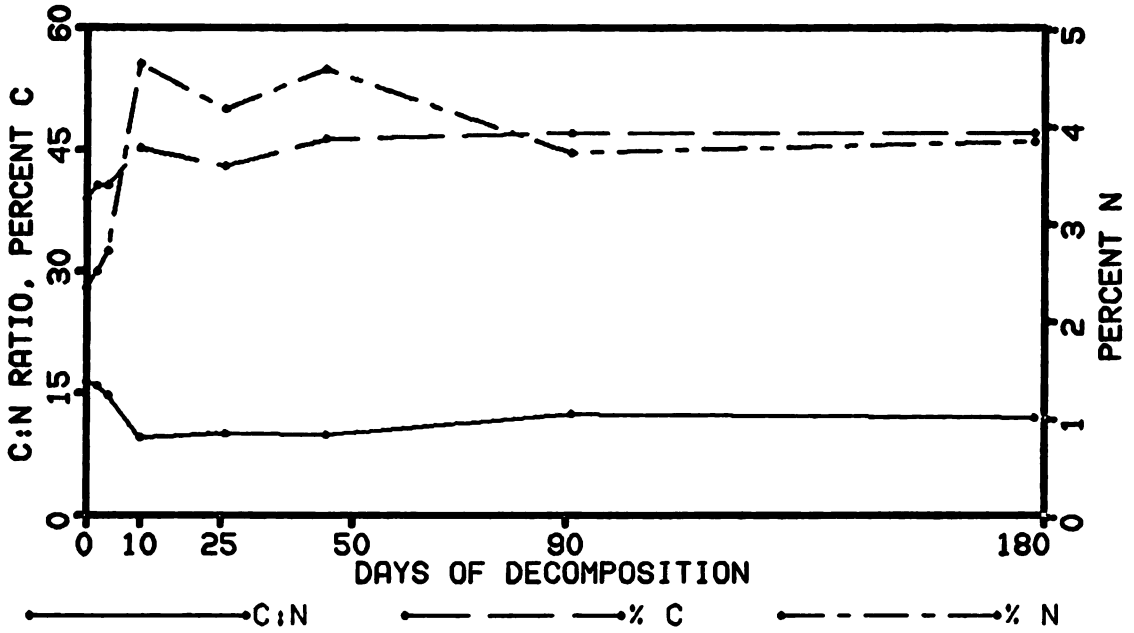
Appendix Figure 286. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



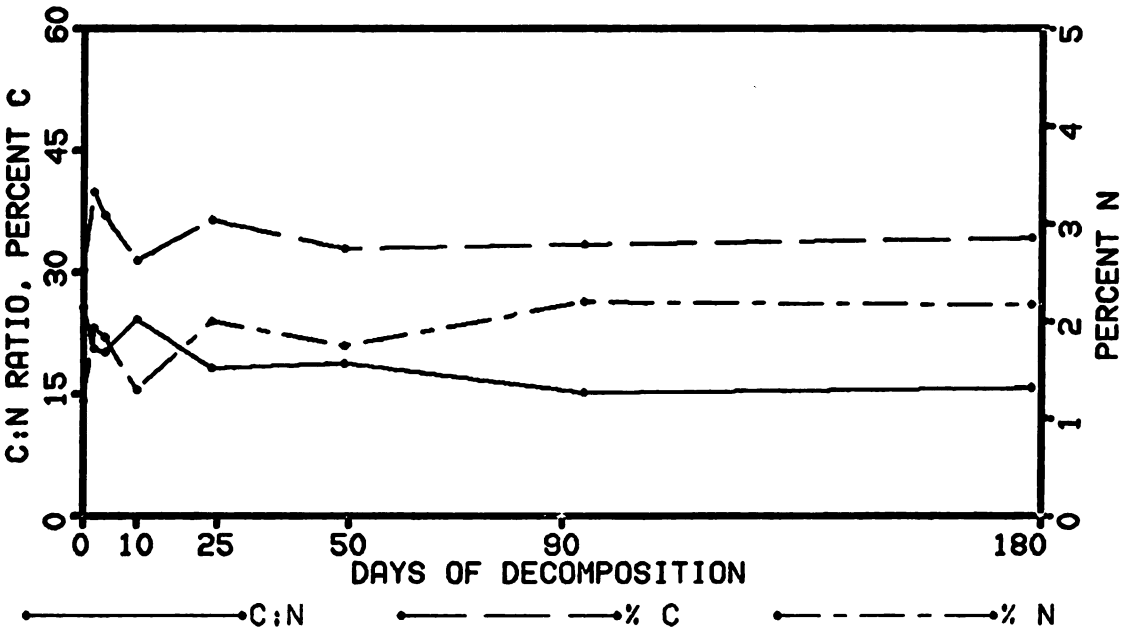
Appendix Figure 287. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



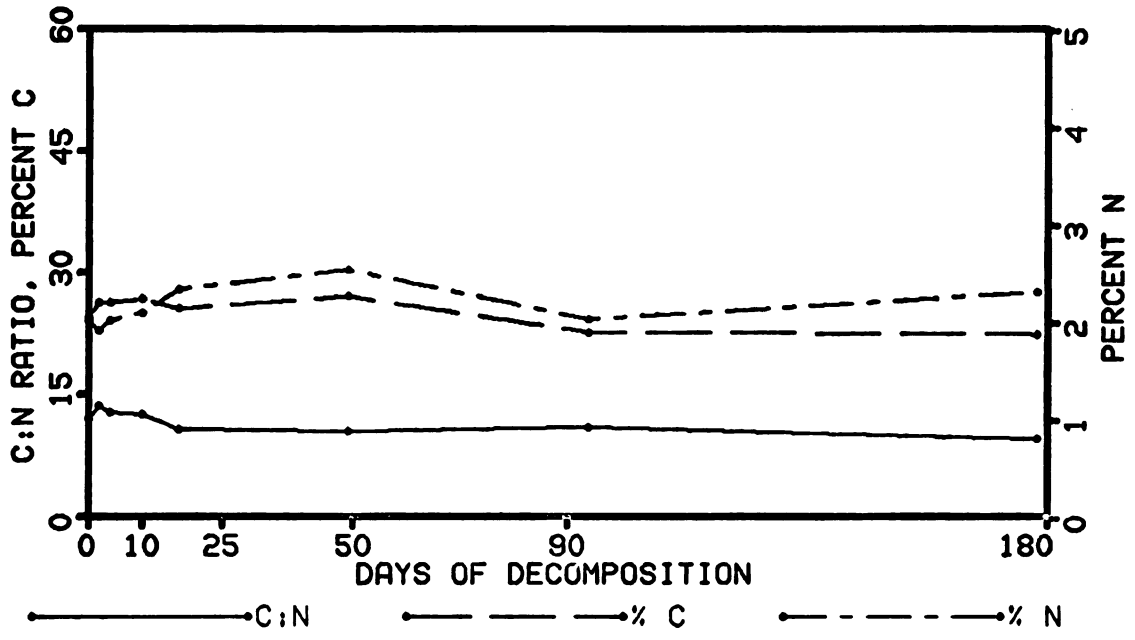
Appendix Figure 288. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



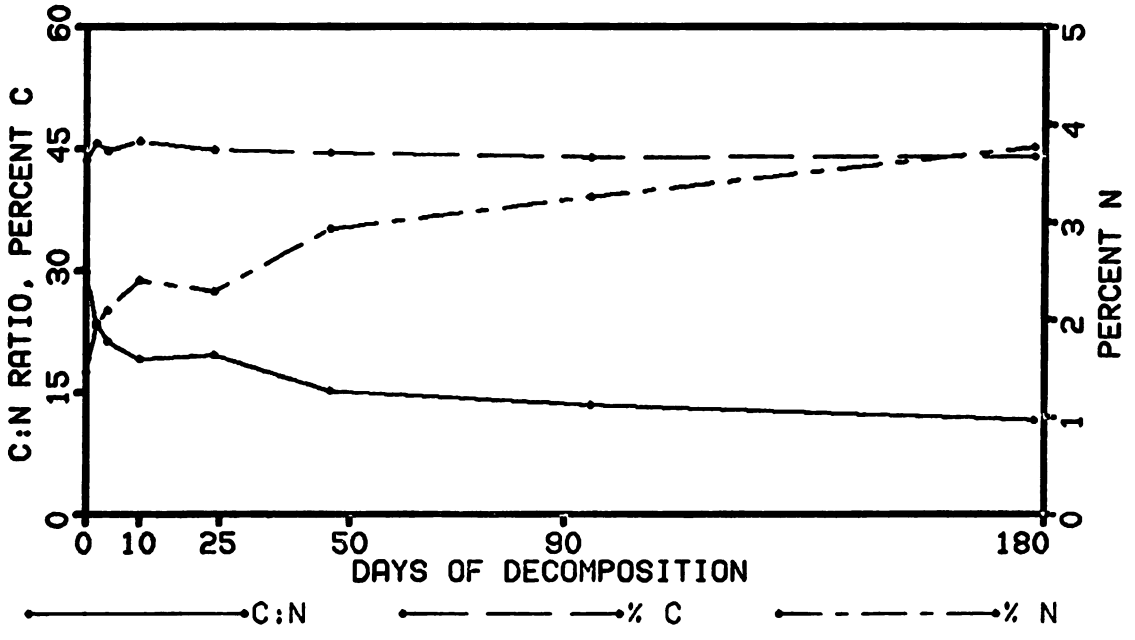
Appendix Figure 289. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



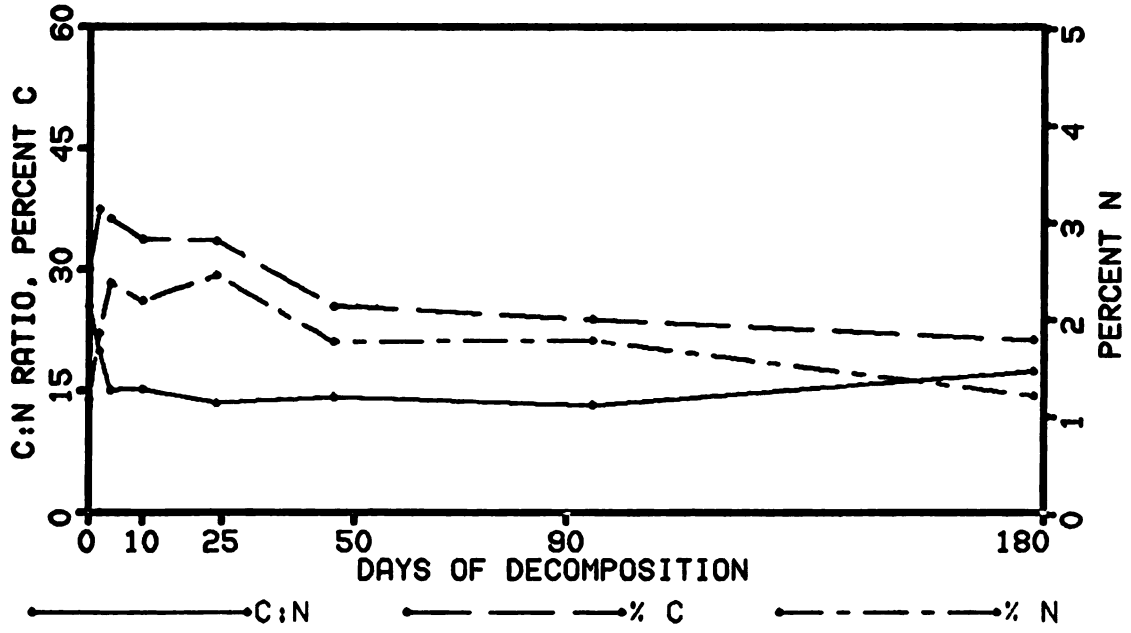
Appendix Figure 290. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



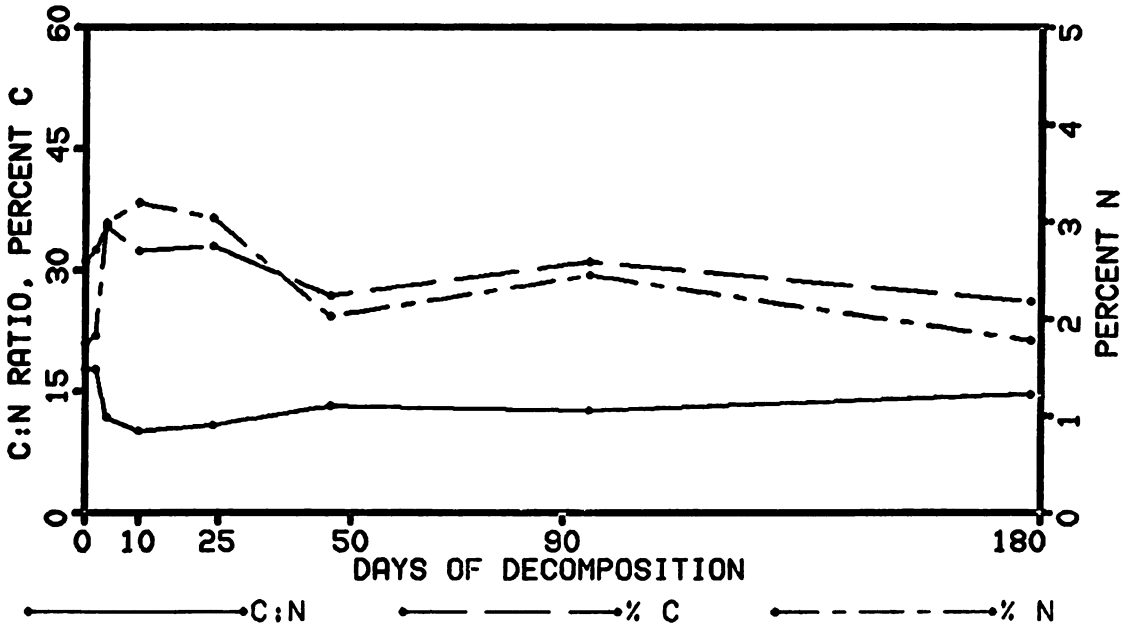
Appendix Figure 291. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



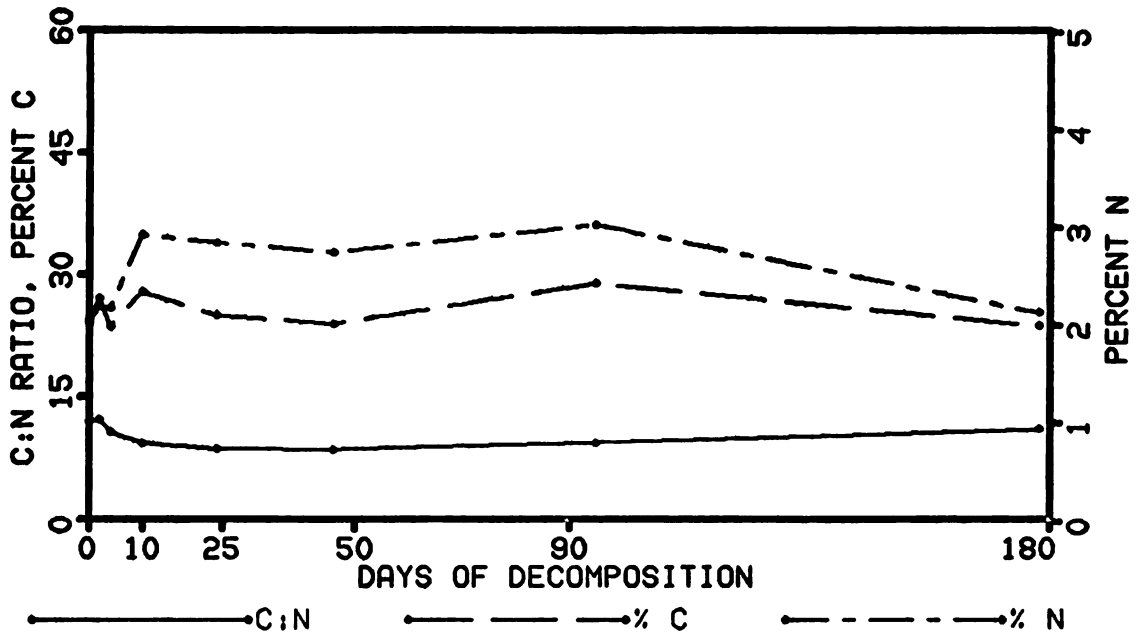
Appendix Figure 292. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



