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DECOMPOSITION IN SALT MARSH ECOSYSTEMS: THE PHASES AND MAJOR FACTORS AFFECTING DISAPPEARANCE OF ABOVE-GROUND ORGANIC MATTER

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Abstract: Decay of litter of salt marsh grasses occurs in three phases. First there is an early phase lasting less than a month, with fast rates of weight loss, during which 5 to 40% of the litter is lost, probably by leaching of soluble compounds. A second slower phase lasts up to a year. In this second phase, microbial degradation of organic matter and subsequent leaching of hydrolyzed substances remove an additional 40 to 70% of the original material. A third phase may last an additional year; in this phase decay is very slow because only relatively refractory materials remain. By this third stage as little as 10% of the original material may remain.

Differences in the chemical makeup of litter are the major factors affecting the amount of decay during the leaching and decomposer phases. Such chemical differences may be due to differences in the chemistry of the plant species producing the litter or in nutrient supply. *Spartina patens* (Ait.) Muhl., for example, produces litter that decays more slowly than that of *S. alterniflora* Loisel. Increases in internal nitrogen content of litter increase loss of weight during the leaching and decomposer phases, while the external supply of nitrogen increases decay rates only during the decomposer phase. Temperature increases decay rates to some extent during the decomposer phase. The feeding activity of large detritus-feeding invertebrates produces a small but significant increase in decay rate during the decomposer phase.

Decay rate in litterbags mimics decay of litter in the field, and makes possible estimates of litter turnover. The turnover of litter of *S. alterniflora* was $1.1-1.4 \cdot \text{yr}^{-1}$. Litter of *S. patens* turns over more slowly, $2.1 \cdot \text{yr}^{-1}$. Nutrient enrichment accelerates turnover of litter up to 24% compared to control litter. Since eutrophication of salt marshes both enriches litter and changes species of plants, it has broad consequences for ecological processes dependent on decomposition of organic matter.

Key words: salt marsh litter; detritus; decay; *Spartina alterniflora*; *Spartina patens*; *Distichlis spicata*

¹ Contribution No. 5681 from the Woods Hole Oceanographic Institution.

INTRODUCTION

Primary production by salt marsh vegetation can be very high, reaching $4\text{--}5 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Valiela *et al.*, 1976), but only a few percent of the annual above-ground production is consumed by herbivores (Teal, 1962). In a New England salt marsh, an amount of organic matter equivalent to $\approx 20\%$ of the above-ground production is removed annually from the marsh surface by tidal flushing (Valiela *et al.*, 1982). About 5% of the annual production accumulates below ground as peat (Valiela & Teal, 1979). Thus, $\approx 80\%$ of the biomass produced above ground and 95% of that produced below ground must decay within the marsh. In view of the relatively high rates of primary production, decomposition has to be a very active process in salt marsh ecosystems.

The relatively small herbivore consumption means that most of the annual production in salt marshes becomes litter and then detritus, and this dominance of the detrital path of organic matter over the herbivore path makes salt marshes a suitable environment to study interactions between decomposers and detritus.

In this paper we deal with the pattern of disappearance of above-ground litter in the field and evaluate some major variables determining rates of loss of litter: time under water, internal and external nitrogen content, temperature, and activity of detritivores.

The decay of plant litter starts with an initial fast phase during which soluble substances are leached out of the litter (Dickinson & Pugh, 1974; Anderson & MacFadyen, 1976; Godshalk & Wetzel, 1978; Swift *et al.*, 1979; Andersen & Hargrave, 1984). Following this is a slower, more protracted phase during which losses of organic matter are mediated by activity of decomposers (Saunders, 1976). These organisms consume litter and make some of its components soluble and thus leachable. Decomposer activity proceeds until only the more refractory compounds remain.

Major variables likely to determine rates of disappearance of organic matter in each phase are listed by Swift *et al.* (1979). Experiments with salt marsh detritus suggest that the time that litter is under water (Kruczynski *et al.*, 1978; White & Trepani, 1982) and type of litter (White *et al.*, 1978; McKee & Seneca, 1982) are important. Decay increases in the laboratory when nitrogen supply is higher (Haines & Hanson, 1979; Marinucci *et al.*, 1983), as occurs with other kinds of organic matter (Mann, 1976; Park, 1976; Berg *et al.*, 1982). Feeding of detritivores may also enhance decay (Lopez *et al.*, 1977; Briggs *et al.*, 1979). Temperature of the water also may change the rate of decay of marsh detritus (White & Trepani, 1982).

In this paper we describe the use of litterbags and various experimental procedures in the field to manipulate the time that litter was under water, vary the initial percent nitrogen in the litter and the nitrogen concentration in the environment where litter was decaying, and also set up experiments that excluded large invertebrate detritus-feeders. We also took advantage of seasonal changes in temperature of tidal water to see if decay rate changed as temperature changed. In each case, we followed the course of decay over time to see the effect of the various factors during the different phases of decay.

The study was carried out in Great Sippewissett Marsh, a representative New England salt marsh in which we have carried out many studies (Valiela *et al.*, 1976; Valiela & Teal, 1979). Among other things, we have measured primary production (Valiela *et al.*, 1975; Valiela *et al.*, 1976) and discussed some dynamics of decomposition and energy flow (Howarth & Teal, 1979, 1980; Howes *et al.*, 1984, 1985) in Great Sippewissett Marsh.

MATERIALS AND METHODS

CONSTRUCTION AND HANDLING OF LITTERBAGS, ASSESSMENT OF LITTERBAG METHOD

Litterbags were constructed of nylon mesh (2×4 mm opening) and were large enough to hold 50 g of dry litter. The mesh was large enough to admit virtually all the larger detritivores except fish and fiddler crabs. These two groups feed primarily in creek banks and bottoms, and gut analyses show that they ingest only small detritus particles, not litter such as included in litterbags.

Litter was collected in October (the time when plants senesce), except where otherwise indicated, air-dried, and weighed. The litter was placed whole as collected into the litter bags, rather than ground (Gosselink & Kirby, 1974), since the intent of this study was to follow as closely as possible the course of events in natural litter from the time of senescence of the plants until the detritus was largely gone.

All litterbags in the experiments were anchored loosely to the sediment with thin wire wickets, labeled with coded plastic tags, and left in the marsh until collected at the appropriate time.

Litterbags have several drawbacks. Meshes large enough to allow entrance of animals may also allow loss of litter fragments, especially during handling. We measured this loss by running through the usual packing procedures, transport, and installation in the field. The bags were then immediately removed and the litter was reweighed in the laboratory. We used air-dried new litter so that maximum losses could be measured.

Litterbags also contain sediment after exposure in the marsh. The choice is then to include the sediment in the weight and chemical measurements, or to rinse the litter gently and risk washing out some of the litter material. Losses of soluble material by rinsing are not likely to be great, because salt marsh litter is exposed to twice daily immersion in water. We checked to see how much particulate organic material was removed by the rinsing in a separate experiment. We set out four litterbags in the different habitats of the marsh (see below for description). When the litter was 19.5 months old we brought the bags into the laboratory, rinsed one-half of them, and obtained dry weights, ash, water, carbon, nitrogen, and sulfur contents. The concentrations of the latter three elements were determined by a Perkin-Elmer elemental analyzer. All the water used in the rinsing was collected and the particulate matter in the rinse water was filtered, dried, weighed, and ashed. We incubated the bags for 19.5 months so as to use older detritus. This gave us an assessment of the maximum

extent of the problem, because old litterbags would have been exposed to more sedimentation and reworking by animals.

The loss of weight recorded from litterbags is not exactly equivalent to a decay rate. The weight losses may include fragmentation and removal of particles, leaching of soluble materials, as well as degradation of organic matter.

After collection and washing, the litter from each bag was dried at 10 °C until dry and a random subsample milled in a Wiley mill. The percent nitrogen, carbon, and sulfur were measured with a Perkin-Elmer elemental analyzer.

EXPERIMENTAL DESIGN AND TREATMENTS

The experiments in which decay of litter within litterbags was followed were first performed in 1977 and repeated in 1979. Litterbags for 1979 experiments were set out soon after the stands of marsh plants senesced in early fall. Enough bags were initially set out in each treatment combination (described below) to allow for sampling at 2 wk, 1 month, and four or five other dates up to 600–700 days. Two litterbags per treatment combination were collected at each date.

