

Effects of Litter Quality and Nutrient Availability on the Rate of Belowground Decomposition in a Nutrient-enriched Salt Marsh¹

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Abstract. Belowground decomposition of *Spartina alterniflora* in the control and fertilized plot of Great Sippewissett salt marsh was studied. From the slurry experiments performed under laboratory condition, the rate of decomposition is found to be positively related to litter quality, namely C:N ratio and lignin content. Low C:N ratio and low lignin content leads to high rate of decomposition. However, nutrient availability studied with three levels of nutrient concentrations does not have show an effect on the decomposition rate. In addition, two approaches were used to estimate the belowground decomposition. First, a mass-balance approach estimate the rate of belowground decomposition as the difference between the rate of primary production¹ and the rate of organic matter accumulation. Rates of 1289.32 and 1182.85 g C m⁻² yr⁻¹ were estimated. Second, the rates estimated from the slurry experiments are 229.8 and 319.3 g C m⁻² yr⁻¹ for the control and fertilized plots. These low values measured under laboratory condition are definitely underestimated. It is believed that sulfate reduction plays a major role in the decomposition process in the salt marsh. Since the slurry experiment did not imitate the anaerobic condition, only low estimates were obtained.

Key words: Decomposition; Litter quality; Nutrient availability; *Spartina alterniflora*; Great Sippewissett salt marsh.

¹ A collaborated study on “The Effects of Litter Quality and Temperature on Belowground Decomposition of Northern and Southern Salt Marshes” was conducted by Catherine O’Connor, Lafayette College, Easton, Pennsylvania.

Introduction

Coastal salt marshes are important habitats that provide nutrients for the surrounding estuarine ecosystems. In many systems, detritus produced in the salt marshes are responsible for supporting the estuarine food web because of their richness in organic carbon and nitrogen. Vegetated salt marshes also play crucial roles as buffer zones to reduce shoreline erosion. However, in recent decades, fossil fuel burning and land-use changes significantly increase the production of carbon dioxide in the atmosphere, resulting in global rise of temperature, melting of polar ice cap, and acceleration in sea level rise. As transitional zones between the marine and terrestrial ecosystems, coastal salt marshes are threatened by erosion and submergence by the rising sea level (Craft et al., 1993). As a result, salt marshes can only be maintained by landward migration, vertical accretion, or both (Craft et al., 1993).

Two major factors determine the vertical accretion of salt marshes: sediment deposition and organic accumulation. Supplies of new sediment from the coastal ocean and land can be deposited on the salt marsh surface. In addition, Redfield (1972) observed that organic matter accumulation is crucial in the development of salt marshes. Net primary production of marsh vegetation results in the formation of peaty and fibrous sediment, which is effective in retaining water and in providing structural support (Redfield, 1972). As very little sediments deposit on the Atlantic coast, the rate of organic matter accumulation becomes crucial in the maintenance and growth of the salt marsh (Bricker-Urso et al., 1989). For the site of this study, Great Sippewissett salt marsh, Buzzards Bay, MA, organic matter accumulation is expected to be the major contributor to vertical accretion of the marsh. Since the aboveground biomass either decomposes *in situ* or is flushed away by tides (Valiela et al., 1982), accumulation from belowground is thought to be critical for vertical accretion.

The rate of decay and the rate of primary production belowground are crucial factors that determine the rate of organic matter accumulation in the salt marsh. Although the rate of belowground production in the salt marsh has been actively studied, the rate of belowground decomposition has not been investigated in details. The decomposition process is generally described as three phase: a leaching phase that last for a month, a decomposer phase that last for a year, and a refractory phase that last for an additional

year (Valiela et al., 1985). It is believed that different factors are important in controlling the decay rate at different phases. For example, during the decomposer phase, temperature and the availability of nutrients are two major factors. In addition, studies of decomposition of aboveground marsh plants concluded that litter quality plays an important role in controlling the decomposition rate (Wilson et al, 1986).

In this study, I examine the role of litter quality and nutrient availability in controlling the rate of belowground organic matter decomposition. I investigate two hypotheses in the Great Sippewissett salt marsh. My first hypothesis is that higher litter quality, meaning low C:N ratio and low lignin content, enhances belowground decomposition. I expect that lower C:N ratio in the roots, which is closer to that of the microbes, allows microbes to obtain nitrogen easily during decomposition. My second hypothesis is that higher nutrient availability in the sediment provides the easily accessible nutrients for the microbes. Both of these result in a higher decomposition rate. I attempt to approach these questions by setting up slurry incubations under laboratory conditions.