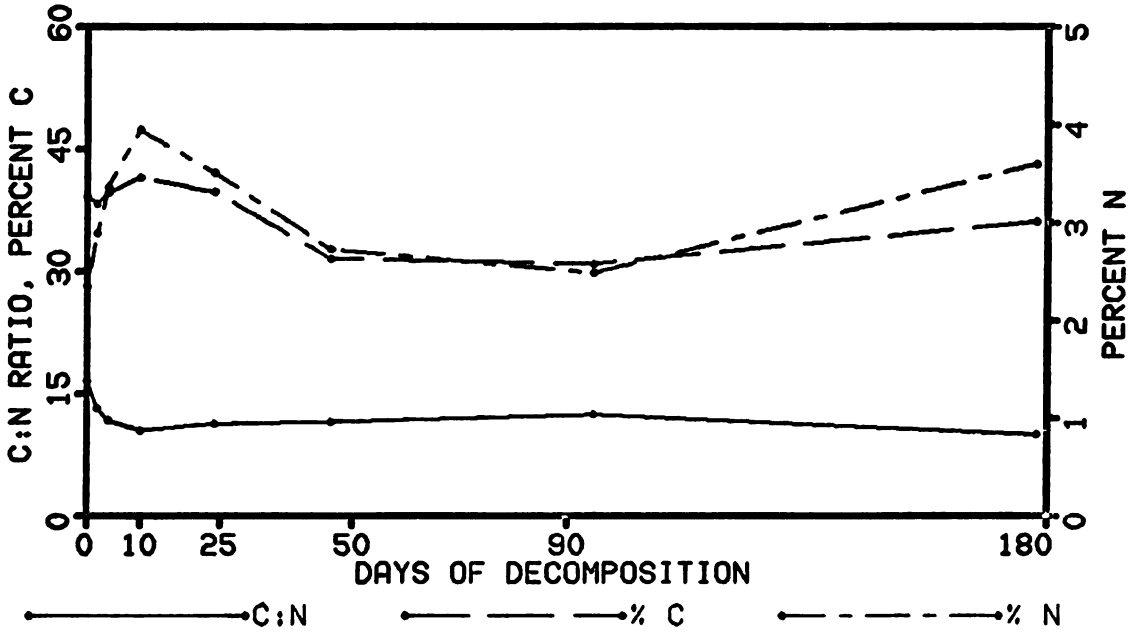
Appendix Figure 293. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



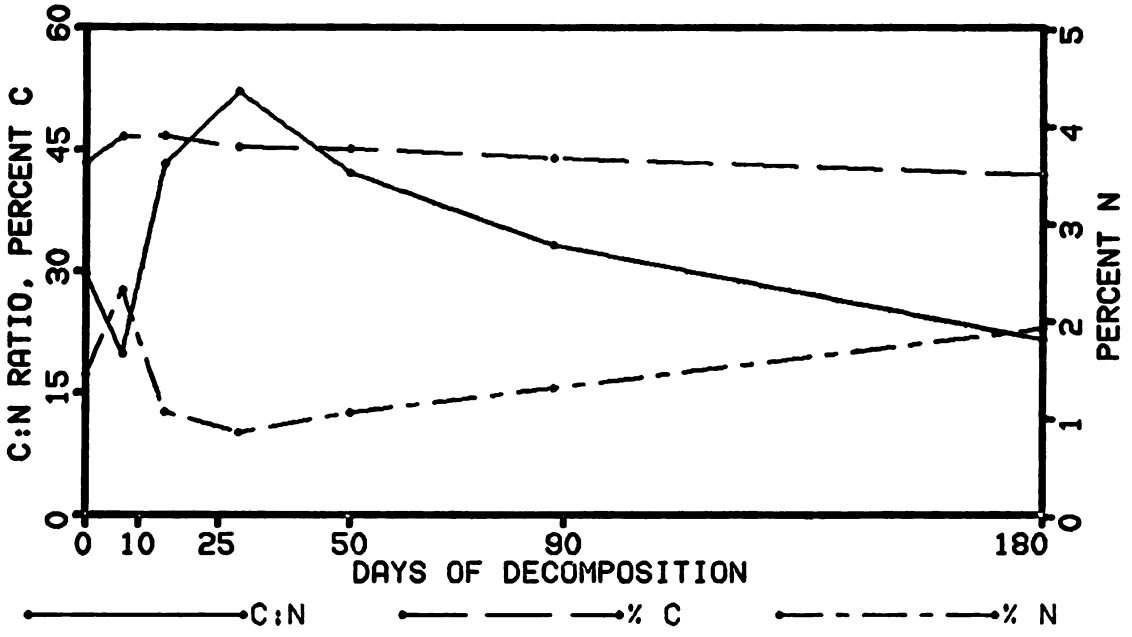
Appendix Figure 294. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



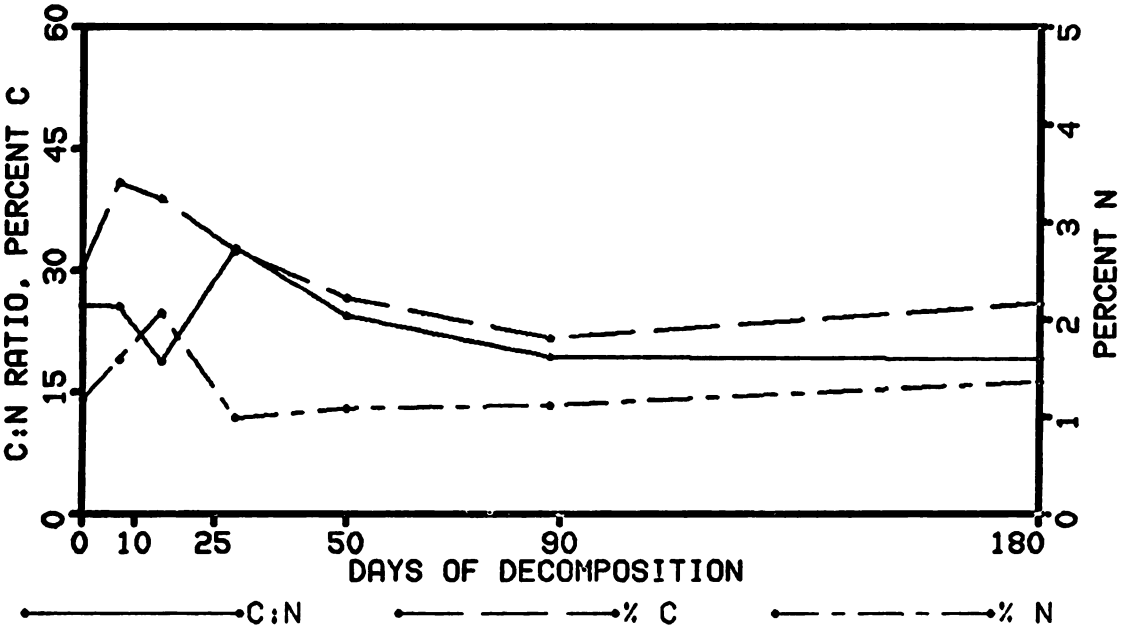
Appendix Figure 295. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



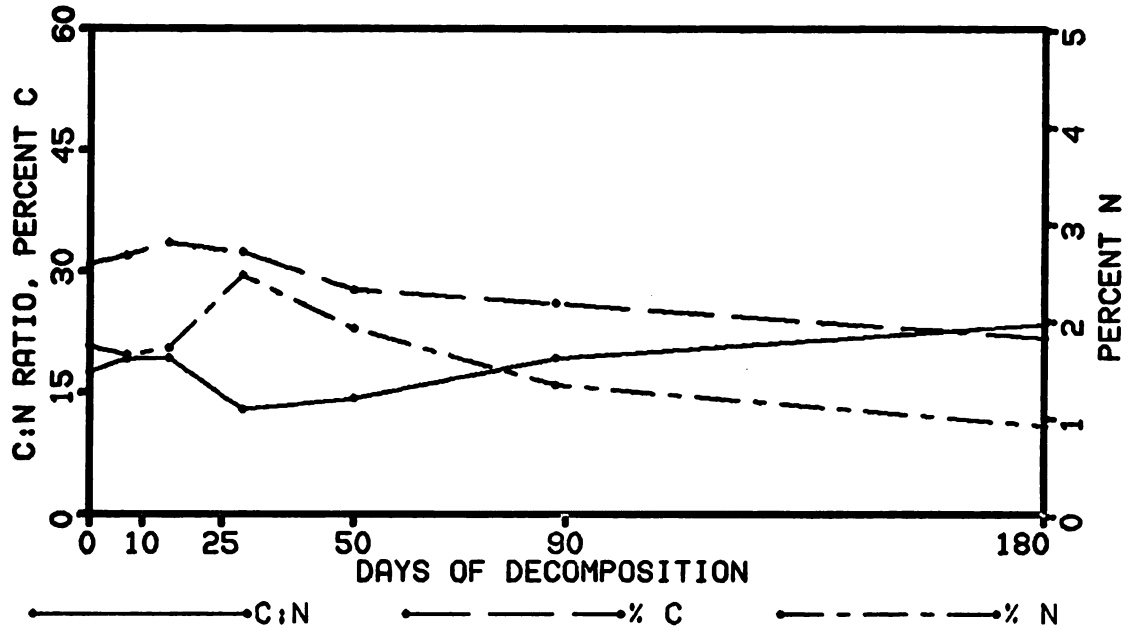
Appendix Figure 296. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



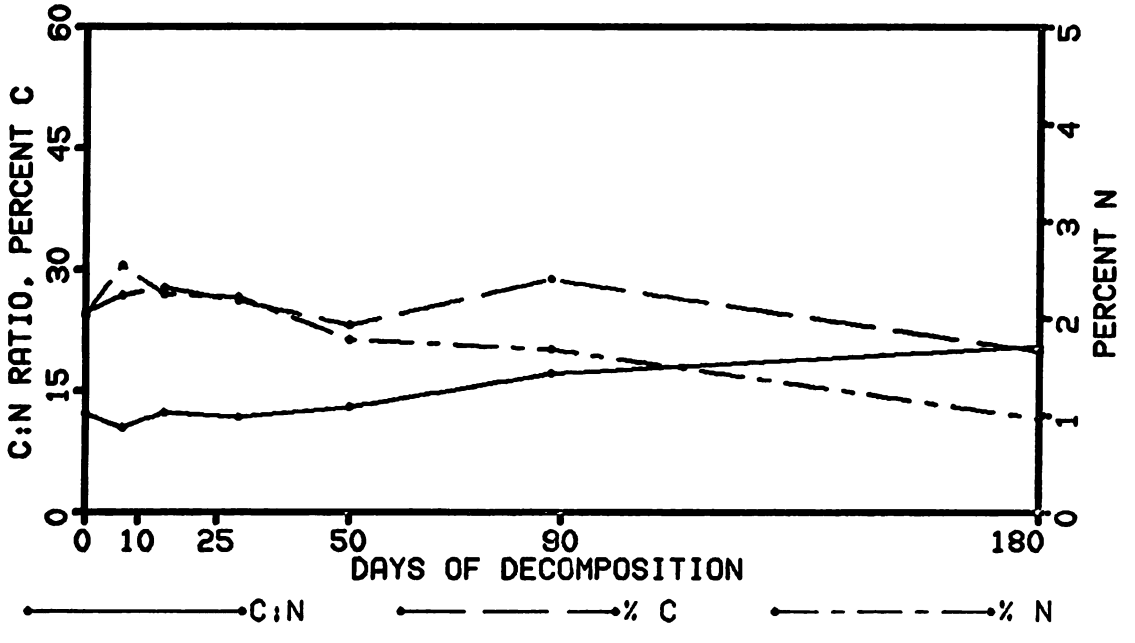
Appendix Figure 297. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during spring and summer. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



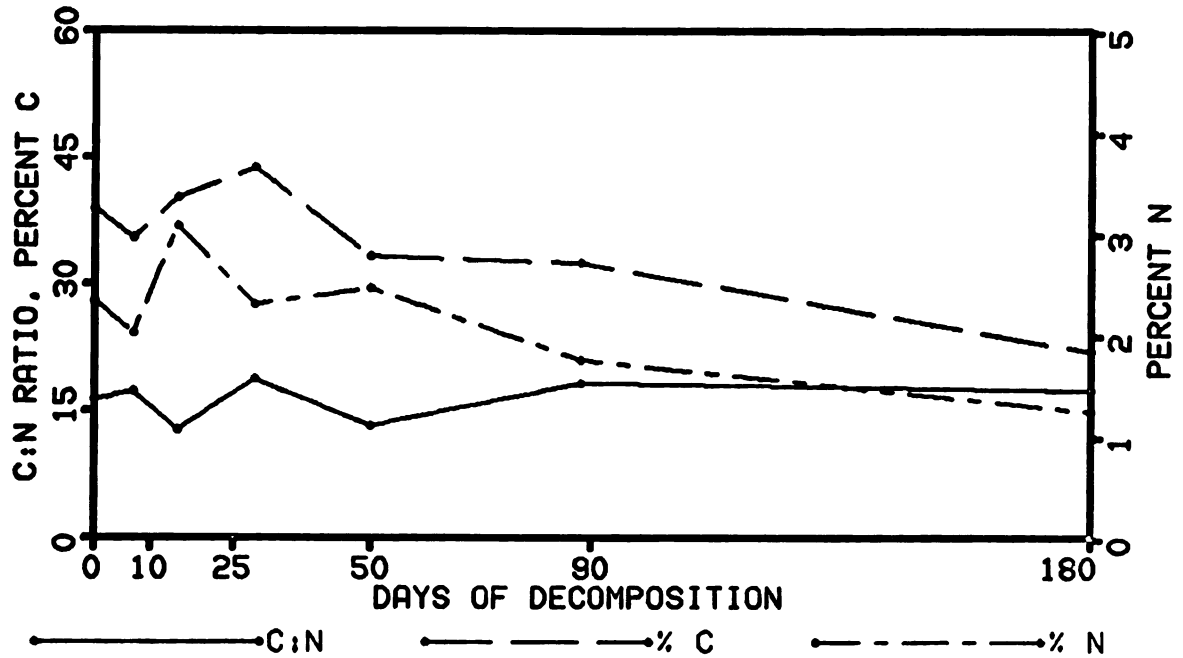
Appendix Figure 298. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during spring and summer. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



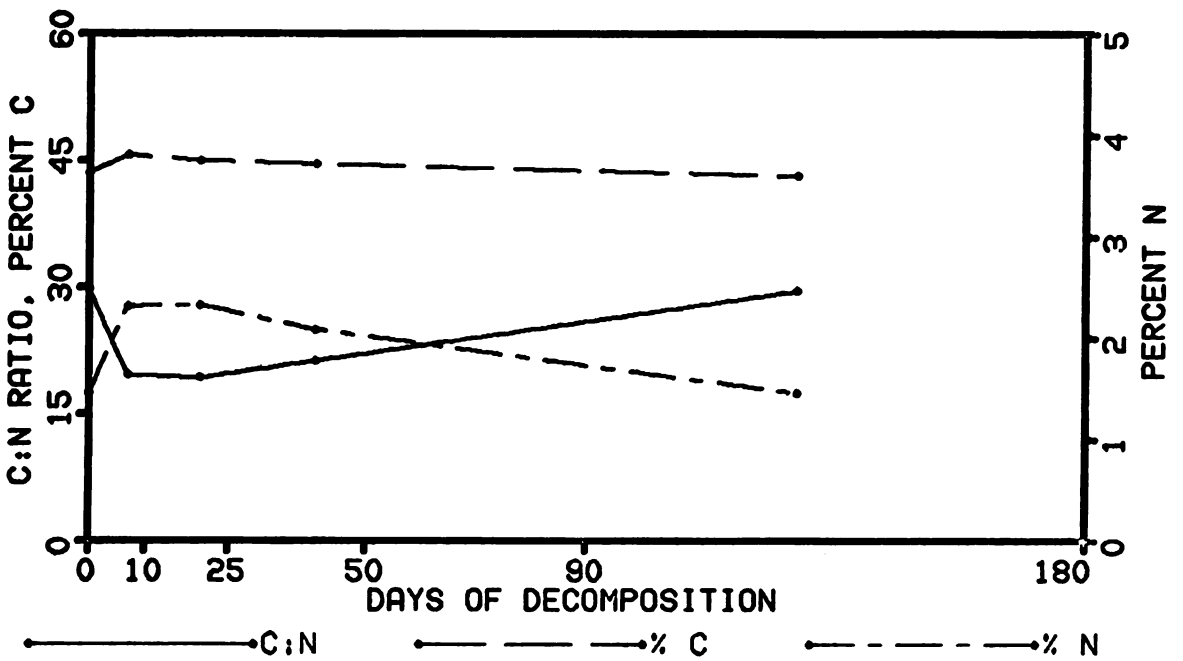
Appendix Figure 299. Decay of *Najas flexilis* in Lawrence Lake littoral zone during spring and summer. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