The 1977 experiment consisted of two series of measurements on litterbags. One was carried out during an initial period (0–270 days) and was done with bags started October 1977 with recently dead litter. The second was carried out with bags started in June 1977, containing litter from plants that died the previous October, so the age of the litter was 240 days at the start of the experiment and 590 at the end. These two series were combined so as to represent one sequence of decay from recently dead to very old detritus.

The 1979 litterbag experiment was started in October with recently dead litter and followed for up to \approx 700 days. In the 1979 experiments, litterbags from inside the enclosures were only sampled from 300 days onward, because we knew from the 1977 experiment that there were no effects of detritus-feeders during earlier phases of decay.

The experiments of 1977 and 1979 were carried out within treatments that tested how decay was affected by time under water, plant type, internal and external nitrogen supply, detritus-feeders, and temperature.

EFFECTS OF AMOUNT OF TIME UNDER WATER AND PLANT TYPE

The effect on decay of time under water and grass type was studied by incubating litterbags at different elevations within the intertidal range. Three major habitats within Great Sippewissett Marsh were used in this study. The high intertidal zone is dominated by *Spartina patens* (Ait.) Muhl. and is flooded by tides only a few times a month; we refer to this area as the high marsh (HM). The creekbanks (CB) at the lower end of the vegetated zone are covered by tall plants (1–2 m) of *S. alterniflora* Loisel. These tall plants are found about mean high tide level, and are submerged almost twice daily. The vegetation of sediment at intermediate elevations is characteristically dominated by shorter (\approx 10–50 cm) plants of *S. alterniflora*; this habitat we refer to as the low marsh (LM).

Litterbags were located in each of the three sites, and were, therefore, exposed to a different length of time under water. At each site we measured tidal height so that we could calculate the length of time that litter was submerged. Tide height was recorded by painting tide staffs with a water-soluble paint and measuring the height on the staff to which the tide water removed paint.

The bags incubated at each elevation contained litter from the particular elevation. There was some overlap in the elevational range of the three vegetation types in our sites. Comparison of litterbags containing different types of litter but located at the same elevation enabled separation of effects of litter type from elevational effects.

EFFECTS OF INTERNAL AND EXTERNAL NITROGEN SUPPLY

To test the effect of nitrogen supply, we used plots that we eutrophied experimentally. We have maintained since 1971 a series of experimental plots 10 m in radius to which fertilizers are added (Valiela *et al.*, 1975; Valiela *et al.*, 1976). Two control plots (C) and two plots (F) that receive $75 \text{ g} \cdot \text{m}^{-2} \cdot \text{wk}^{-1}$ of a mixed fertilizer (N: 10%; P: 6%; K: 4%) from March through November were used in this study. The vegetation in the fertilized plots is enriched in percent nitrogen (Vince *et al.*, 1981) as is the litter that appears after senescence of the plants. We therefore had available litter that contained different initial amounts of % N. Litterbags were set out in the treated plots from which the litter was obtained. The fertilization treatments continued through the present study, so the external supply of nitrogen available to the litter was also higher for litter located in the fertilized plots compared to litter in control plots.

To test whether the initial internal nitrogen content of the tissues or the increased nitrogen in the environment had a more important effect on decay rate, we carried out a supplemental litterbag transplantation study. We collected litter from CB habitats within fertilized and control plots, and installed bags containing this litter within the donor plot and in the alternate treatment. Thus there was enriched litter undergoing decay in a fertilized plot and in a control plot, and unenriched litter decaying in a control and a fertilized plot. These litter transplantation experiments were carried out in 1979. The litterbags in these transplantation experiments were anchored in intertidal creek bottoms, just below the creekbanks. Twenty-four bags were started, and two bags per treatment combination were harvested at intervals.

Marsh plants contain different amounts of nitrogen at different times of year (Vince *et al.*, 1981). To see if loss of organic matter and nutrients of litter differed when plant death took place at different times of year, we ran these transplantation experiments with a set of bags started in July and a second set of bags started in October. Litter for the July litterbags was obtained by collecting newly dead leaves around the base of live plants. This design provided two differing types of litter as well as two very different temperature regimes for the decay processes.

INTERACTION OF SPECIES OF LITTER, ENRICHMENT, AND ELEVATION

So far we have focused on main effects of variables, but there may be important interactions among the variables. To examine the effect of elevation and enrichment in litter of different species we carried out a second supplementary transplantation experiment. These experiments were started in the fall soon after senescence of the sward in 1982 and 1983, and included litter of *S. alterniflora*, *S. patens*, and a third marsh grass, *Distichlis spicata* (L.) Greene. The design consisted of locating bags containing litter of each of the three species high in the tidal range (HM) and low in the tidal range (CB). The experiments were done with control and enriched litter.

Replication and handling of the litter bags from this experiment was as described in earlier experiments.

EFFECTS OF DETRITUS-FEEDERS

To assess the importance of feeding by detritivores, we ran the litterbags of the 1977 and 1979 experiments within and outside of exclosures. Circular exclosures 1 m in diameter were constructed to exclude invertebrate and fish detritus-feeders > 2 mm in length. The exclosures consisted of a metal apron sunk 20 cm into the sediment. Welded to this apron were upright iron bars that supported plastic window screening (mesh opening \approx 1.5 mm) sides for the exclosure. A band of thin aluminum sheeting was stapled to the top edge of the exclosure and then the band was creased outward along the upper edge of the exclosure to prevent invertebrates from crawling up the mesh into the exclosure.

Before the growing season each year the exclosures were treated once with a light application of a short-lived molluscicide and an insecticide (marlate). Any remaining large invertebrates were picked out by hand. The hand removal was repeated at intervals and effectively removed large detritus-feeders from the exclosures, but it was not possible to prevent larvae from settling into the exclosures. Young snails (*Melampus bidentatus* Say) were removed during the repeated checking as soon as they were large enough to be seen. Our manipulation markedly reduced densities of large detritus-feeders compared to those outside the exclosures.

Caging experiments in soft sediments often may lead to artifacts due to the cages themselves. In our case, the mesh never became fouled and we checked repeatedly to make sure that the drainage inside the exclosures was normal. There was no noticeable change in the sediment inside the exclosures relative to outside the exclosures. There were also no changes in the vegetation inside the exclosures, another indication that the sediment was not greatly affected.

TEMPERATURE OF TIDAL WATER

We used the seasonal changes in sea-water temperature as a way to examine how temperature alters decay rates. Continuous records of sea-water temperature at Woods

Hole are kept by the Woods Hole Oceanographic Institution. We have an additional series of intermittent temperature records obtained during a study of tidal flow in Great Sippewissett Marsh, and these were correlated to the Woods Hole temperatures. The relationship was excellent ($r = 0.97$) and enabled an extrapolation to average temperatures of tidal water at Great Sippewissett Marsh at any time. This procedure allowed us to estimate the temperature of the water over the litterbags throughout the study.

RESULTS

EVALUATION OF LITTERBAG PROCEDURES

The changes in litter weight due to handling procedures were quite small (CB: -0.3 ± 0.1 ; LM: 0.5 ± 0.2 , HM: -0.3 ± 0.2 , all mean \pm SE of percent of initial weight). Losses of organic matter during handling were thus not significant relative to other losses.

Rinsing sediment off the 19.5-month-old litter removed between about half the dry weight found in litterbags retrieved from creekbanks and 4% of the weight of litterbags from high marsh (Table I). The litter that was rinsed had a lower ash content compared to unrinsed litter in creekbanks and low marsh (Table I, column 2), suggesting that rinsing removed sediment. The material rinsed off the litter had a considerably higher ash content than plant litter (Table I, column 3), but not quite as high as the surrounding marsh sediment (Table I, column 4). Using the ratios between percent ash in rinsed litter and sediment, we calculated the amount of inorganic sediment in the material rinsed off the bags (Table I, column 5). Sediment made up 83% of the weight of the rinsed material from creekbank litter, and about half the weight rinsed off low marsh litter. Rinsing thus caused a loss of 14 and 16% of weight of litter in creekbanks and low

TABLE I

Effects of rinsing litter from each of the three habitats to remove sediment prior to analysis.