Finally, I attempt to compare the measured rate of decomposition in this study with another estimation obtained from a mass-balance approach. This study is conducted in Great Sippewissett salt marsh, Buzzards Bay, MA. Long-term fertilization in some plots of the salt marsh may imply on the effect of nutrient loading due to the increasing influence of urbanization on the rate of organic matter accumulation in the salt marsh.

Methods

I conducted the study in Great Sippewissett salt marsh, Buzzards Bay, MA. A fertilized plot was compared to an untreated plot. The fertilized plot (XF) has received $75\text{g m}^{-2}\text{ wk}^{-1}$ of a commercially available sewage sludge-based material (N: 10%; P: 6%; K: 4%) by broadcast from March through November since 1971 (Valiela and Rietsma, 1995). The fertilized plot and the control plot were located at the creek bank and low marsh, and were dominated by the long and short form *Spartina alterniflora* respectively. Since the long and short forms of *S. alterniflora* are only ecophenes with no genetic differences (Valiela and Teal, 1974), the effect of varying species was eliminated.

As part of the calculation of the decomposition rate, the bulk density and root mass in the sediment were studied. Two core samples of 3.6cm and 6.5cm in diameter and 20-30cm deep were collected at each site for bulk density and root mass measurements respectively. Bulk density samples were divided into 0-10cm, 10-20cm, 20-25 cm and beyond 25cm intervals. Wet and dry weights for each interval were obtained. From the 6.5cm cores, white, translucent and fairly rigid live roots and rhizomes were carefully separated from yellowish-brown and flaccid recently dead roots and rhizomes by rinsing water through a 1mm sieve. Roots were dried at 60°C for 36 hours and weighed.

In this study, qualities of three types of belowground litter, live roots and rhizomes, recently dead roots and rhizomes, and the remaining dead materials, were assessed by carbon, nitrogen and lignin contents. Litters that were used for the root mass estimation and the slurry experiment were tested. All samples were dried at 60°C and grounded with a Wig-L-Bug. Percents carbon and nitrogen were determined using a Perkin-Elmer elemental analyzer. Acid-soluble lignin content was analyzed following Effland's modified procedure (1977). 1 g of each sample was dried at 450°C to obtain the ash content.

Since different litter type results in different rate of decomposition, the rates for each litter pool, live roots and rhizomes, recently dead roots and rhizomes and dead material, of *S. alterniflora* were measured under laboratory conditions. Sediment samples from the control and fertilized site were collected and separated into the three pools according to the method described previously. Roots and rhizomes were then cut with scissors to eliminate the variations in surface area to make slurries. 240ml bell jars were used as incubation containers. The live and recently dead root and rhizome microcosm were composed of 6-8g wet weight of sample and a small volume of sediment to complete microbial consortium (=10% by wet weight). Microcosms of dead materials contained 30-50g wet weight of sample. Water was then added to barely cover the sample (~ 30ml).

For each litter type, the effect of nutrient availability was studied at three levels. The three nutrient levels were control (seawater), low (100µM NH₄Cl and 60µM K₃PO₄), and high (500µM NH₄Cl and 300µM K₃PO₄). Nutrient solutions were made up with

seawater. During the incubation, water lost by evaporation was replenished with de-ionized water. To get the background nutrient concentrations of each plot, pore water samples were collected to estimate the background ammonium and phosphate concentrations. Samples were acidified with hydrochloric acid (1µl acid / ml sample), and were tested for ammonium and phosphate following the procedures of Strickland and Parsons (1972) and Murphy and Riley (1962) respectively with a spectrophotometer.

In this study, I evaluated the rate of belowground organic matter decomposition by measuring the rate of carbon dioxide production. In each microcosm, CO₂ production was measured by a gas chromatographer with a thermal conductivity detector and a POROPAK-Q column, or an infrared gas analyzer (LI-CORTM, LI-6200). All incubations were kept at 21°C and were in the dark beginning on Day 5 after a potential effect of photosynthesis was observed. CO₂ production in sample chambers was measured over varying intervals for 3 weeks using two methods, depending on the rate of production. When rates were sufficiently high, CO₂ increase was measured over 4-minute intervals. Otherwise, incubations of 12-hour duration were measured at the beginning and end of duration. Sample containers were left open at other times. All microcosms were handled carefully to avoid disturbing the CO₂-HCO₃ equilibrium and the anaerobic layer of the microcosms.