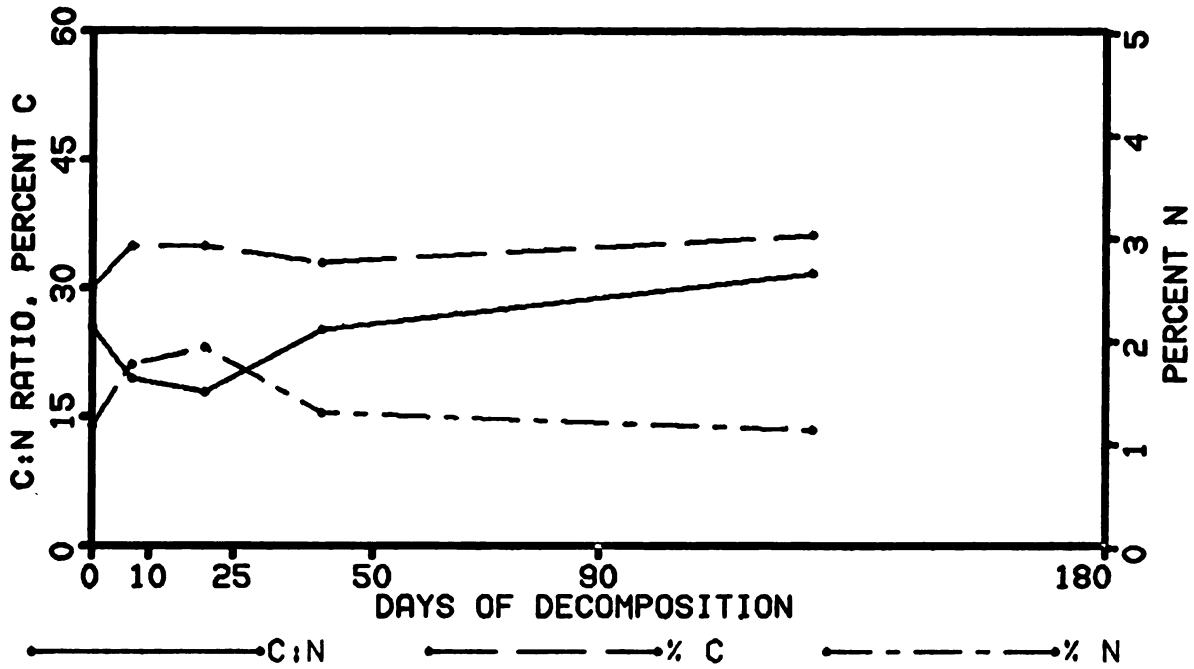
Appendix Figure 300. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during spring and summer. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



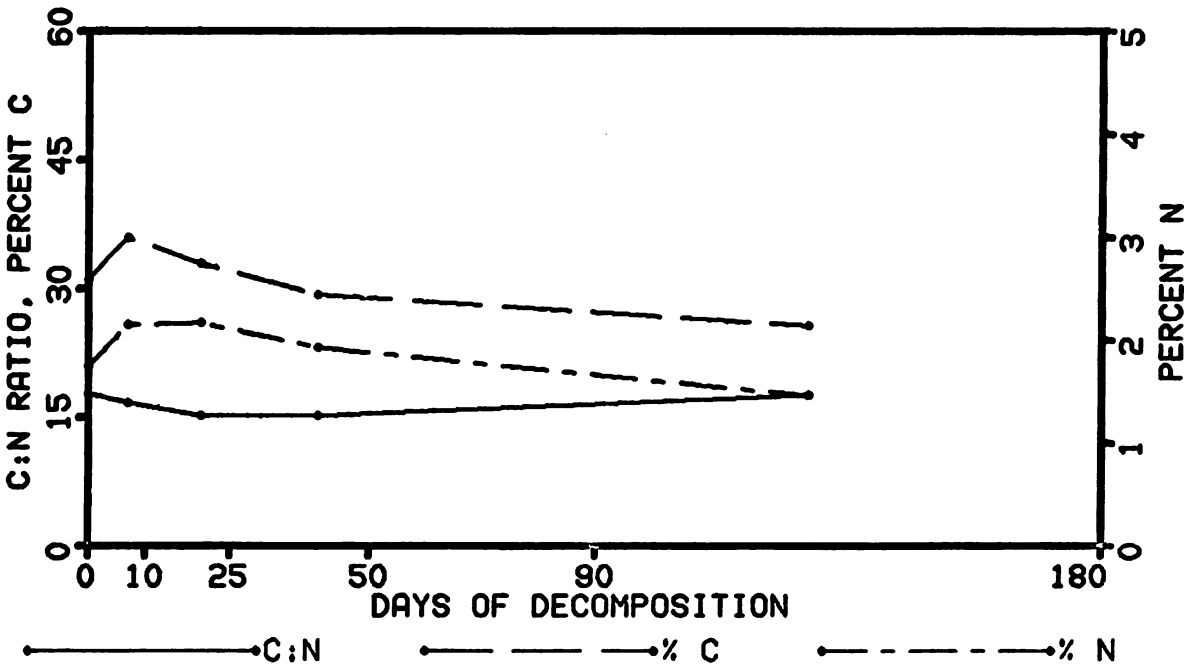
Appendix Figure 301. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during spring and summer. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



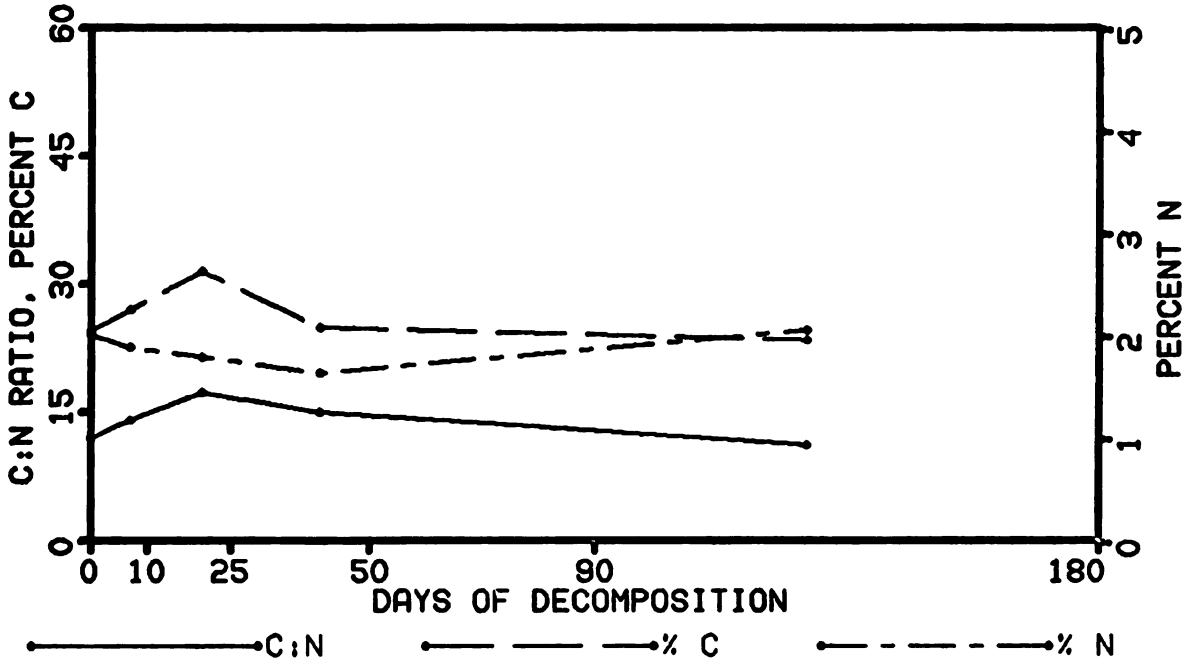
Appendix Figure 302. Decay of *Scirpus acutus* in Lawrence Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



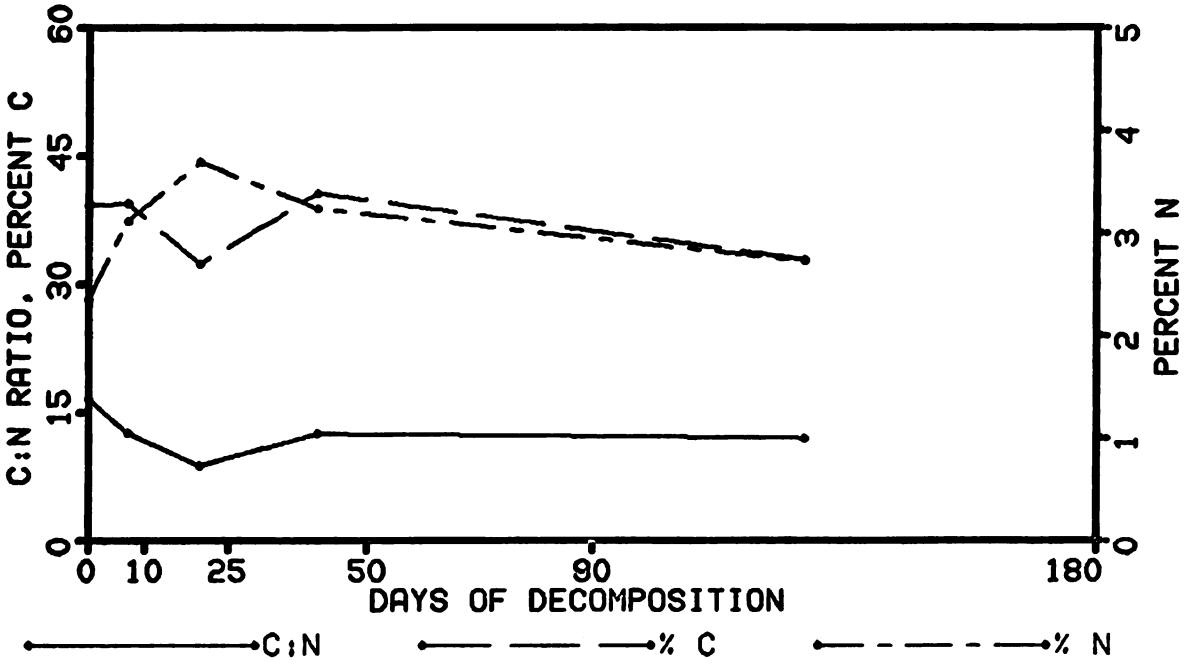
Appendix Figure 303. Decay of *Scirpus subterminalis* in Lawrence Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



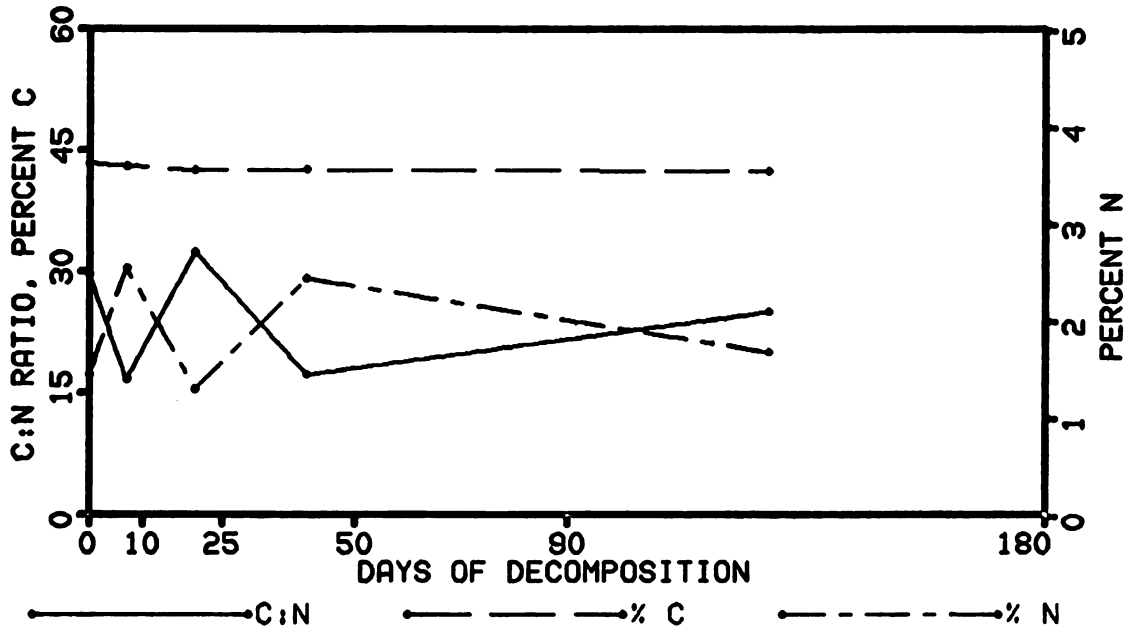
Appendix Figure 304. Decay of *Najas flexilis* in Lawrence Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



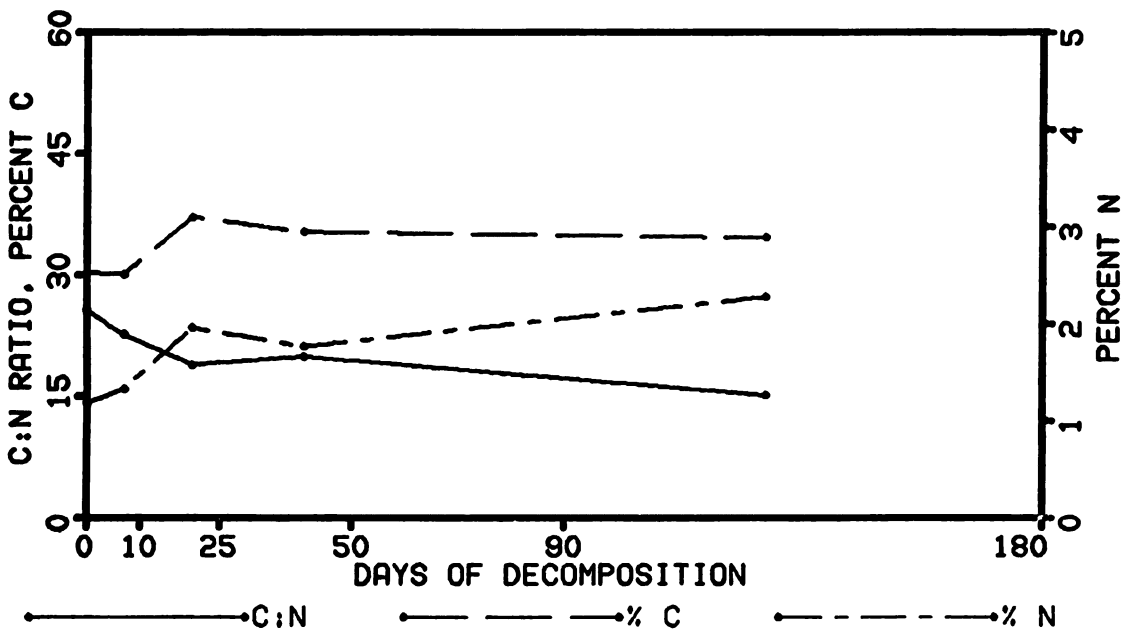
Appendix Figure 305. Decay of *Myriophyllum heterophyllum* in Lawrence Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