	Weight lost by rinsing (%)	Ash (%)	Ash in material rinsed from bags (%)	Ash in salt marsh sediment (%)	Sediment in material rinsed from bags (%)	Loss of litter weight (%)
Creekbank						
Rinsed	45.8	31.3 ± 0.7	56.6 ± 0.2	86.6 ± 1.4	83 ± 0	14 ± 2
Unrinsed		55.4 ± 3.2				
Low marsh						
Rinsed	38.2	39.4 ± 0.4	53.8 ± 1	66.1 ± 1.1	46 ± 10	16 ± 4
Unrinsed		54.1 ± 0.1				
High marsh						
Rinsed	4	15.1 ± 2	28.7 ± 2.9	59.8 ± 1.9	20 ± 2	5 ± 1
Unrinsed		12.4 ± 0.9				

marsh, respectively. These losses are not greater than the variation among replicate litterbags. In the case of the litter from high marsh, there was only $\approx 20\%$ sediment in the material rinsed from the bags (Table I, column 5), due to reduced sedimentation and resuspension in high marsh. Here, the amount of litter lost by rinsing was only 5%. The washing is thus justified in view of the large weights of sediment we would otherwise have included in our measurements of weight and composition of material within the bags. Because we chose rather old litter exposed to much sedimentation to carry out this check on the method, the calculations of Table I are a worst-case example. Thus the method used was an adequate procedure to remove sediment from the litter while minimizing losses of the original organic matter.

WEIGHT LOSS OVER TIME

The pattern of loss of organic matter consisted of a fast early phase, lasting 2–4 wk, a slower phase up to 350 days (perhaps longer in high marsh), and a phase in which losses of weight were much slower (Fig. 1). We will refer to these as the leaching, decomposer, and refractory phases. These are to an extent misnomers, because leaching of hydrolyzed compounds takes place during the decomposer stage and some decay of the organic matter must take place even in the “refractory” phase. The point, however, is that loss of organic matter follows a sequence of fast, intermediate, and low rates, and that the major mechanisms leading to loss of organic matter in each phase differ.

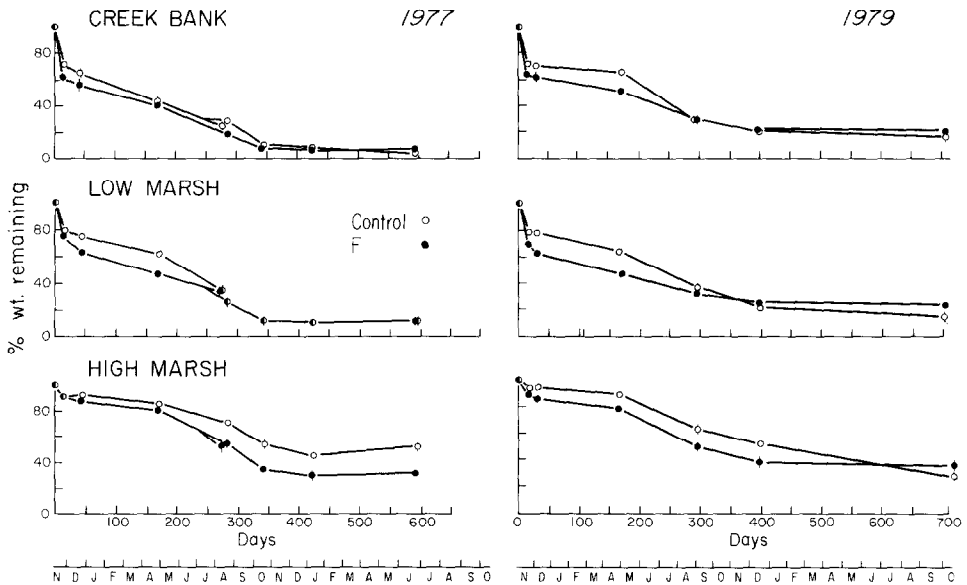


Fig. 1. Percent of weight remaining in litterbags incubated in three different habitats (creekbanks where tall *Spartina alterniflora* grows, low marsh where short *S. alterniflora* grows, and high marsh where *S. patens* grows): the litter in the bags was native to the habitat where the bag was incubated; litter from control and experimentally fertilized (F) plots was used.

These three phases occurred, with some variation, in all habitats and all treatments. During these three stages, the litter imperceptibly became fragmented detritus and resembled the organic matter on the sediment surface but was still microscopically recognizable as originated from marsh grasses.

In the decomposer phase there was a slower rate of loss during the winter months, with an acceleration during spring (Fig. 1). This may be due to the effect of temperature on activity of organisms.

CONCENTRATIONS OF CARBON, SULFUR, AND NITROGEN THROUGH TIME

The carbon content of the litter was unvarying throughout the various treatments (Fig. 2, top three graphs). New litter of *Spartina alterniflora* averaged 40% carbon and slowly decreased to 30–35% by 600 days. Litter of *S. patens* averaged 41% carbon initially and decreased to 40% after 600 days.

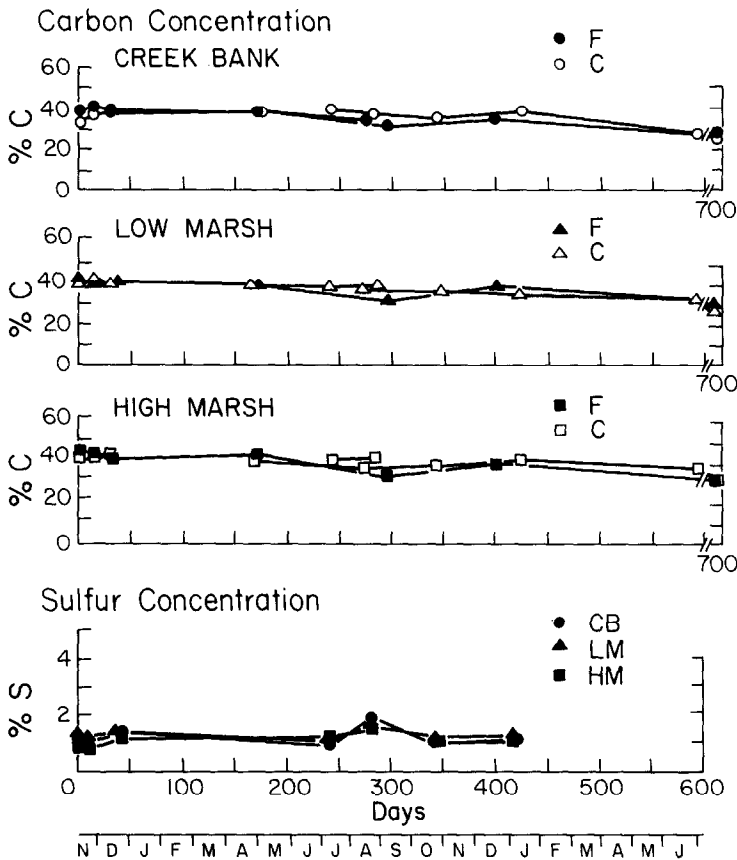


Fig. 2. Carbon and sulfur concentration (% by wt) of litter from the various treatments during the course of decay: carbon content of the experimentally fertilized (F) and control (C) plots are shown, for litterbags incubated in each of the three different habitats; for sulfur, there were no differences between C and F, so that data were pooled, and included for creekbank (CB), low marsh (LM), and high marsh (HM).

The sulfur content of litter was not changed by the treatments or time, and averaged 1% (Fig. 2, bottom). Values for the various treatments were thus not differentiated in Fig. 2.