In order to estimate the total decomposition rate from the three litter types, the rate of CO₂ production (mg CO₂-C g⁻¹C d⁻¹) was plotted against time. In this calculation, a wet weight to dry weight conversion unit (for roots and rhizomes, a 70% of dry weight was assumed) and the percent carbon from the bulk density samples were used. The mass of carbon in the sample at each time interval was corrected for the CO₂ loss per time interval. The resulting exponential curve was then integrated to obtain the total production of CO₂ (mg CO₂-C g⁻¹C) at each time interval. With the total CO₂ production, the percent original carbon remaining was calculated and plotted against time. It is represented by the following equation:

$$\ln (W_t / W_0) = -kt \quad \text{Eq. (1)}$$

where W_t = percent original carbon remaining; W_0 = weight of original carbon; k = decomposition rate constant; t = time. The log transformation of W_t at each time interval

was regressed over time to obtain the k value and the corresponding standard errors (Wilson et al., 1989).

This decomposition rate constant, k , for each distinct treatment was used as an index to evaluate the difference in decomposition rate between nutrient treatments, litter types and treatment plots. The k value determined from Eq.(1) for each litter type was used to calculate a weighed k to estimate the total decomposition rate from belowground biomass:

$$k^* = (k_L \cdot m_L + k_{RD} \cdot m_{RD} + k_D \cdot m_D) / (m_L + m_{RD} + m_D) \quad \text{Eq.(2)}$$

where k^* = weighed k ; m_L = mass of live roots and rhizomes; m_{RD} = mass of recently dead roots and rhizomes; m_D = mass of dead materials. Total rate of decomposition is then calculated:

$$D = k^* \cdot (m_L + m_{RD} + m_D) \quad \text{Eq.(3)}$$

Finally, this decomposition rate was compared with another estimates, which is obtained in a mass-balance approach (Figure 1). Rate of belowground decomposition was calculated:

$$D = P - A \quad \text{Eq. (4)}$$

where D = Rate of Decomposition; P = Rate of primary production belowground; A = Rate of organic matter (OM)accumulation. This OM accumulation rate was calculated as follows:

$$A = R_{sl} \cdot Bd \cdot C \quad \text{Eq. (5)}$$

where R_{sl} = Rise of sea level (cm yr^{-1}); Bd = Bulk density (g cm^{-3}); C = Percent carbon.

Results

In order to calculate the total decomposition rate, the mass and the carbon content of each litter type was measured. Since the samples I collected only allow accurate comparisons above 20cm of sediment, the final estimations of decomposition rate are only consider up to this depth. Bulk density for the top 20cm is about 0.16 g cm^{-3} and 0.26 g cm^{-3} respectively for the control and fertilized plot. As depth increases, bulk density seems to decrease in the control plot but increase in the fertilized plot (Figure 3). Beyond 20cm, it is twice as high in the fertilized plot than the control plot (Figure 3). Overall,

bulk density is consistently higher in the fertilized plot than the control plot. In both plots, the mass of live roots and rhizomes is half of that of the recently dead for the 0-20cm interval (Figure 4). There are more live roots in the control plot than in the fertilized plot whereas the mass of recently dead roots is similar between the two. Beyond 20cm, the mass of recently dead roots seems to decrease in the control plot but remain the same in the fertilized plot. No live root was found beyond 20cm. Percent carbon does not deviate between plots or live and recently dead roots and rhizomes (Figure 5). However, it dropped considerably by about 10% from recently dead roots to dead materials (Figure 5).