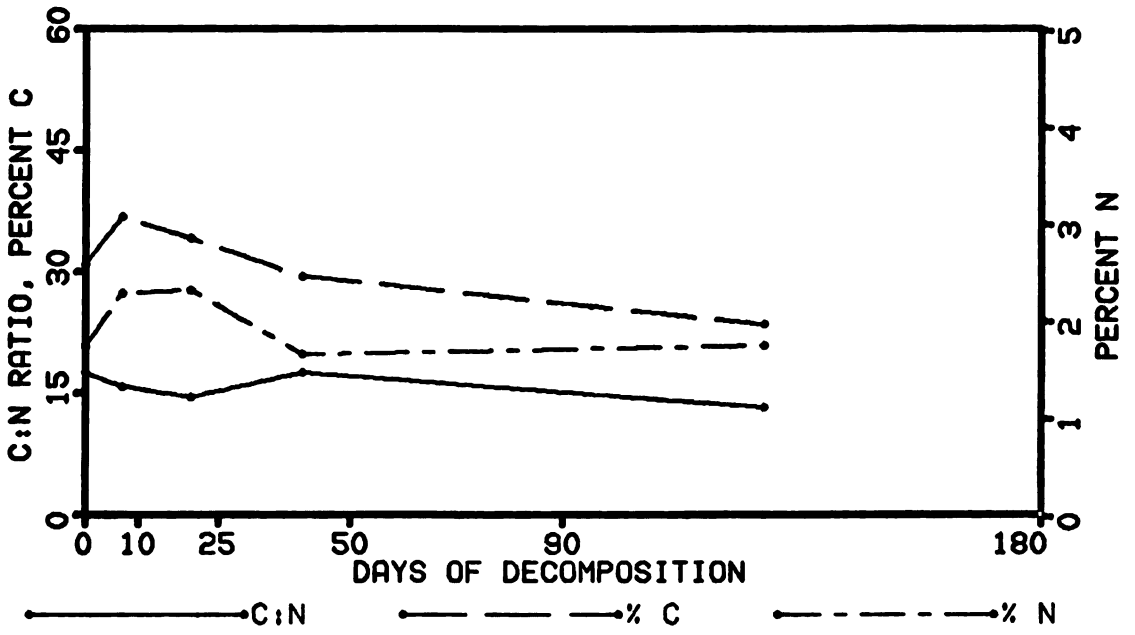
Appendix Figure 306. Decay of *Nuphar variegatum* in Lawrence Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



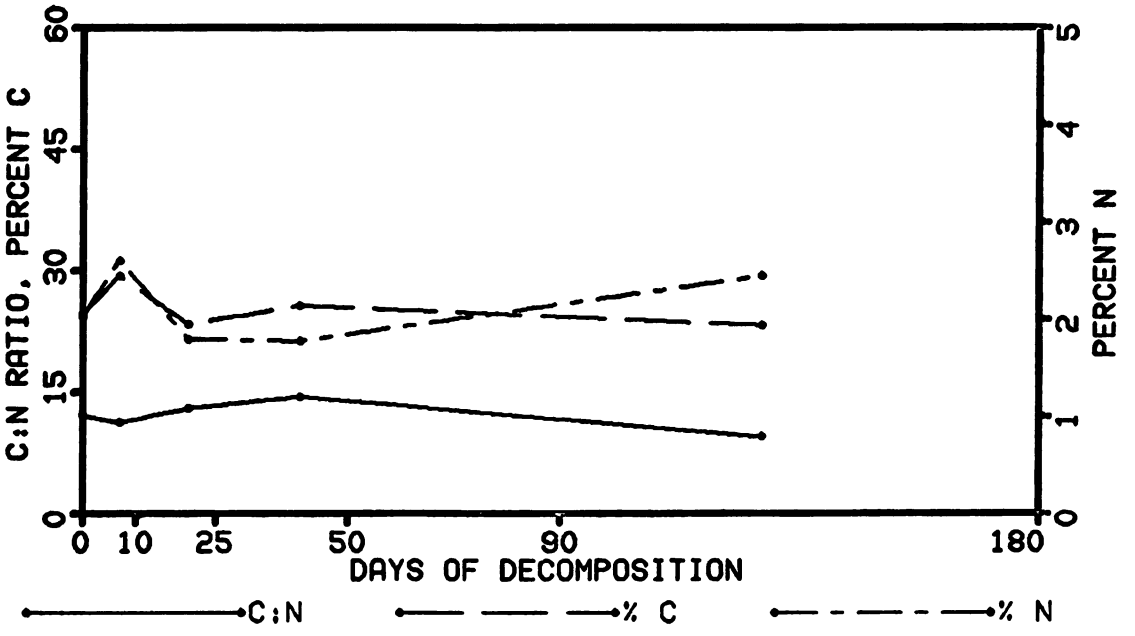
Appendix Figure 307. Decay of *Scirpus acutus* in Lawrence Lake pelagial zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



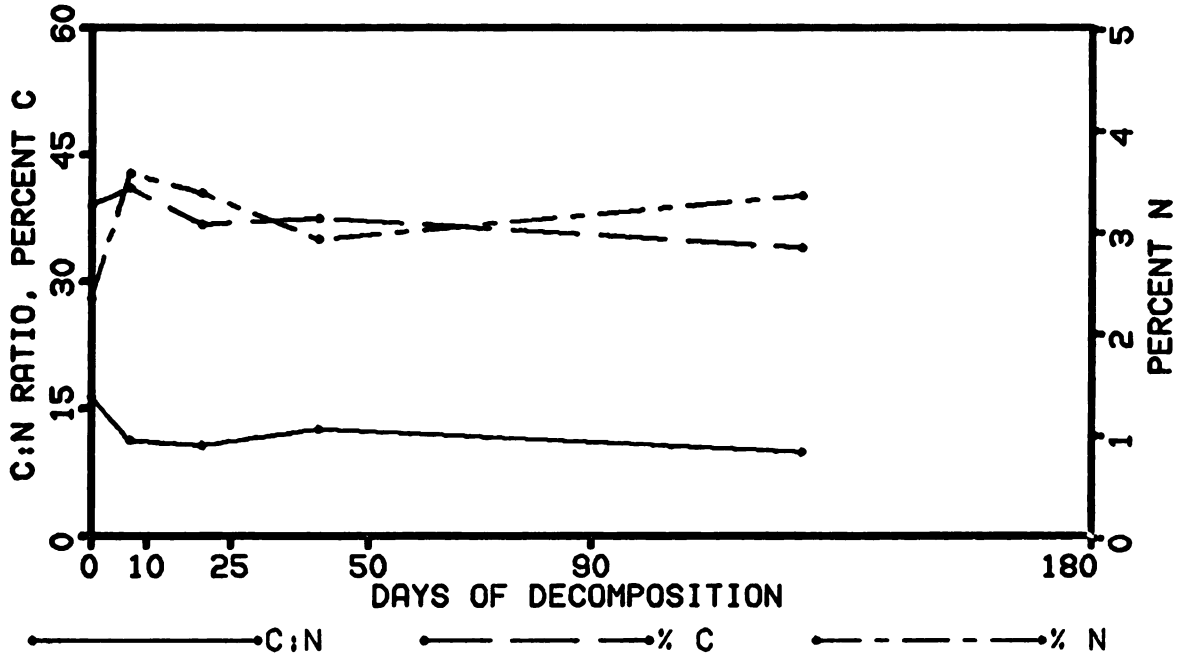
Appendix Figure 308. Decay of *Scirpus subterminalis* in Lawrence Lake pelagial zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



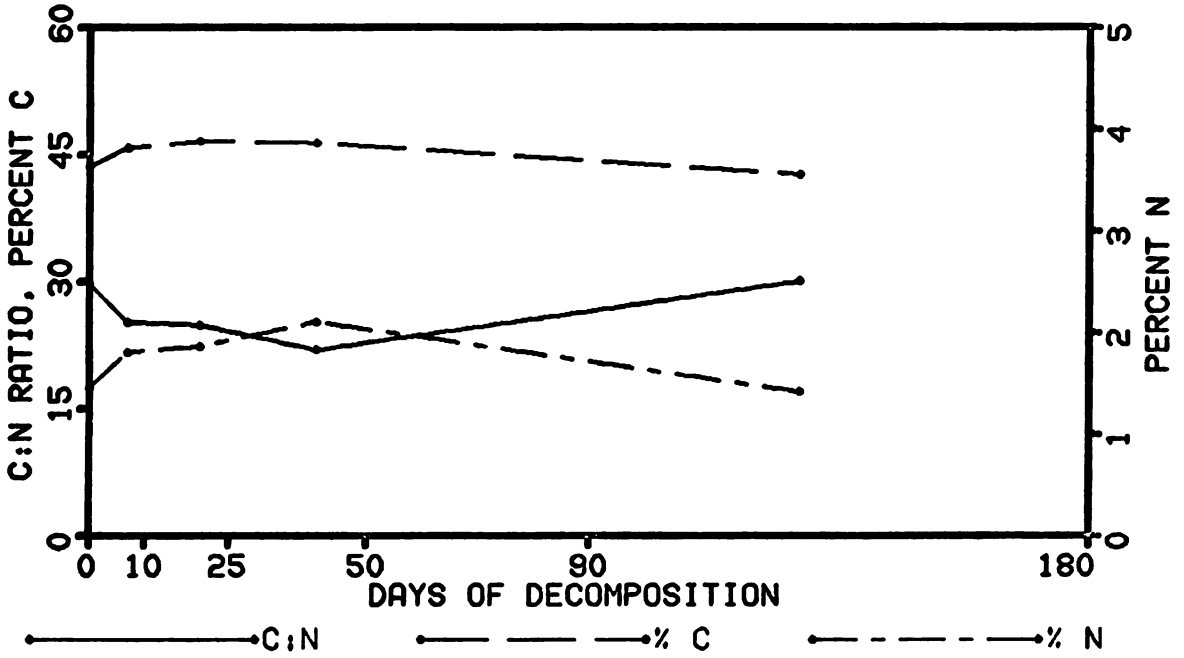
Appendix Figure 309. Decay of *Najas flexilis* in Lawrence Lake pelagial zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



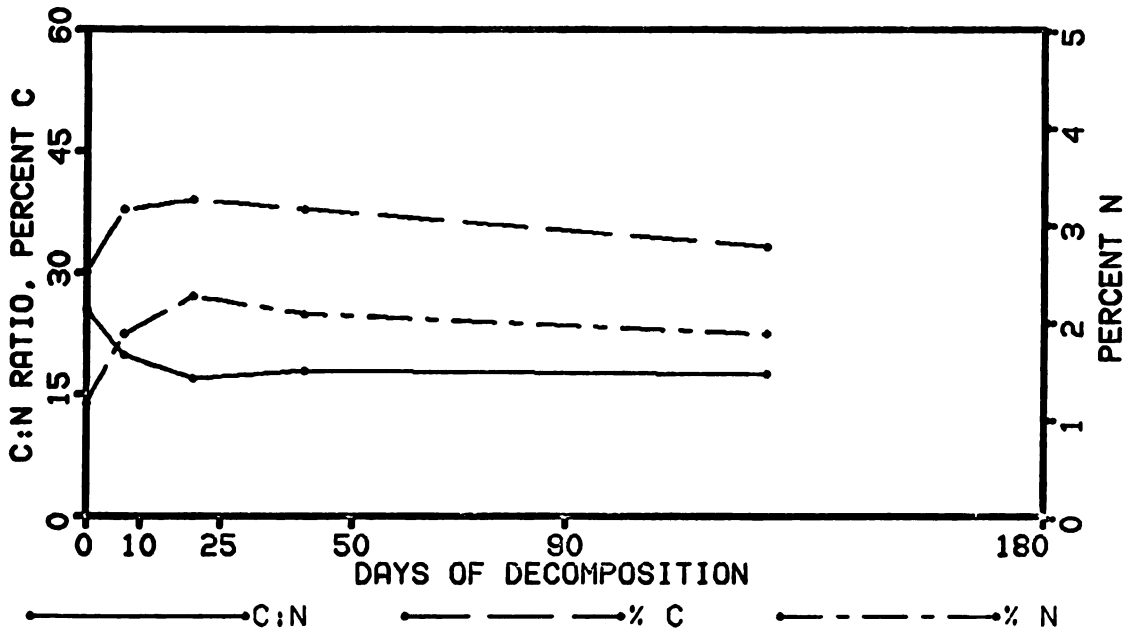
Appendix Figure 310. Decay of *Myriophyllum heterophyllum* in Lawrence Lake pelagial zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



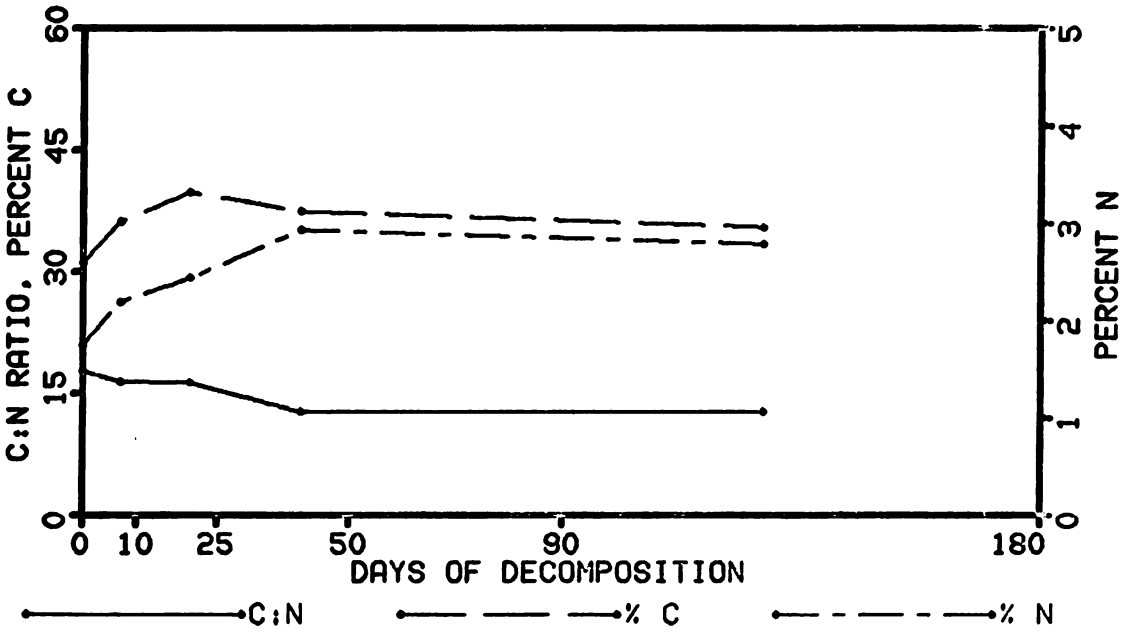
Appendix Figure 311. Decay of *Nuphar variegatum* in Lawrence Lake pelagial zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



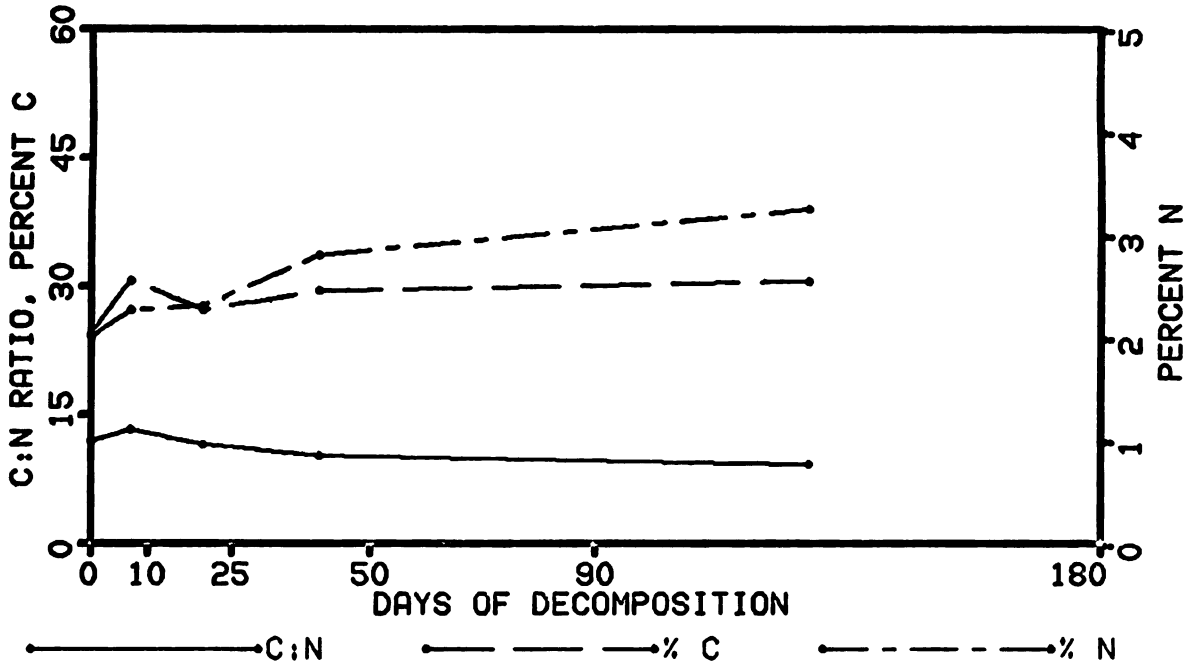
Appendix Figure 312. Decay of *Scirpus acutus* in Wintergreen Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