The nitrogen content varied over time and with treatment. The initial percent nitrogen in fertilized litter was about three times that of control litter (Fig. 3). There were no prominent differences between the 1977 and 1979 results or between bags inside and outside exclosures, so these sets of data are not differentiated in Fig. 3. During the first

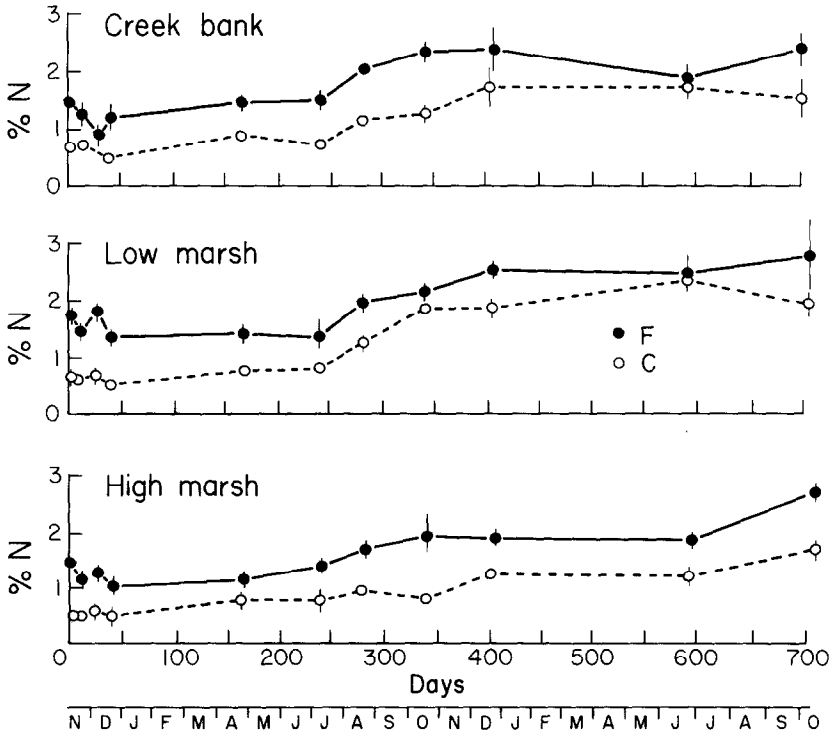


Fig. 3. Nitrogen concentration (mean % \pm SE by wt) of litter from the various treatments during the course of decay: the data from fertilized (F) and control (C) litter are shown for each of the three habitats.

month there was a net loss of $\approx 0.5\%$ N in fertilized litter and about half that in control litter. Nitrogen content changed little during the first winter, while by the end of the warm months nitrogen content increased in all habitats, exceeding initial amounts of nitrogen. This net increase in nitrogen content in summer took place at the same time that an accelerated net loss of weight was observed (Fig. 1). There was a convergence of percent nitrogen in litter of *S. alterniflora* during the second fall and winter (Fig. 3, top and middle), but not in litter of *S. patens* (Fig. 3, bottom). *S. patens* litter rarely exceeded 1% nitrogen while untreated litter of *S. alterniflora* exceeded 2% nitrogen. All litter types showed increases in nitrogen content over time, as found in other studies (Godshalk & Wetzel, 1978; Rice & Tenore, 1981).

We should reiterate here than our measurements of weight and elemental contents are values obtained at one time. The actual weights or element molecules could or could not have been those originally present in the litter.

MAJOR VARIABLES AFFECTING LOSS OF ORGANIC MATTER FROM LITTER

Effects of time under water and litter type

The rate of weight loss during the leaching phase was greatest the lower the litter is found in the intertidal zone. Litterbags low in the intertidal range (CB) lost 30–40% of their weight during this phase (Fig. 1, top), while bags in HM lost only \approx 5–15% of their weight (Fig. 1, bottom); 1977 and 1979 results were similar.

Leaching of soluble materials may be related to the time that litter is submerged in tidal water. The measurements of tidal elevation of each of the sites where the litterbags were placed were used in combination with continuous tide gauge records available from previous work on the same site to calculate the number of hours that each litterbag was

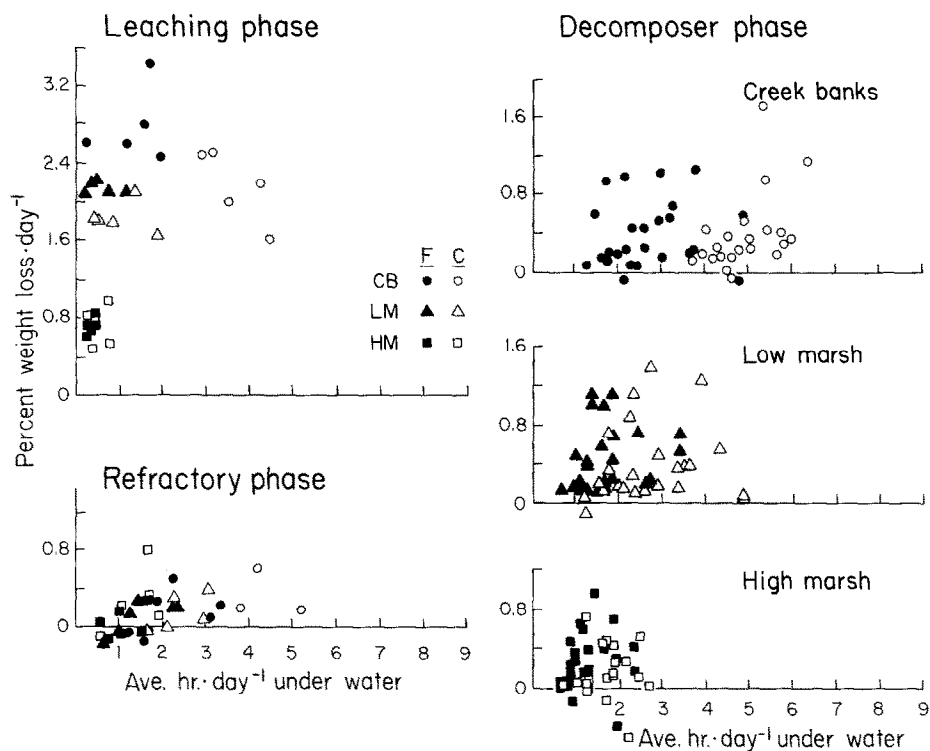


Fig. 4. Rate of weight loss as a function of time under water plotted separately for the three phases of decay: fertilized (F) and control (C) litter, incubated in each of the three habitats (CB, LM, HM); because of the large numbers of points, the data for the decomposer phase are shown in separate graphs for each of the three habitats.

covered by marsh water. We also calculated the rate of loss of organic matter for each habitat and treatment from the slopes of Fig. 1.

Changes in duration of time under water did not change rates of weight loss within any one habitat or phase of decay (Fig. 4). The differences in rates are unrelated to submergence but depend on type of litter. For instance, during the leaching phase (Fig. 4, top left) the ratio of weight loss of litter of *S. alterniflora* (CB and LM) was more than twice that of litter of *S. patens* (HM). This was true even within the range of tidal elevation ($< 1 \text{ h} \cdot \text{day}^{-1}$ under water) where the CB, LM, and HM litterbags were covered by water for the same period of time. Thus, *S. patens* must have smaller amounts of easily leachable compounds than *S. alterniflora*.

Increases in amount of time under water did not increase decay rate of the litter from fertilized or control treatments during the leaching phase (Fig. 4, top left). There were no differences in rates of loss during the leaching phase due to the presence or absence of detritus-feeders, so these two treatments are not differentiated in Fig. 4.

The rates of weight loss during the decomposer phase were slower than during the leaching phase, and were not increased by increases in length of time under water (Fig. 4, right panels). For instance, the decay rates of the three litter types are very similar within the overlapping range of elevations ($1\text{--}3 \text{ h} \cdot \text{day}^{-1}$). The only difference was that the maximum rate of weight loss was somewhat smaller in high marsh than for other litters. The rates of loss of weight during the refractory phase were very low (Fig. 4, bottom left). There is no trend associated with increases in time under water.

Time under water in Great Sippewissett Marsh does not account for differences in decay rate among litterbags set in the various elevations. Rather, the different rates of decay during the decomposer phase in each litter type probably reflect differences in chemical makeup of the litter.

EFFECTS OF NITROGEN ENRICHMENT

Fertilized litter lost more weight during the leaching stage than control litter (Fig. 1). The effect was more prominent in litter of *S. alterniflora* than of *S. patens*.

To show how decay rate was related to %N, data of Fig. 1 were expressed as percent loss of weight per day and were graphed versus the nitrogen content at the start of each time interval (Fig. 5). During the leaching phase (Fig. 5, top left) the daily rate of weight loss increased with increased nitrogen content in litter of *S. alterniflora* (CB and LM), but not for *S. patens* (HM). During the leaching phase the %N would affect loss of weight only if there were larger amounts of soluble nitrogen containing compounds present in the fertilized litter.

During the decomposer phase nitrogen content did not greatly affect rate of weight loss (Fig. 5, right panels) and the correlations of loss of weight to nitrogen content of the litter were low (r values are inset in Fig. 5). The slight effect of nitrogen content is to an extent surprising, because we expected that increases in nitrogen would more substantially stimulate microbial degradation. The slight effect and large scatter suggest

that other factors also influence rates of weight loss. It is likely that not all the nitrogen present in the litter was available to decomposers, being bound to compounds such as lignins (Rice, 1982; Wilson, 1985). A more clear-cut effect could have resulted if we had used available instead of total nitrogen in Fig. 5.