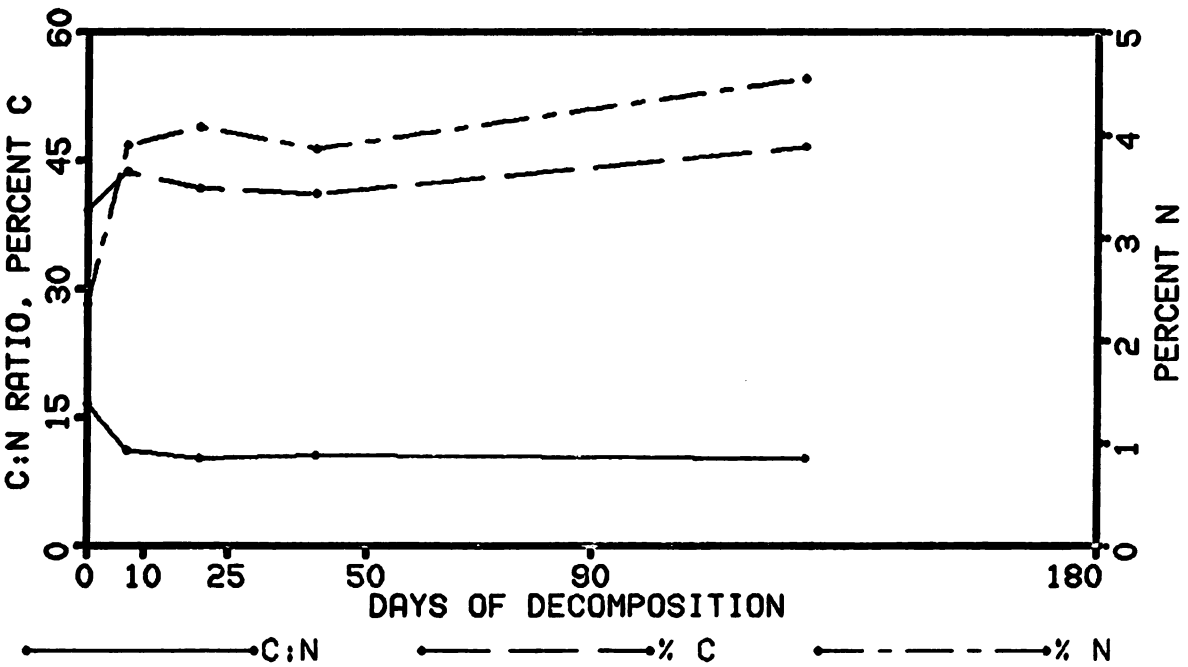
Appendix Figure 313. Decay of *Scirpus subterminalis* in Wintergreen Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



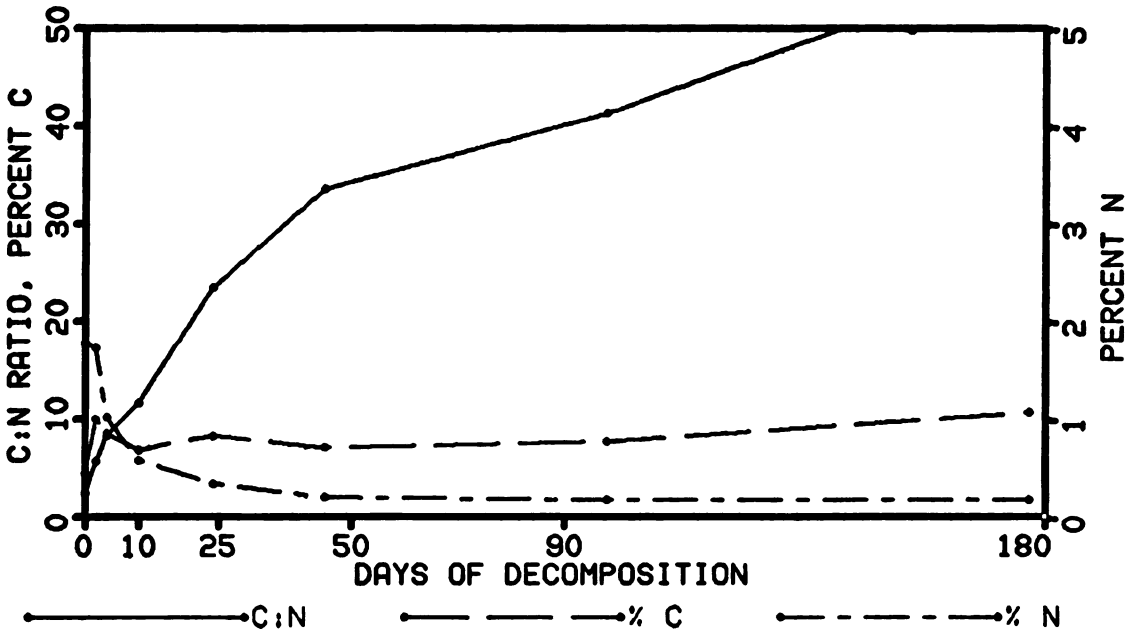
Appendix Figure 314. Decay of *Najas flexilis* in Wintergreen Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



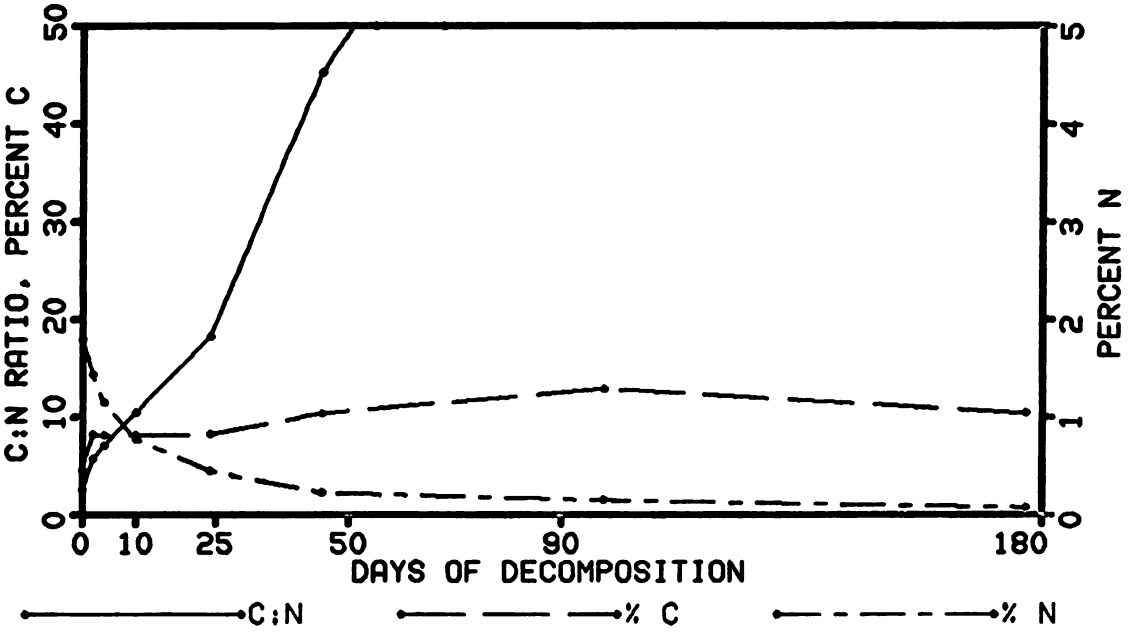
Appendix Figure 315. Decay of *Myriophyllum heterophyllum* in Wintergreen Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



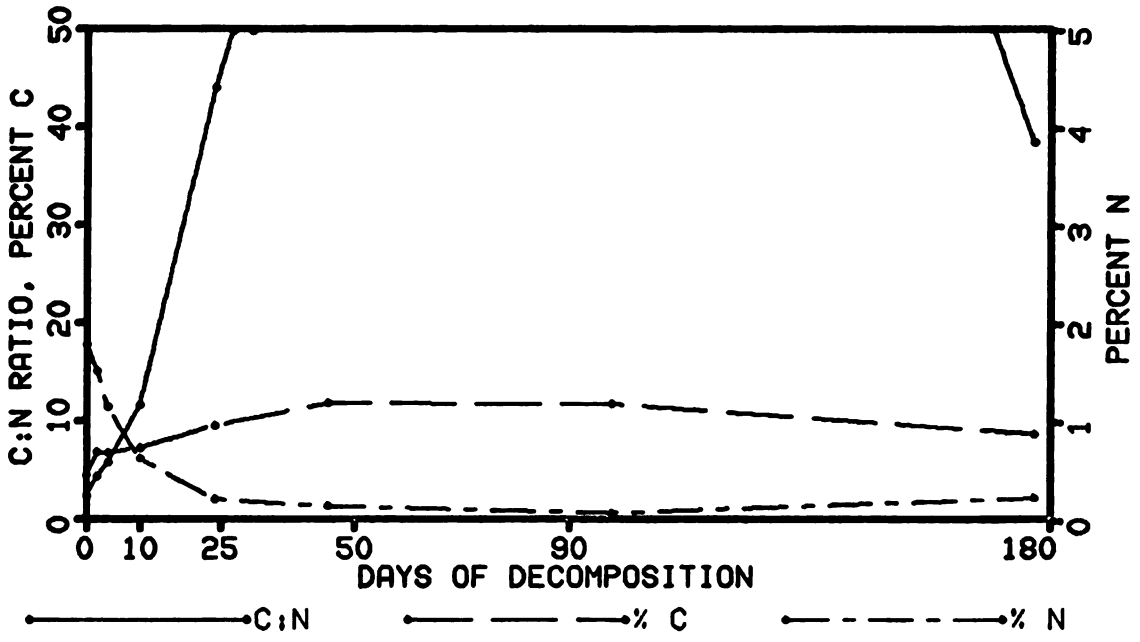
Appendix Figure 316. Decay of *Nuphar variegatum* in Wintergreen Lake littoral zone during fall and winter. Carbon and nitrogen, as percent of total dry weight, and C:N ratio of plant tissue.



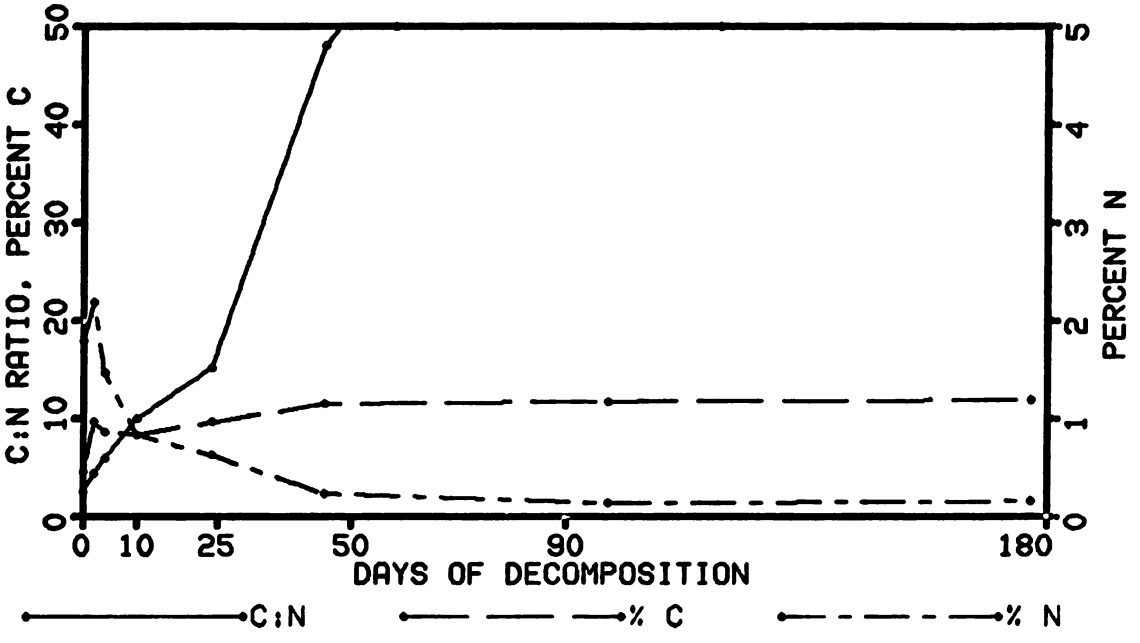
Appendix Figure 317. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



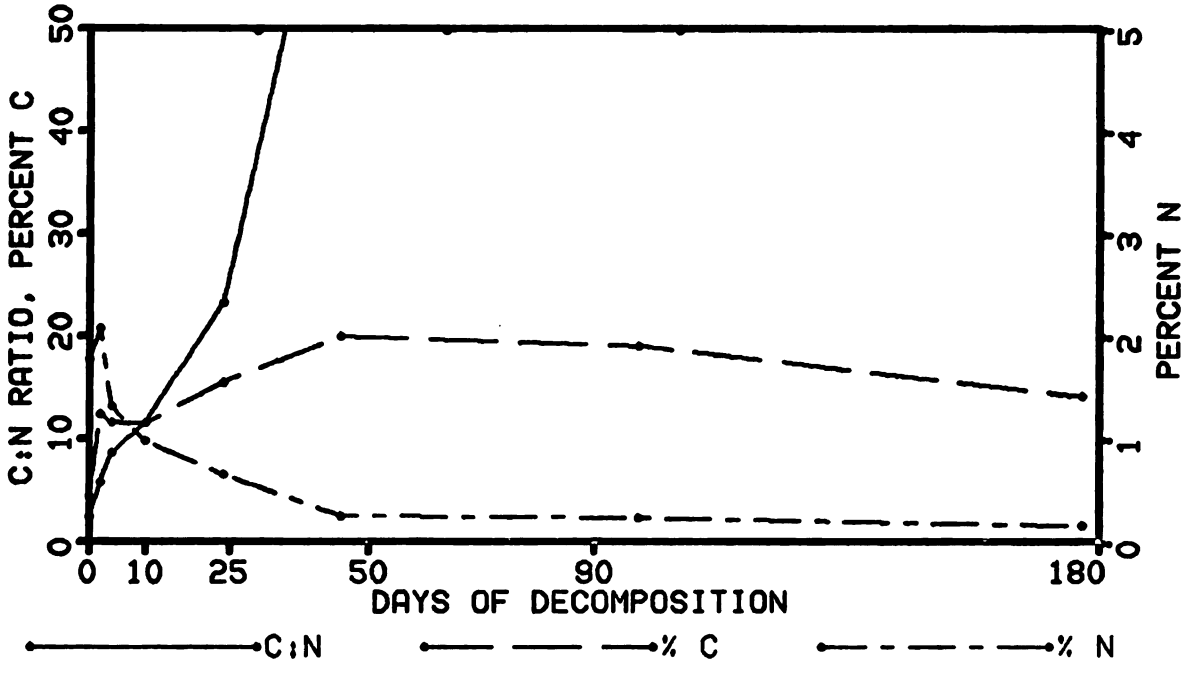
Appendix Figure 318. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



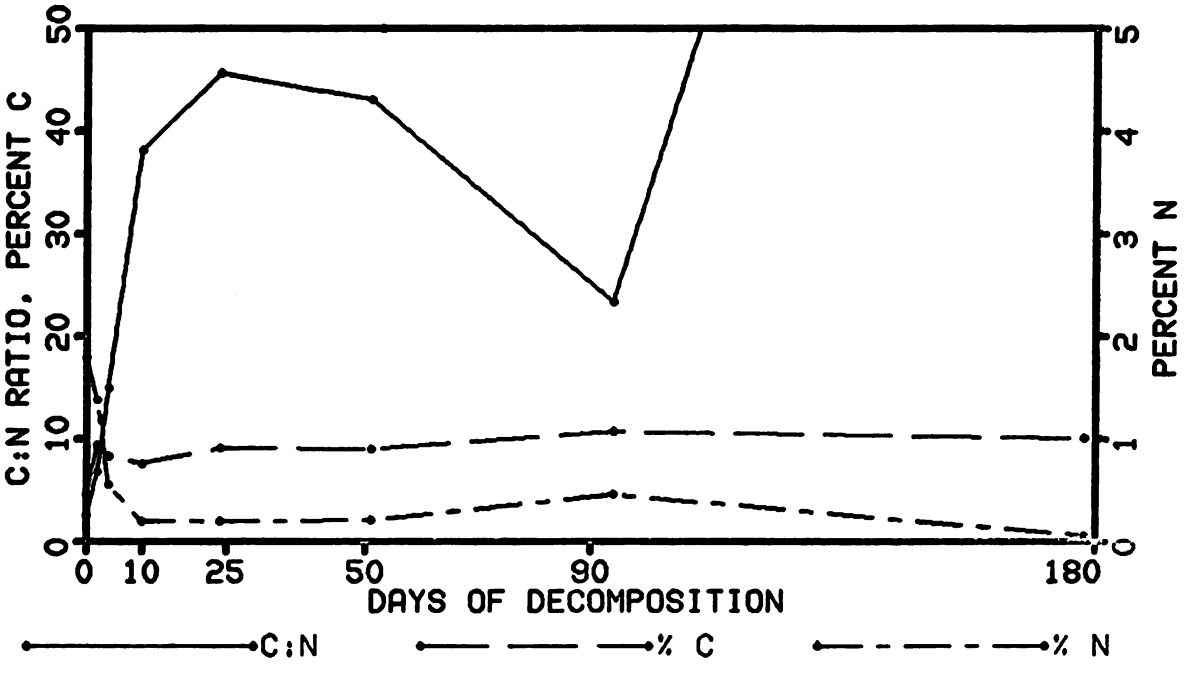
Appendix Figure 319. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



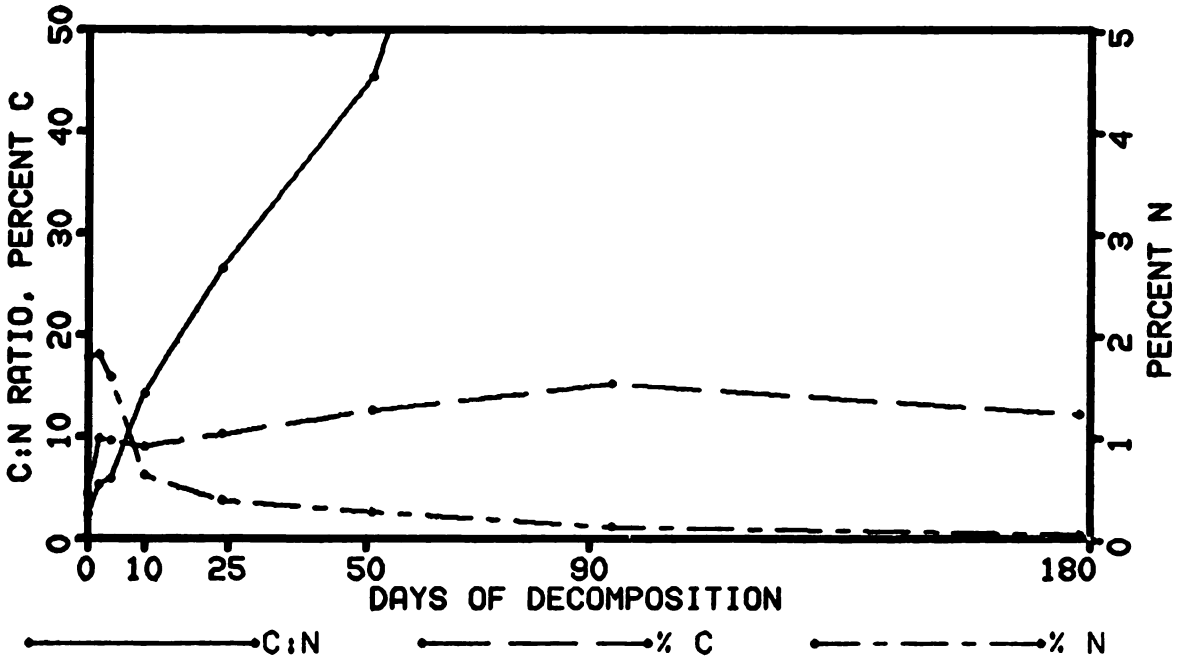
Appendix Figure 320. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



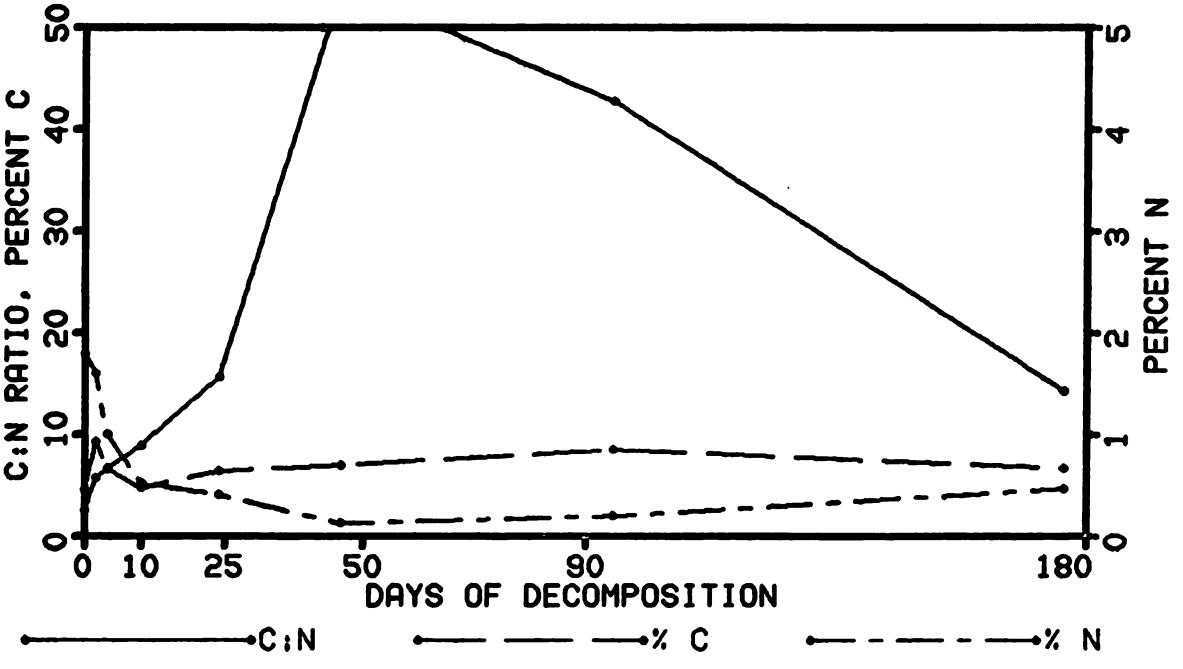
Appendix Figure 321. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



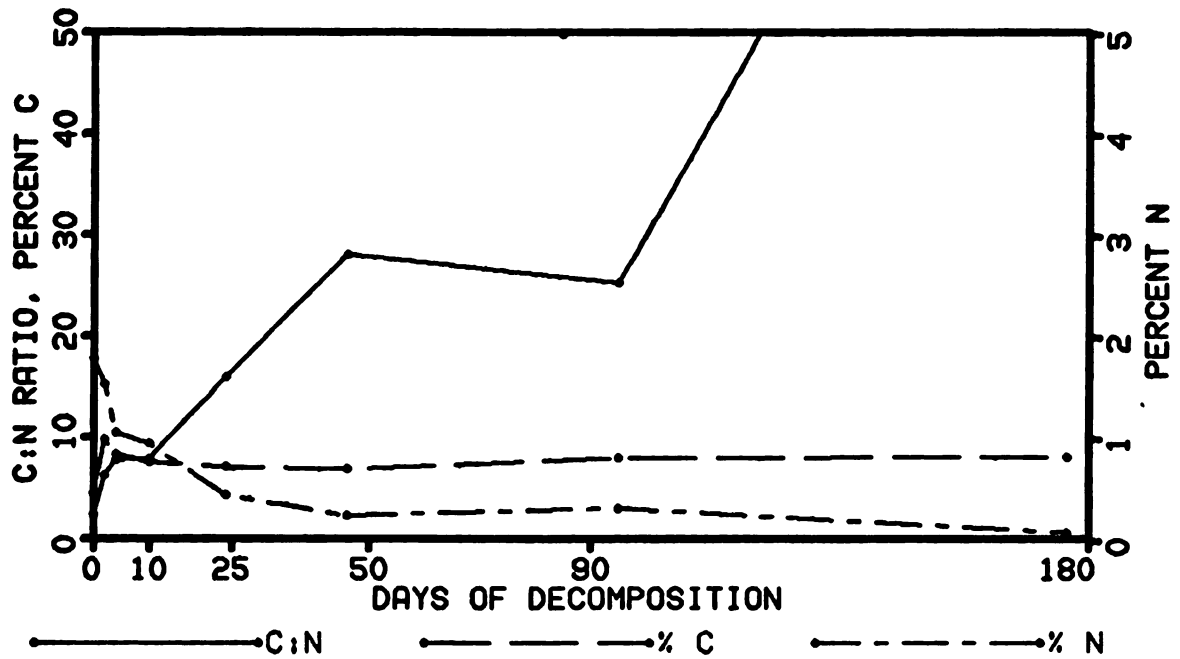
Appendix Figure 322. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



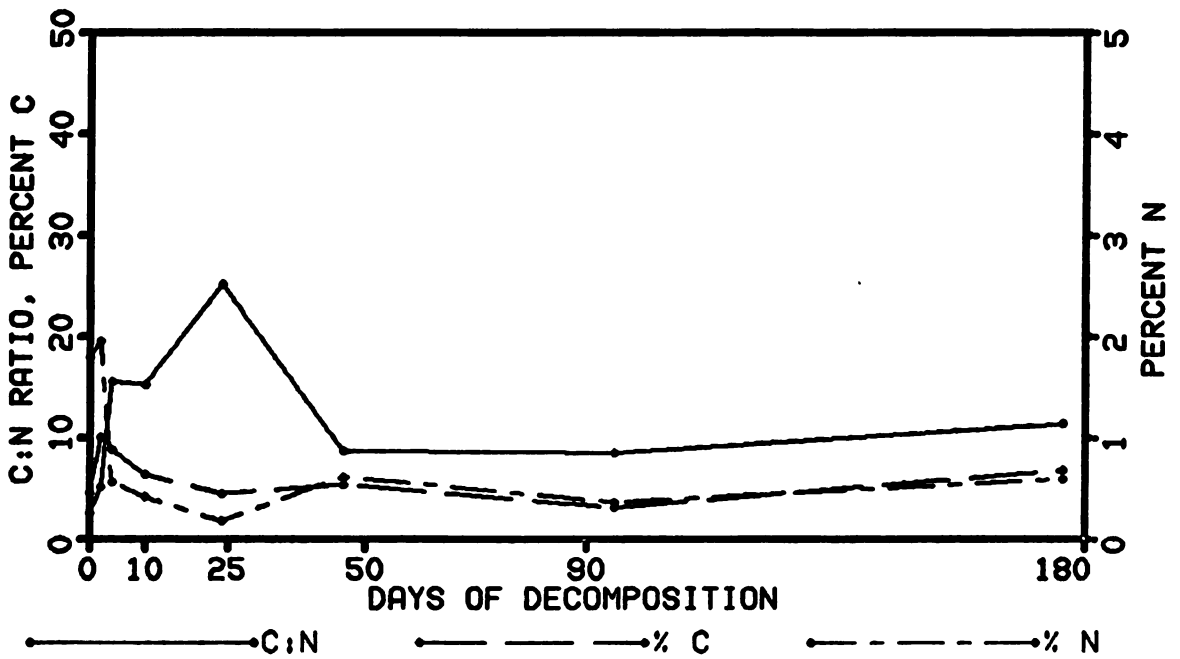
Appendix Figure 323. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



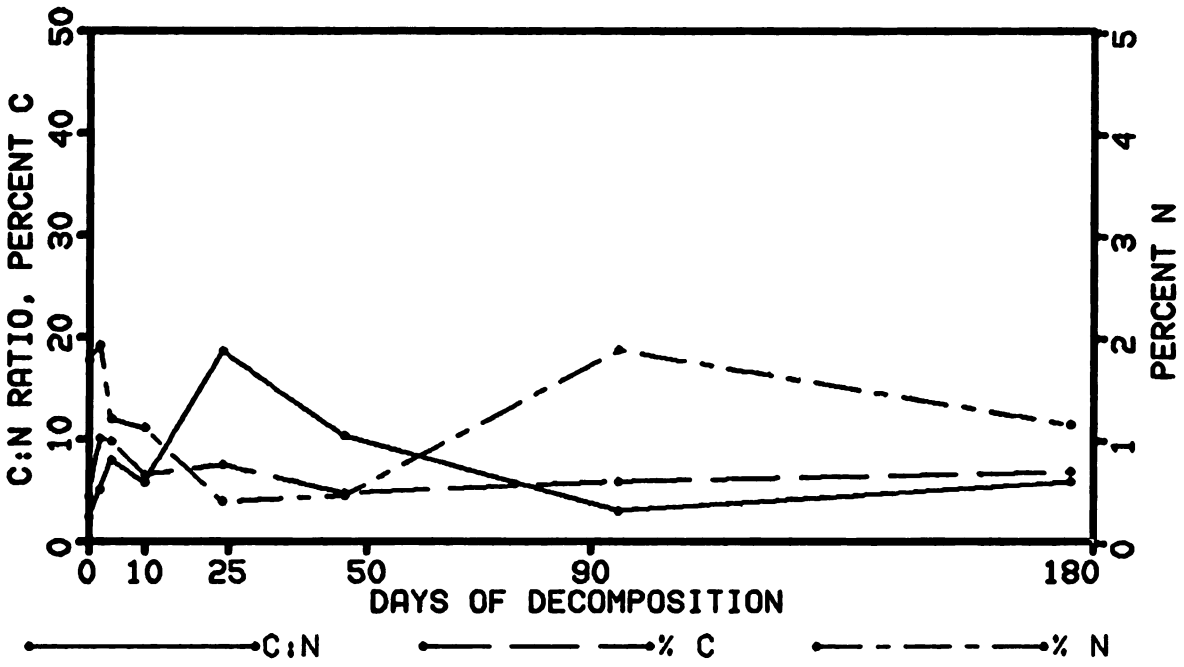
Appendix Figure 324. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



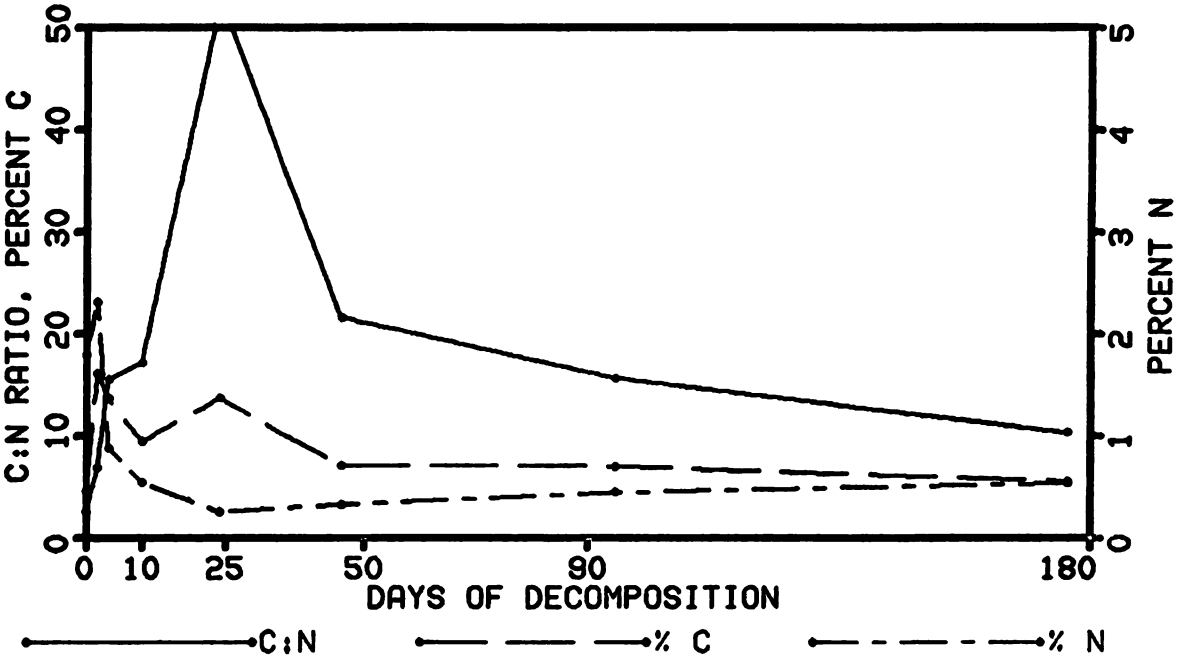
Appendix Figure 325. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