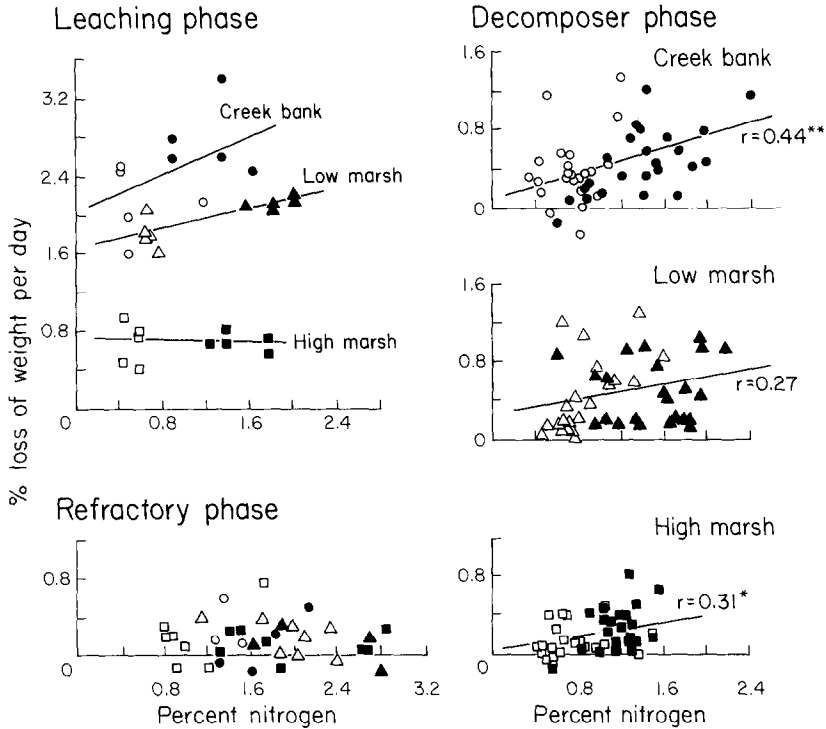


Fig. 5. Rate of weight loss plotted as a function of percent nitrogen during each phase of decay: lines are regressions; *, regression significant at 0.05 level; **, regression significant at 0.01 level.

The amount of nitrogen in control litter varied from ≈ 0.4 to 1.4% in all three habitats (Figs. 3,5). Fertilized litter had a similar range in high marsh but reached 2.4% in creekbanks. Either more nitrogen was bound to litter lower in the intertidal or there were significant differences among the three types of litter. Further experiments involving litter transplantation are needed to clarify this point.

During the refractory phase (Fig. 5, bottom left), even where the nitrogen content increased to over 2.8% (cf. Fig. 3), there was no effect of nitrogen content on weight loss. The nitrogen present may have accumulated as refractory compounds not accessible to microbial degradation (Rice, 1982).

The effects of initially larger nitrogen content on decay can be assessed in more detail by graphing the percent weight remaining in fertilized vs control litter (Fig. 6) for each

of the three phases of decay. During the leaching phase (Fig. 6, top right) decay increased in enriched litter relative to control litter in *S. alterniflora* (CB and LM) but not in *S. patens* (HM) litter (the squares are on the 1 : 1 line, but the circles lie below the 1 : 1 line). In the decomposer phase (Fig. 6, bottom) the losses of organic matter in

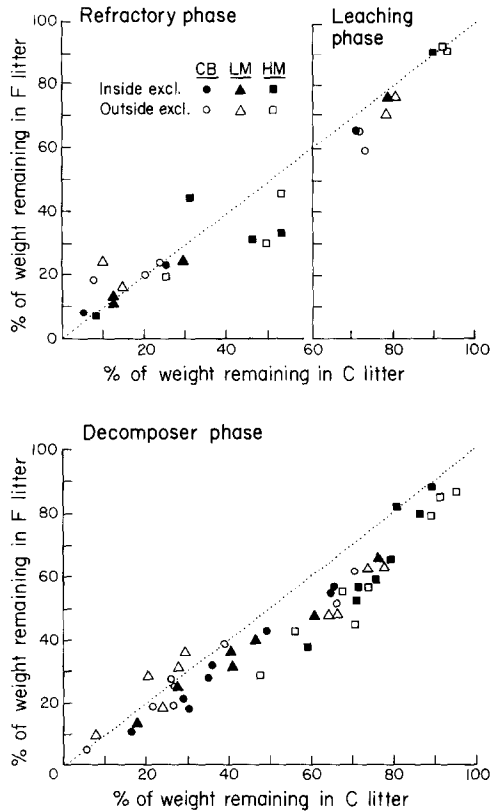


Fig. 6. Relation of weight remaining in fertilized litter vs. control litter, for each phase of decay: all treatments are included here; dotted line is the 1 : 1 line.

fertilized litter were greater than in control litter, until $\approx 40\%$ of the litter was left (the points at the start of the decomposer phase on the right of the graph lie below the 1 : 1 line until 40% of the litter is gone). After that, all points fell nearer the 1 : 1 line. Except for the leaching stage, in all instances the slopes of regressions differed significantly from equality (Table II). These results show that litter enriched in nitrogen lost weight at significantly faster rates than unenriched litter. Note that we have included points in the decomposer phase over a wide range of percent weight remaining (Fig. 6, bottom). This in part explains the scatter of points in the regression of Fig. 5 (right panels). Had we used only the points up to 40% remaining, the scatter around the regressions would have been reduced substantially. The point, however, is that increased nitrogen content

significantly affected loss of weight, and that this effect was prominent early in the decomposer phase.

TABLE II

Regression equations and correlation coefficient for data of Figs. 7 and 8: on the right-most column are the results of a comparison of the slope of the calculated regressions versus a 1 : 1 slope (Draper & Smith, 1966); the three habitats are pooled in the regressions for the leaching and refractory phases.

	Regression equation	<i>r</i>	<i>t</i> -test, <i>b</i> vs. slope of 1
Fertilized vs. control litter			
Leaching phase	$Y = -31.45 + 1.33X$	0.96	2.25 ns
Decomposer phase			
Creek bank	$Y = -0.45 + 0.86X$	0.98	2.83*
Low marsh	$Y = 9.00 + 0.67X$	0.97	6.02**
High marsh	$Y = -37.61 + 1.33X$	0.96	3.12**
Refractory phase	$Y = 7.16 + 0.58X$	0.89	4.80**
Inside vs. outside exclosures			
Leaching phase	$Y = 11.97 + 0.87X$	0.95	1.41 ns
Decomposer phase			
Creek bank	$Y = 7.77 + 0.90X$	0.95	1.52 ns
Low marsh	$Y = 13.71 + 0.75X$	0.88	2.91**
High marsh	$Y = 20.67 + 0.77X$	0.93	3.67**
Refractory phase	$Y = 4.26 + 1.01X$	0.88	0.05 ns

The significant difference in loss rate of enriched litter compared to control litter during the refractory phase (Table II) is due only to some of the high marsh values (Fig. 6, top left). Perhaps the lower intensity of leaching (Fig. 1), the somewhat dryer, perhaps less favorable habitat for microbes, and chemical makeup of *S. patens* combine to maintain the large difference in the %N (Fig. 3) throughout the history of HM litter.

The supplementary transplantation experiments (Fig. 7, left panels) done to separate the effect of internal from external nitrogen enrichments showed a pattern of loss of weight over time similar to that of the main experiments of 1977 and 1979. Two experiments are included in Fig. 7, one started in the fall, and a second started in mid-summer.

Litter grown in fertilized plots, and hence internally enriched in nitrogen (Fig. 7, top right), decayed at the same rate regardless of whether it was incubated in a control or fertilized plot (Fig. 7, top left). At the end of a year, <40% of the weight remained in both treatments.

Control litter incubated in the fertilized plot showed losses of weight quite similar to those found for enriched litter (Fig. 7, bottom left). In contrast, control litter incubated in the control plot lost less weight than the other three treatments. At the end of the experiment this treatment still retained >60% of the initial weight while the other treatments still retained ≈40% of the initial weight. Decay rate was thus slower where nitrogen supply, either internal or exogenous, was lower.

The effect of internal supplies seemed more important in the leaching phase since there were more soluble nitrogenous or other compounds to be leached in fertilized litter (Figs. 5 and 6). The effect of internal nitrogen was more important for litter of tall

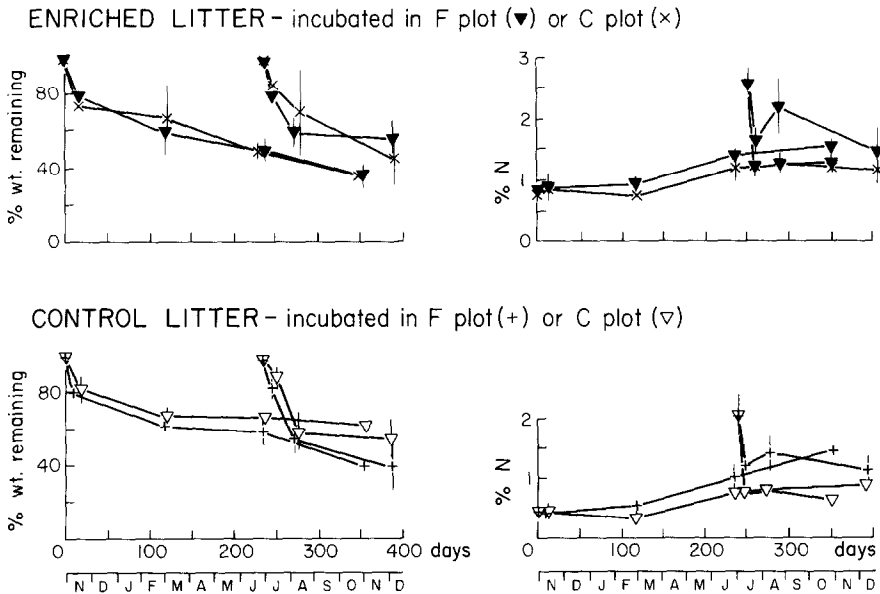


Fig. 7. Supplementary transplantation experiment to evaluate effect of internal vs. external nitrogen on decay of litter.

S. alterniflora than with other litter types (Fig. 5, top right). External supplies of nitrogen increased rates of weight loss during the decomposer phase (note that the lines for control litter incubated in control and fertilized plots diverge during the decomposer phase, Fig. 7, bottom left). The effect of the added external nitrogen during the decomposer phase was to roughly double the rate of weight loss of litter.

As in Fig. 1, the percent nitrogen of litter in the transplantation experiments increased slightly over 350 days (Fig. 7, right panels). Litter incubated in the enriched plots maintained higher nitrogen content than litter incubated in the control plot. The nitrogen content of the control litter incubated in the enriched creek increased so that by the end of the experiment its nitrogen content approached that of the enriched litter. In contrast, control litter incubated in the control plot had lower nitrogen content (Fig. 7, bottom right).

The weight remaining after a year in these transplantation experiments was larger than that of the main experiments (compare with Fig. 1). This was probably due to our having started the transplantation experiments later in the year than those of Fig. 1, so that the litter in the transplantation experiments had been exposed to leaching one or two weeks longer. This would have reduced the easily leachable fraction.

The transplantation experiment that started in June (Fig. 7) showed a time course similar to that seen in other experiments; summer litter lost more material during the leaching phase and had higher nitrogen content than fall litter. Fall litter may be lower in soluble compounds and nitrogen because by then the plants have translocated nutrient and energy reserves to the perennial underground parts. Litter originating at other times of year may have a different initial chemical makeup, but this difference is soon lost by removal of soluble compounds (Fig. 7, bottom right).

INTERACTIVE EFFECTS OF LITTER QUALITY AND ELEVATION

The interactive effects of litter quality (species and chemistry) and time under water (elevation) on decay were examined by the second supplementary transplantation

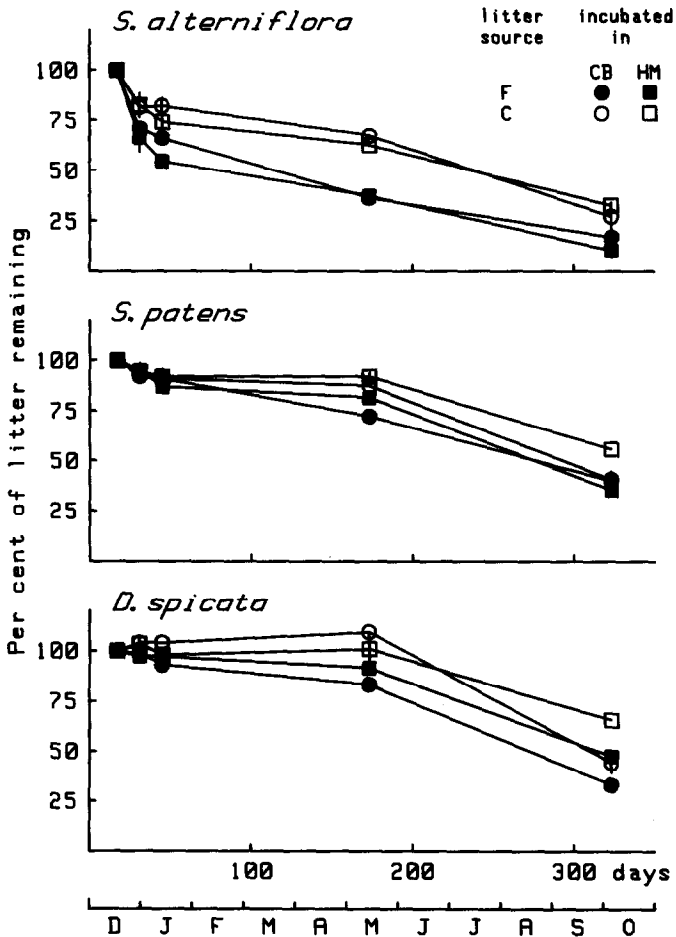


Fig. 8. Supplementary transplantation experiment to evaluate the effect of high (HM) or low (CB) elevation within the tidal range on decay of litter of three species of marsh grasses: mean % remaining \pm SE; the SE not shown where smaller than symbol.

experiment. Litter of *Spartina* grasses decayed at the same rate, regardless of location high (HM) or low (CB) in the intertidal range (compare circles to squares in Fig. 8). For a further comparison, we added another species, *Distichlis spicata* in this experiment. The differences due to elevation were also small for this species.

Enriched litter decayed faster than control litter in all three species (compare black to open symbols, Fig. 8). The effect of enrichment led to up to 20% differences in weight remaining at the end of the experiment (Fig. 8).

The clearest differences seen in Fig. 8 were due to the type of litter. First, the three grasses differed in the leaching phase, with a clear loss (as seen in Figs. 1 and 7) in *Spartina alterniflora* and a less pronounced loss in *S. patens*. *Distichlis spicata* showed no clear leaching phase (Fig. 8, bottom). Secondly, litter of *Spartina alterniflora* degraded more than that of *S. patens* and *Distichlis spicata*.

These results show that the loss of weight is influenced, as concluded earlier, by type of litter and nitrogen content. Elevation per se did not have an important main effect, nor did it clearly interact with type of litter or nitrogen enrichment.

EFFECTS OF TEMPERATURE

The importance of temperature varied depending on the phase of decay. Temperature had little effect on the rate of weight loss during the leaching phase (Fig. 9, top left). During the decomposer phase, however, there was increased weight loss when water

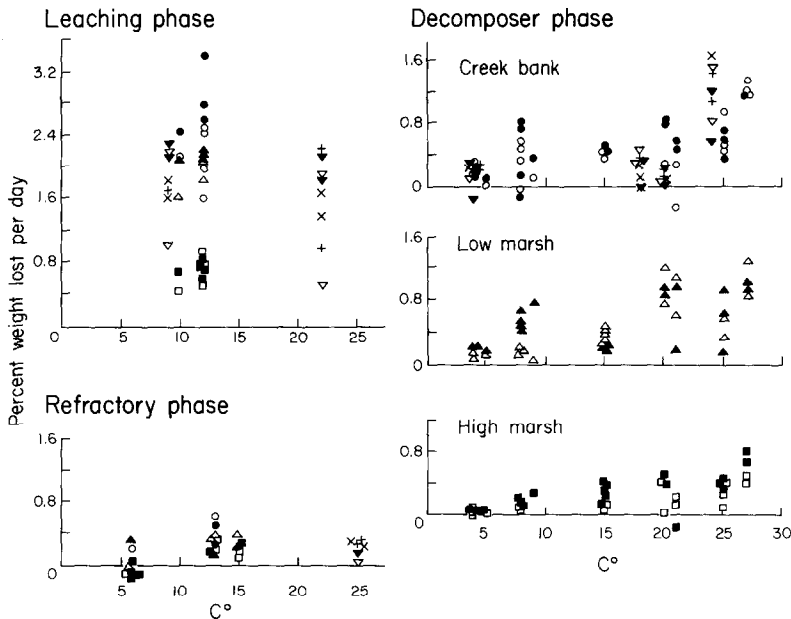


Fig. 9. Rate of weight loss as a function of temperature during each phase of decay: symbols as in Fig. 7 and all other figures.

temperature increased (Fig. 9, right panels). This can be seen in Figs. 1 and 8, and suggests that, as expected, decomposer activity is enhanced by higher temperatures. Temperature had no discernible effect on the low rate of weight loss during the refractory stage (Fig. 9, bottom left).