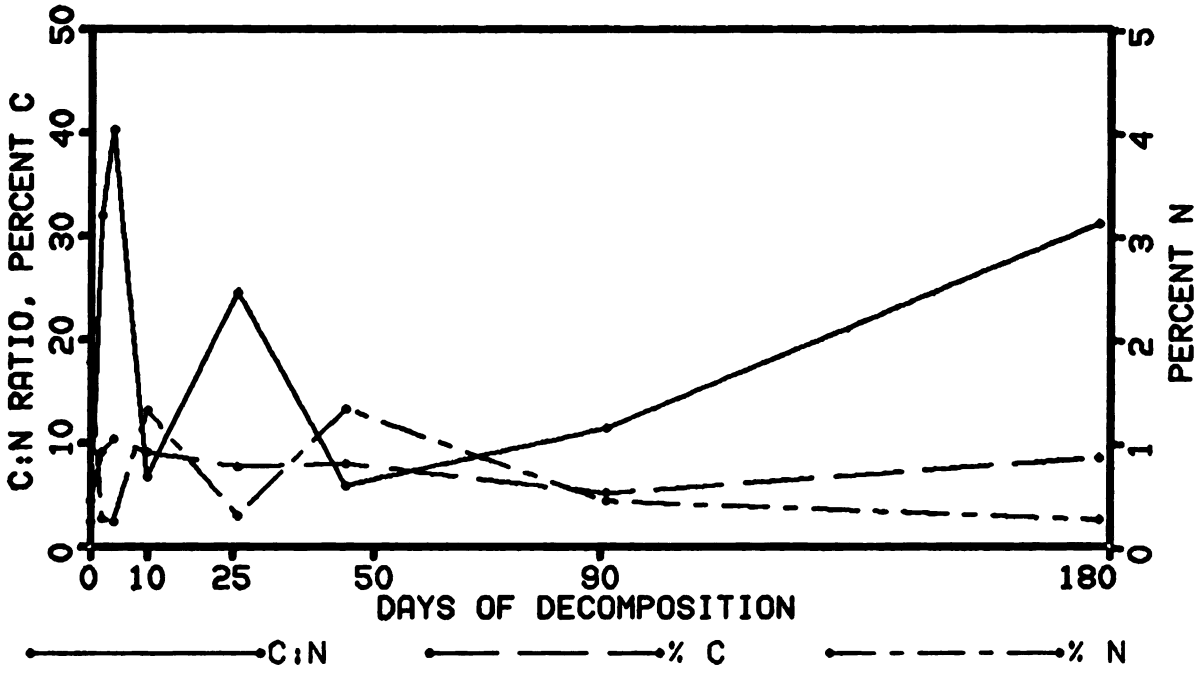
Appendix Figure 326. Decay of *Najas flexilis* in laboratory under aerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



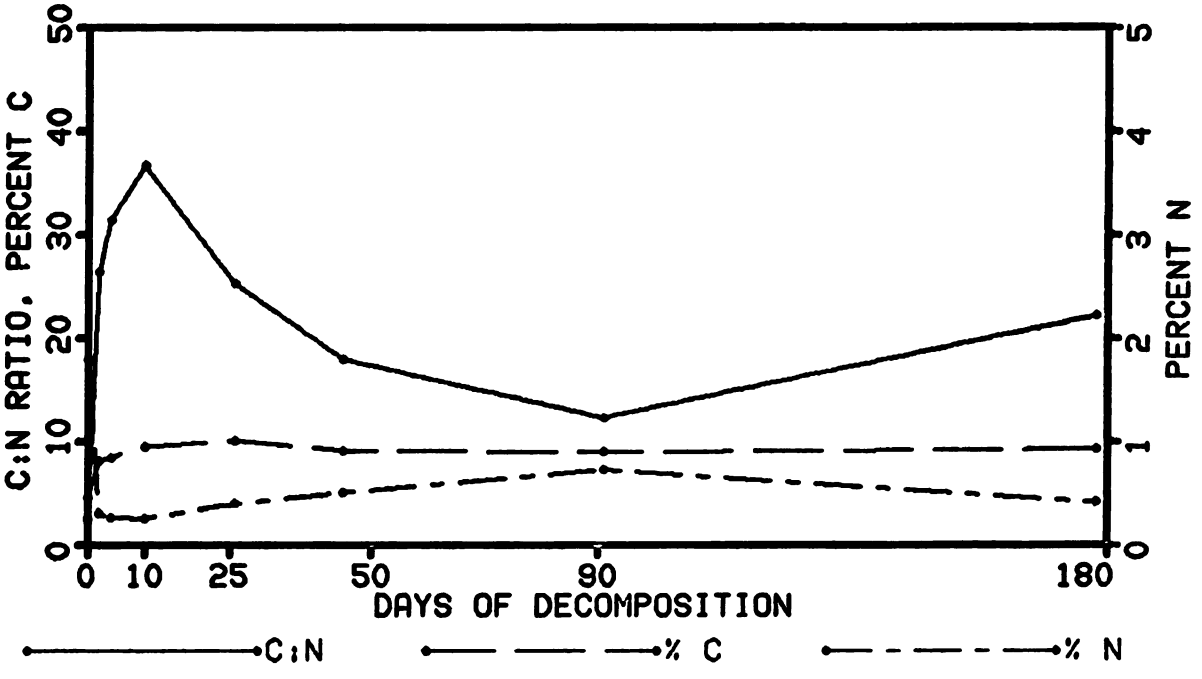
Appendix Figure 327. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



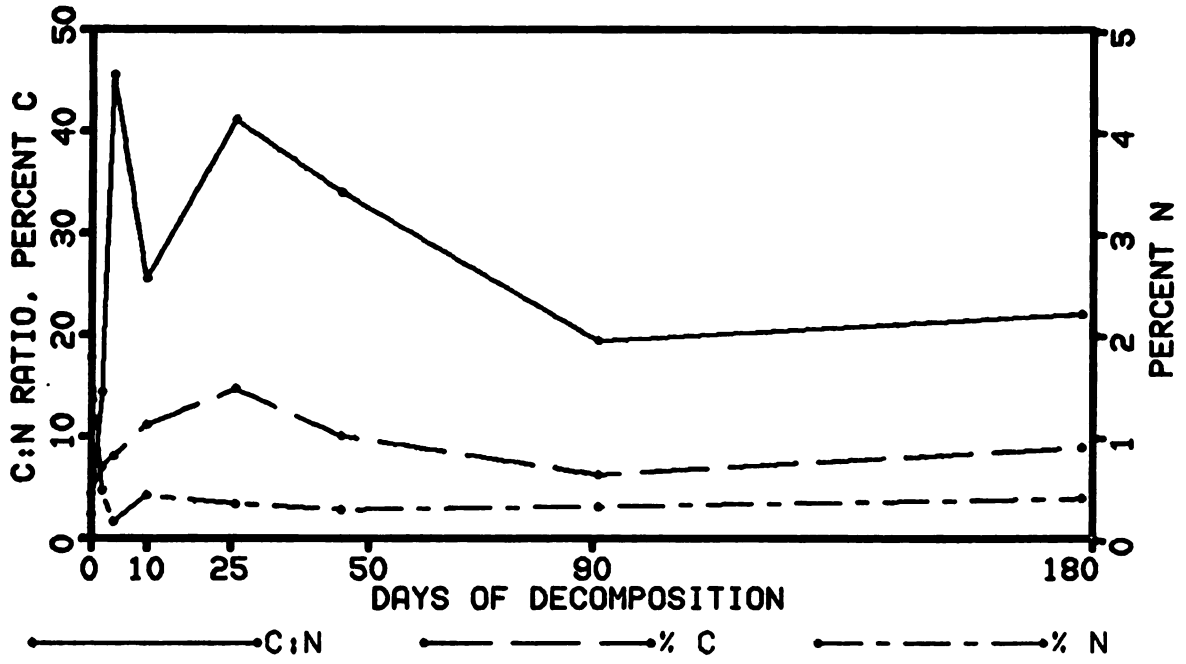
Appendix Figure 328. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 10°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



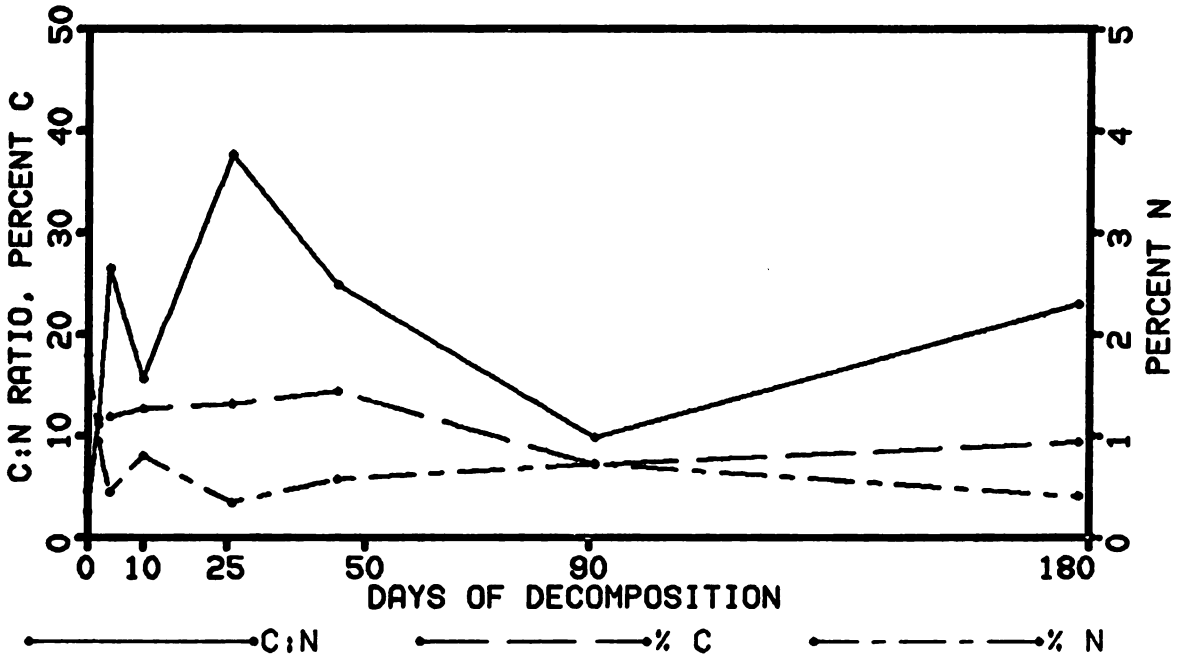
Appendix Figure 329. Decay of *Scirpus acutus* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



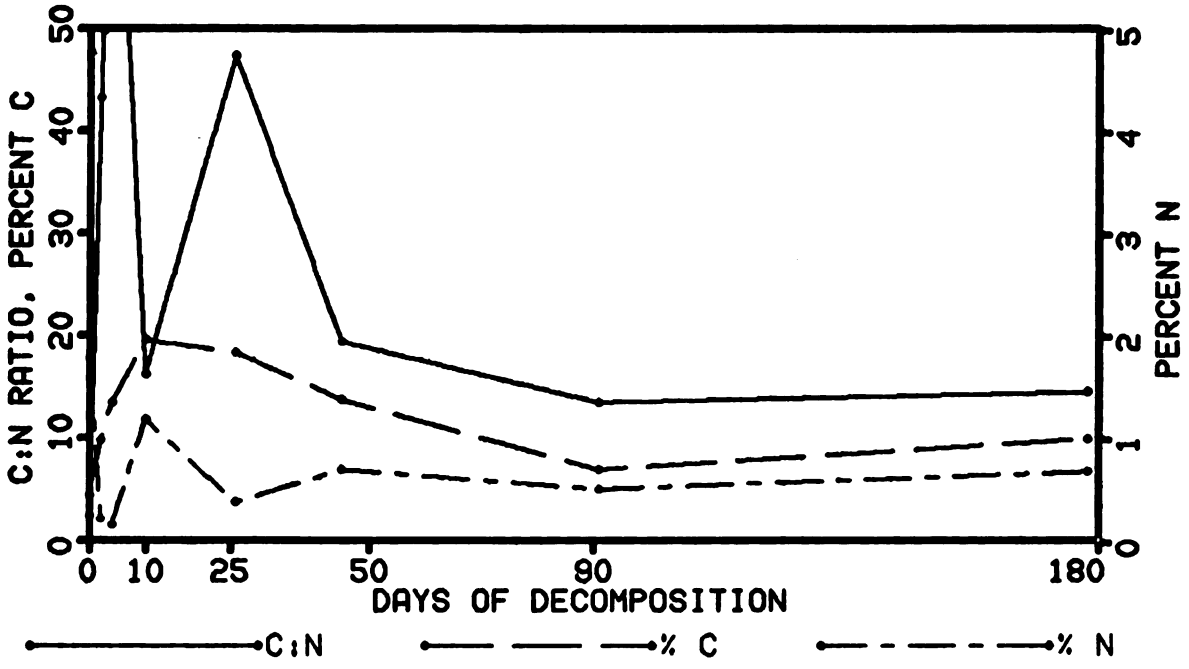
Appendix Figure 330. Decay of *Scirpus subterminalis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



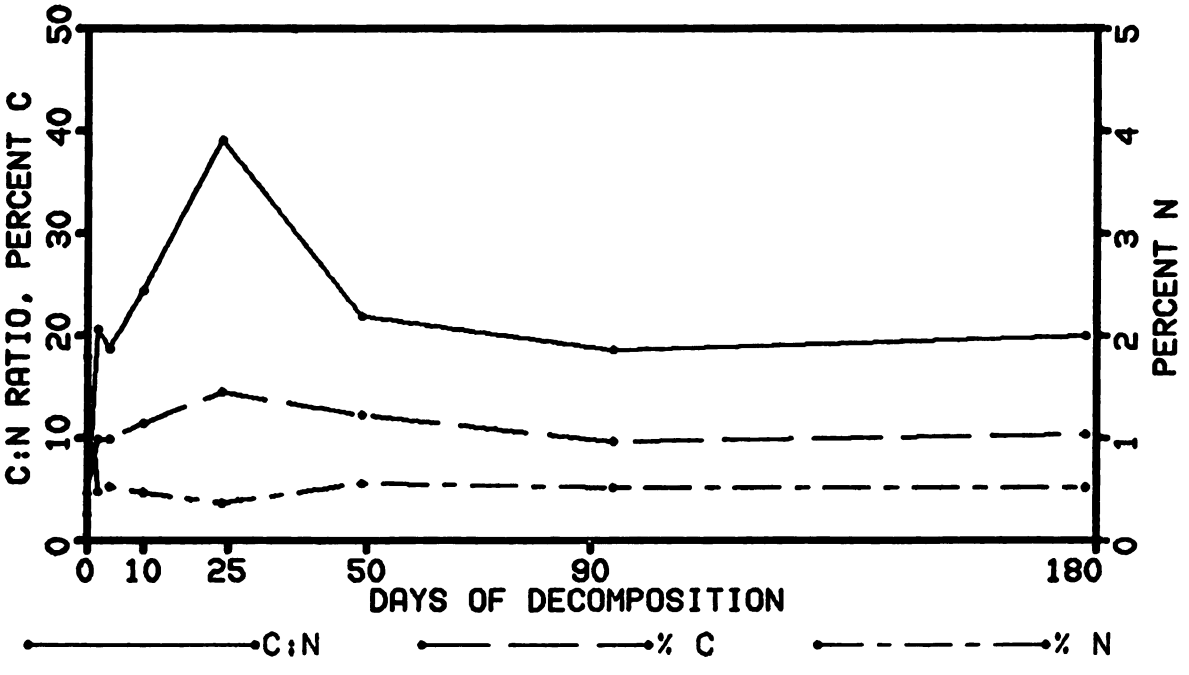
Appendix Figure 331. Decay of *Najas flexilis* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