EFFECTS OF REDUCED DENSITY OF LARGE DETRITIVORES

The effect of lowered abundance of detritivores could be estimated by plotting the weight of litter remaining in bags inside exclosures versus weight of litter remaining in bags outside exclosures (Fig. 10). Losses of weight during the leaching phase were not affected by activity of large detritus-feeders (Fig. 10, top right). During the leaching phase there were no significant effects of exclosures – the slope of the regression does not differ from a slope of 1 (Table II, bottom).

In the decomposer phase (Fig. 10, bottom) weight losses tended to be smaller inside than outside exclosures, as seen earlier (Fig. 6). The slopes of the regression of the low and high marsh points were significantly different, while that for creek bank was not

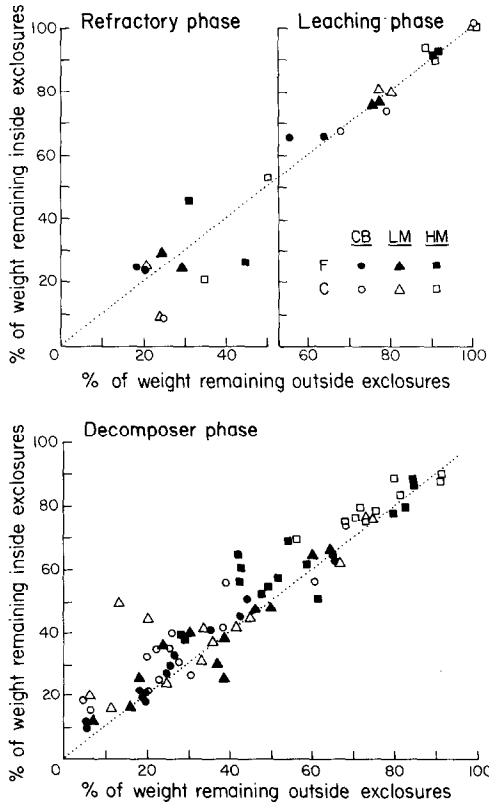


Fig. 10. Relation of weight remaining in litterbags located inside vs. outside exclosures, for each phase of decay: dotted line is 1 : 1 line.

(Table II, bottom). This suggests that the effects of detritus-feeders are more important in the upper reaches of the intertidal range; lower in the intertidal range other factors increased rates of weight loss and overwhelmed the effect of detritus-feeders.

The effect of detritus-feeders during the decomposer phase was not influenced by the nitrogen content of litter. There were no differences in weight remaining between litter inside and outside exclosures in the case of fertilized or control litter (Fig. 10, bottom), as shown by comparisons of the slopes of the regression lines fit to the F and C points within each habitat (Table III). None of the three *t*-tests was significant.

The differences in litter loss inside and outside the exclosures were independent of elevation or type of litter. We tested this by calculating the residuals from the line where loss of weight inside equaled loss of weight outside an exclosure. The contingency chi-square value for the frequency of residuals of different size in the three habitats was not significant. The scatter of the points was about the same in all three environments,

TABLE III

t-test for comparison of two slopes of regression lines (Steel & Torrie, 1960); the two regressions contrasted are the enriched and control values of the percent weight remaining during the decomposer phase.

	df	<i>t</i>
Creek bank	23	0.69 ns
Low marsh	22	1.21 ns
High marsh	23	1.00 ns

TABLE IV

Percent of weight (\pm SE) of litter remaining in bags exposed within exclosures (In) and outside exclosures (Out) at each of the three habitats: CB, creekbank; LM, low marsh; HM, high marsh; F and C, fertilized and control litter.

		Weight remaining (%)					
		CB		LM		HM	
		In	Out	In	Out	In	Out
Experiment started in 1977							
After	F	21.2 \pm 0.5	18.9 \pm 0.9	36.6 \pm 1.1	31.0 \pm 7.6	59.0 \pm 4	44.8 \pm 2.9
272 days	C	28.8 \pm 3.7	21.5 \pm 1.4	40.3 \pm 3.7	35.3 \pm 0.3	75.6 \pm 0.2	70.4 \pm 2.6
After	F	10.9 \pm 0.4	5.1 \pm 0.1	13.4 \pm 2.0	10.9 \pm 4.8	38.2 \pm 0.3	28.6 \pm 0.7
340 days	C	16.2 \pm 1.4	5.2 \pm 0.8	17.6 \pm 1.7	8.0 \pm 2.0	58.9 \pm 1.4	47.3 \pm 4.3
Experiment started in 1979							
After	F	32.8 \pm 0.1	26.7 \pm 0.4	29.8 \pm 0.9	36.9 \pm 0.3	56.5 \pm 0.1	42.5 \pm 0.6
291 days	C	35 \pm 1.4	25.5 \pm 4.6	40.6 \pm 2.8	34.2 \pm 0.8	70 \pm 0	56.3 \pm 1.6
After	F	24.3 \pm 1.5	22.2 \pm 0	24.4 \pm 1	28.9 \pm 0.4	45.6 \pm 2.3	26.2 \pm 4.3
395 days	C	24.1 \pm 2.2	20.2 \pm 0.4	24.9 \pm 3.8	20.2 \pm 3.2	53.6 \pm 3	49.6 \pm 2.3

so that the effect of detritus-feeders was not influenced by elevation or plant species.

These statistical manipulations evaluate trends, but do not provide information on the magnitude of the effect of the exclosures. Table IV provides the actual values of percent of the litter weight left after various periods of time. The variation within litterbags treated alike is low. In 22 out of 34 cases the amount of litter left was smaller where large detritivores were more abundant. The differences range from 0.07 to 50%, most of them falling in the 0–15% range (Fig. 10, bottom). The presence of large detritus-feeders thus leads to about a 0–15% decrease in the weight left in litter after about a year of decomposition.

DISCUSSION

The pattern of fast rates of loss during early decay, followed by slower rates, has been found for many kinds of litter, including litter of salt marsh plants (Burkholder & Bornside, 1957; Gosselink & Kirby, 1974; Odum & Heywood, 1978; White *et al.*, 1978; Haines & Hanson, 1979; Lee *et al.*, 1980; Montagna & Ruber, 1980; McKee & Seneca, 1982; Marinucci *et al.*, 1983). The pattern of decay can be interpreted as three phases, in which different processes dominate each phase. Leaching of soluble materials may be the major mechanism during the fast early phase. Microbial degradation of organic matter, with leaching of decay products, are probably the major sources of weight loss in the second stage. The third stage is characterized by slow decay of fairly refractory materials.

The percent nitrogen in litter was initially lowered but then slowly increased, as is well known in other cases (Godshalk & Wetzel, 1978; Rice & Tenore, 1981), so as to exceed initial values. Carbon and sulfur contents were virtually constant over 2 yr of decay.

Our experiments showed that different factors influenced decay rates at different times during the process of decay. A rough ranking of the factors, and the phases during which these factors act, is shown in Table V. During the leaching phase elevation within the marsh – or time under water – had a marked effect on losses: the litter situated lowest

TABLE V

Relative ranking of importance of the variables studied in regard to their effect on rate of decay, and phase in which the variables act: 0, not significant; +, significant at 0.05 level.

	Phase of decay		
	Leaching	Decomposer	Refractory
1. Species of litter	+	+	0
2. Temperature	0	+	0
3. Internal nitrogen	+	+	0
4. External nitrogen	0	+	0
5. Large detritus-feeders	0	+	0

in the tidal range lost more than twice the weight than that in the highest location. This effect, however, was – within the range of submergence times in our site – mainly due to the nature of the litter from different elevations rather than to time of submergence per se, as demonstrated by our transplantation experiments. Within a single type of litter there were no increases in rate of decay at longer submergence times. Salt marsh litter seldom dries out; the organic matter is generally at least moist, microbes and other decomposers are probably active throughout the tidal range, and additional wetting by increased hours underwater did not directly increase decay. Similar results were obtained by White *et al.* (1978), who studied decay of litter of *Spartina alterniflora* and *Distichlis spicata* in litterbags placed side by side at the same elevation. Tenore *et al.* (1982) also conclude that type of detritus is the key factor setting decay rates.