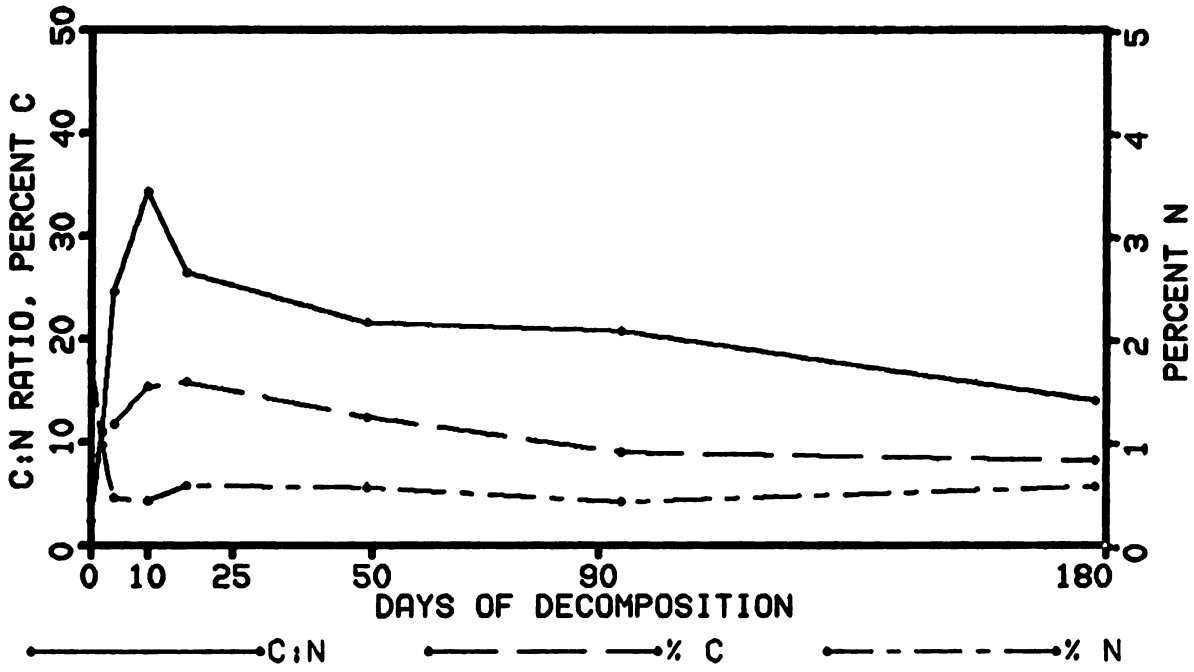
Appendix Figure 332. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



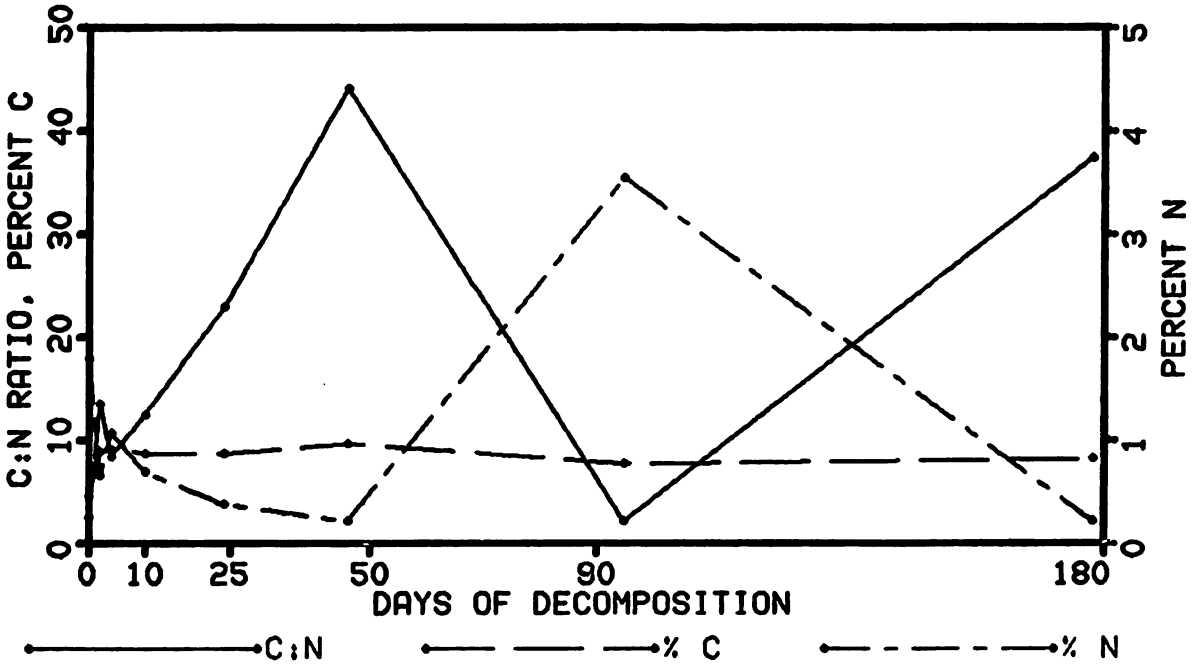
Appendix Figure 333. Decay of *Nuphar variegatum* in laboratory under aerobic-to-anaerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



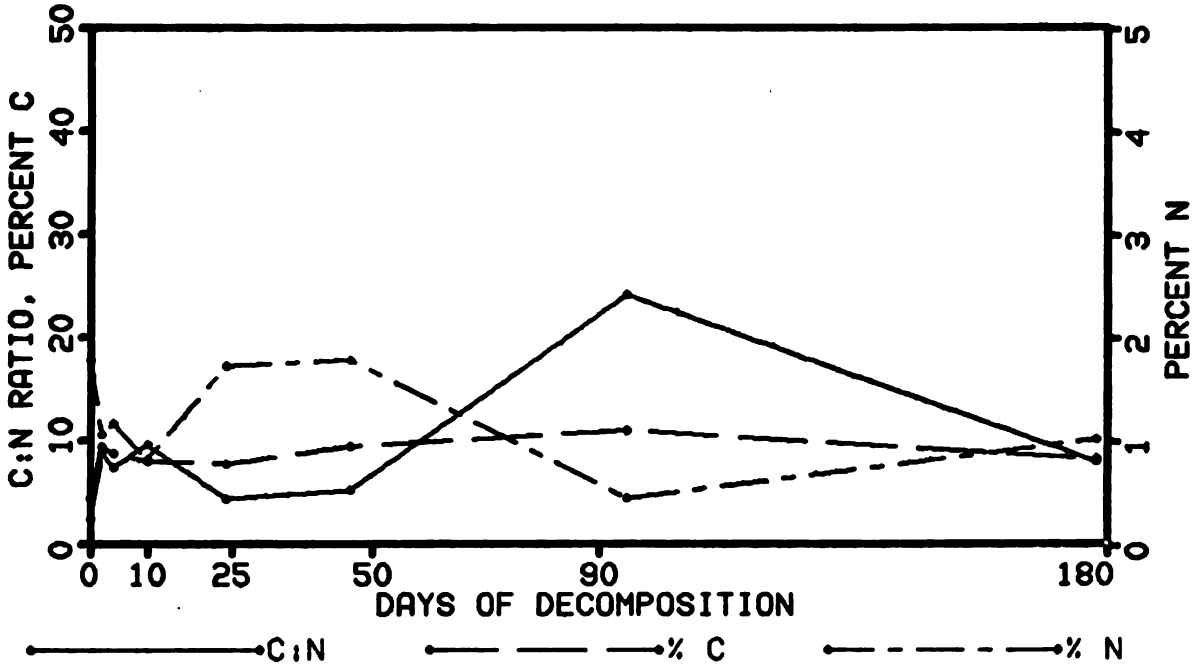
Appendix Figure 334. Decay of *Scirpus subterminalis* in laboratory under anaerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



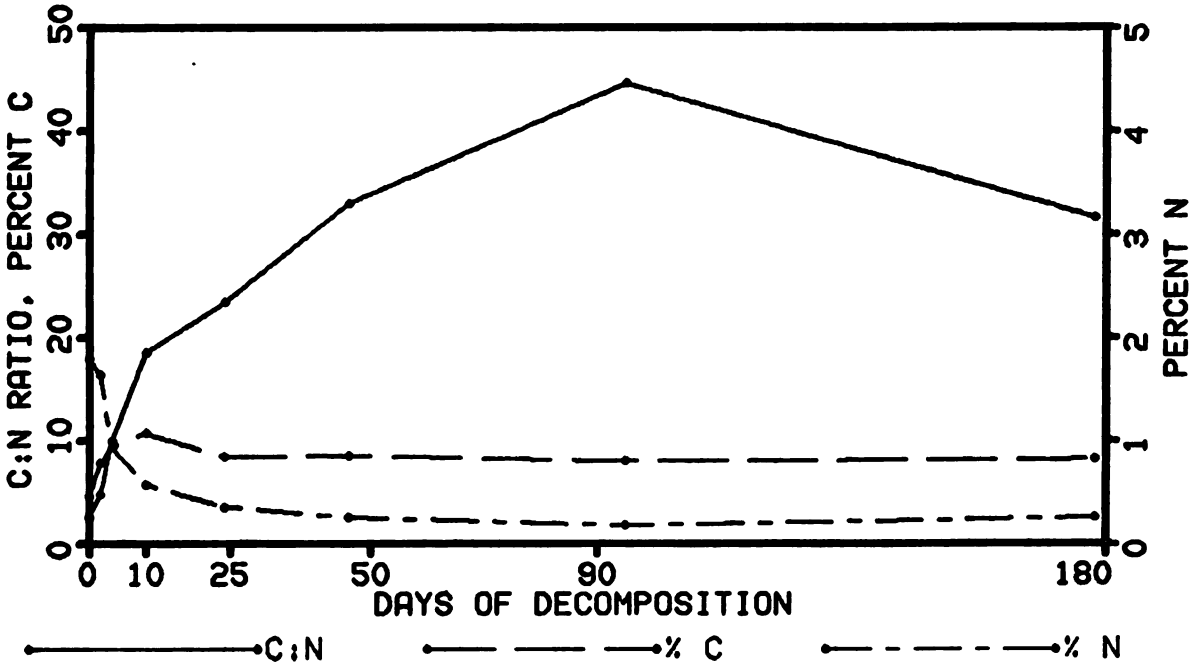
Appendix Figure 335. Decay of *Myriophyllum heterophyllum* in laboratory under anaerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



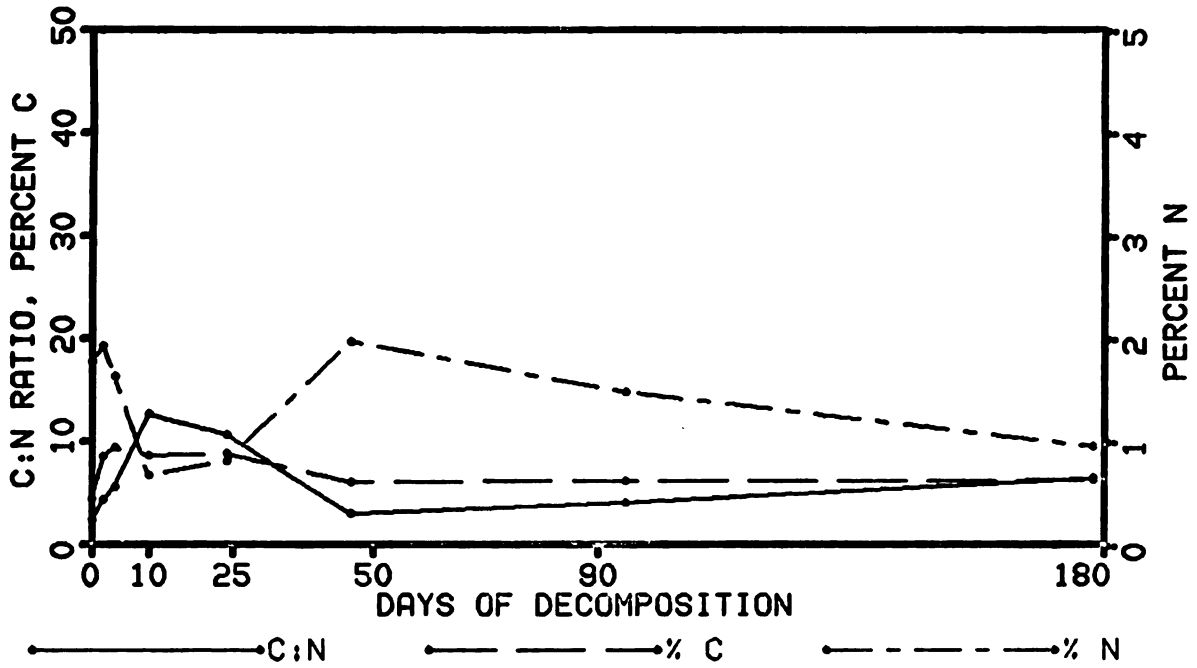
Appendix Figure 336. Decay of *Scirpus acutus* in laboratory under aerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



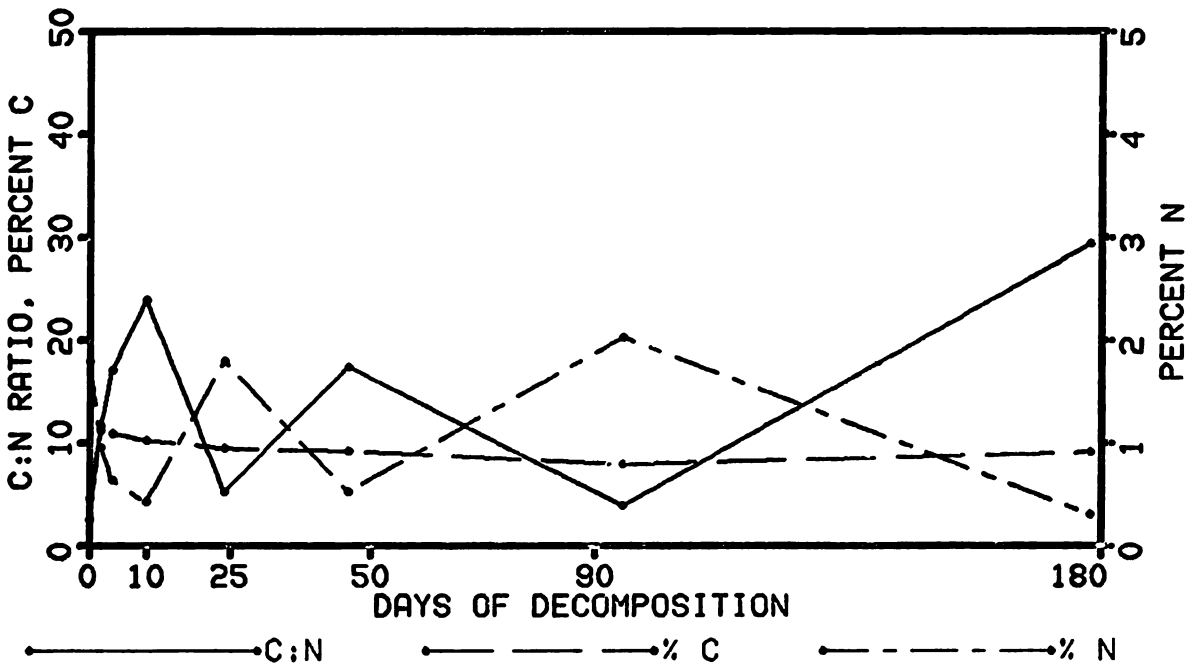
Appendix Figure 337. Decay of *Scirpus subterminalis* in laboratory under aerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



Appendix Figure 338. Decay of *Najas flexilis* in laboratory under aerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



Appendix Figure 339. Decay of *Myriophyllum heterophyllum* in laboratory under aerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.



Appendix Figure 340. Decay of *Nuphar variegatum* in laboratory under aerobic conditions at 25°C. Percent carbon and nitrogen and C:N ratio of residue of filtered (pore size 0.2 µm) lyophilized media.