White & Trepani (1982) concluded that time under water affected rate of decay of *Spartina alterniflora*, since loss of weight decelerated when tidal circulation decreased in winter. Perhaps a more likely explanation is that, as they show, temperature also decreased in winter and was responsible for the lower decay rates. We saw such an effect of temperature during the decomposer phase when increases in temperature increased rates of weight loss up to ≈ 10 times compared to colder temperatures (Fig. 9, right panels). The temperature-induced high rates of decay, however, apparently did not last long enough in our experiments to exceed the effect of litter type.

Fertilized plots produced enriched litter that lost more weight than control litter. The differences during leaching were primarily due to differences in losses of soluble materials. During the decomposer phase the rate of weight loss in litter enriched in nitrogen doubled (in *S. patens*) or quadrupled (in tall *S. alterniflora*) compared to nitrogen-poorer litter (Fig. 5, right panels). This again emphasizes that losses in weight during the leaching phase are affected by the chemical nature of the original plant tissues.

Nitrogen for degradation of detritus can be supplied internally or externally. Increases in internal or external nitrogen supply led to similar quantitative increases in decay rates and nitrogen content (Fig. 7, left panels). There were greater soluble losses during the leaching phase associated with higher internal nitrogen contents, so that the internal nitrogen probably has a somewhat greater overall effect on loss of weight (Table V). We should add here that it would be far better, if possible, to consider the pool of nitrogen available to decomposers rather than the total nitrogen content (Rice, 1982).

The effects of large detritus-feeders were significant but not as large as those of the other factors studied. The biomass of detritus-feeders in fertilized plots was four- to five-fold that in control marsh plots (unpubl. data). The enclosure experiments showed that $\approx 15\%$ loss in weight of litter could be attributed to activity of large detritus-feeders. These experiments, however, did not completely evaluate the effects of all animals. We did not exclude smaller detritivores, nor meiofauna. The presence of ciliates, for instance, may increase oxidation rates of seaweed detritus by $> 60\%$ in the presence of a macrodetritivore (Briggs *et al.*, 1979). Further work with the smaller fauna is needed.

Species of litter, temperature, internal nitrogen content, external nitrogen, and

decomposer activity significantly altered the rate of weight loss in salt marsh litter, in that order (Table V). These variables were not equally important throughout the decay process. A different set of factors affected decay rates in each of the phases of decay (Table V), in agreement with the idea that the dominant mechanism in the early phase of decay was physical leaching, and that activity of decomposers became more important in the second phase.

In spite of differences in decay rates, litter of different types decayed in a clear and identifiable temporal pattern. The consistency of this pattern suggests that the course of decay is strongly influenced by the internal chemical composition of the litter, and is affected only to a small extent by external conditions. The key to understanding decay of litter, in salt marshes and elsewhere (Anderson & McFadyen, 1976) thus seems to be an understanding of the chemistry of organic matter, and how this interphases with external conditions.

It is common practice to fit a first-order kinetic model to decay curves, and calculate a decay constant from the fitted curve. We have not done this because different processes are involved in the loss of litter during the three different stages. Thus, in reality there is no one decay rate characteristic of the whole process. Rather, decay takes place via a sequence of phases, each of which reflects the chemical composition of the litter material left, the changing balance between physical mechanisms and microbial removal, and ambient conditions.

All the above discussion is based on litterbag work, yet, we have not shown if decay in litterbags resembles decay of litter in the actual environment. We have estimates of dead litter present in Great Sippewissett Marsh through the year (Valiela *et al.*, 1982). In Great Sippewissett Marsh the bulk of the live standing crop dies in early November; this is the time when the stock of litter is largest (Table VI, first row). By the following July or August, decay and export by tides have lowered the stock of litter to a minimum (Table VI, second row). The difference between these two (Table VI, third row) is a minimum estimate of litter loss, since there is leaf death and litter decay and export going on through most of the year (Valiela *et al.*, 1975; Kirby & Gosselink, 1976; Reidenbaugh,

TABLE VI

Comparison of the weight loss of litter in the field and calculated loss of weight in litterbags: data on field biomass obtained by harvesting quadrats through the year (Valiela *et al.*, 1982).

	Creek bank		Low marsh		High marsh	
	F	C	F	C	F	C
Maximum live biomass ($\text{g} \cdot \text{m}^{-2}$)	1100	750	760	350	1000	400
Minimum dead biomass ($\text{g} \cdot \text{m}^{-2}$)	100	100	150	120	370	250
Difference	1000	650	610	230	630	150
% weight loss in field $\cdot \text{yr}^{-1}$	91	87	80	66	63	46
% weight loss in litterbags $\cdot \text{yr}^{-1}$	85	84	81	82	65	48
Average turnover time (yr)	1.1	1.1	1.2	1.4	1.6	2.1

1983), and these processes are not included in our net measurement. The calculations shown in Table VI refer to the fate of the pulse of litter produced in the fall. This is what the litterbags simulate. Litter produced at any other time of year will, as shown by the experiments started at times other than the fall, follow a very similar temporal pattern. The autumn pulse comprised 75 to 90% of the annual production (unpubl. data; Valiela *et al.*, 1975; Reidenbaugh, 1983), so the results of Table VI pertain to the bulk of annual litter production.

The losses of litter can be expressed as percentages of the total litter produced in November (Table VI, fourth row). As we found in the litterbag work, disappearance of litter is greater in creekbanks than in low marsh, and losses in both of these habitats were greater than in high marsh. Furthermore, losses were greater where litter was enriched in nitrogen, again as we found in the litterbag work.

We computed the percent of the weight lost from litterbags in each of the treatments during the same time intervals as for the field data (Table VI, fifth row). There is good agreement between the losses measured in litterbags and losses during the autumn pulse of litter measured in the marsh. This suggests that the litterbag method is a reasonable way to assess loss of organic matter, in spite of the many drawbacks.

In each of the three major vegetated habitats of Great Sippewissett Marsh there are different amounts of plant material produced. Because grazing removes only small fractions of net annual above-ground production, the organic matter produced over most of the marsh becomes litter. The average turnover time (Table VI, bottom row) of the litter is $1.1 \cdot \text{yr}^{-1}$ in creekbanks, somewhat higher in low marsh, and $1.6\text{--}2.1 \cdot \text{yr}^{-1}$ in high marsh. In the field it is the rule to find last year's litter still present under a canopy of *S. patens*, for example, while there is usually little litter under canopies of *S. alterniflora* by mid-summer.

The turnover time under eutrophied conditions was shorter in the upper parts of the marsh; in the creekbanks, however, there was no effect of nutrient enrichment (Table VI, bottom). There is such a large increase in biomass produced by the enrichment that it compensated for the faster decay rate. Elsewhere in the marsh (LM and HM), the differences between production and decay rates are such that the turnover of fertilized litter was faster than that of unenriched litter.

Increases in decay rate in nitrogen-enriched litter, and the slower decay of *S. patens* compared to other litter types may have important basic and applied considerations. Eutrophication of salt marshes – a common feature of many coastal areas – results in an almost immediate nitrogen enrichment of tissues of the species present (Valiela *et al.*, 1982). In the longer term – a few years – eutrophication also results in shifts in species composition of salt marsh swards, favoring *S. patens* and *Distichlis spicata* (Valiela *et al.*, in press). Eutrophication could thus initially accelerate rates of decay, but as species are replaced, could in the longer term slow down rates of decay. A further complication is that while eutrophication does not accelerate turnover times of the litter in creekbanks, it does increase the turnover in high marsh up to 24% (cf. Table VI, bottom row). Since rates of accumulation and burial of organic matter in sediments, and regeneration of

nutrients through mineralization depend on decay rates, it is clear that eutrophication could have important but as yet unexplored consequences by its effects on decomposition in salt marsh ecosystems. Further, the recycling and binding of nitrogen and other elements will be greatly different depending on litter type. The point here is that knowledge of how the control of decay takes place, principally via the chemistry of litter, is a key to important ecological features.

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