Variations in percent nitrogen, carbon to nitrogen ratio, and percent lignin are observed between different litter types and treatment plots (Figure 6 - 8). Within the control plot, percent nitrogen increases from live roots to dead roots, and to dead materials, with a considerable increase from recently dead roots to dead materials (Figure 7). However, percent nitrogen remains fairly constant among different litters in the fertilized plot (Figure 6). In both live and recently dead roots and rhizomes, higher nitrogen contents are found in the fertilized plot than the control plot (Figure 6). C:N ratios decline from the live roots, to recently dead roots, and to dead materials in the control plot (Figure 7). However, C:N ratio only decreases from the recently dead roots to the dead materials in the fertilized plot (Figure 7). The live and dead roots and rhizomes have 2.8 and 1.8 times higher C:N ratio in the control plot than the fertilized plot, but dead materials from each plot have similar C:N ratios (Figure 7). Percent lignin is lower in live roots but remain high at a similar level in recently dead roots and dead materials (Figure 8). Variation between plots is only observed in the live roots and rhizomes, in which percent lignin is higher in the control plot (Figure 8).

The rates of CO₂ production of different litters from each plot with different nutrient treatments were measured in the microcosms (Figure 9(a)-(f)). Most microcosms show an exponential decline in the percent original carbon remaining over the 20 days of study (Figure 10(a)-(f)). The decomposition rate constant, k , in Eq. (1) is calculated and compared (Figure 11). For each litter type in each plot, no difference in the k constant was observed among nutrient treatments (Figure 11). Although the k values of the control (seawater) and low nutrient treatments in the live roots of the control plot seem to deviate

from each other (Figure 11(a)), the general pattern from each litter pool of each plot suggests no difference due to nutrient treatments. Therefore, further discussion will be based on the k values obtained from the linear regression of $\ln W_t$ versus t (Eq. (1)) from all data points within each litter type of each plot (Table 1). The range of k among different litter type is large; live roots and rhizomes, recently dead roots, and dead materials are in the order of 10^{-3} , 10^{-4} and 10^{-5} respectively (Table 1). The k constant for live and recently dead roots and rhizomes are 3.9 and 4.0 times higher in the fertilized plot than the control plot (Table 1).

The relationships between the decomposition constant and litter quality are studied. In both live and recently dead roots, lower C:N ratios in the fertilized plot are found with larger values of k (Figure 12). However, no such relationship is observed in dead materials (Figure 12). As the k values are plotted against the percent lignin, lower lignin content is found with higher k values. Moreover, all litter types seem to lie on the same line, with a pattern from live roots, recently dead roots to dead materials as lignin content increases (Figure 13).

In this study, the rate of decomposition measured in the slurry experiment is compared with that obtained from a mass-balance approach (Figure 1). The weighed k calculated from Eq. (2) is obtained for each plot and is used in estimating the total decomposition rate (Table 2). The estimated annual decomposition rates are 229.83 and 319.33 g C m⁻² yr⁻¹ for control and fertilized plot respectively (Table 2). Using estimates of sea-level rise of 0.24 cm yr⁻¹ measured from the Boston Tide gauge over the past 80 years, and that of belowground production in Great Sippewissett salt marsh (Valiela et al., 1976), the rate of OM accumulation is calculated for each plot using Eq. (5). The resulting mass-balance for the rates of belowground decomposition are 1289.32 and 1182.85 g C m⁻² yr⁻¹ for the control and fertilized plot respectively (Table 3). These figures are 5.6 and 3.7 times higher than that measured from the slurry experiment.

Discussion

Litter quality deviates among litter types of *Spartina alterniflora* and between plots. Compared to dead materials, the higher C:N ratio of live and recently dead roots

observed in both plots indicate that immobilization occurs at the later stage of decomposition (Figure 7). As expected, live and recently dead belowground litter from the fertilized plot has a lower C:N ratio because nutrients are not limiting (Figure 7). However, lignin content follows a different pattern; live roots and rhizomes that contain relatively large percentage of soluble or easily decomposed substances lower the lignin content (Figure 8). As most labile materials are decomposed, the refractory lignin is not decomposed in recently dead roots or dead materials; this raises the percent lignin. In both the recently dead roots and dead materials, the consistently high lignin content indicates that the rate of loss is the same for both litter type. Since carbon content decreases substantially from recently dead roots to dead materials (Figure 5), the decline in carbon content in dead materials is probably resulted from decomposition of cellulose. Fertilization also seems to lower the lignin content of live roots and rhizomes (Figure 8). Since percent nitrogen and other substances are higher for live roots from the fertilized plot, the lignin content is relatively lower. Moreover, the similar lignin content in recently dead and dead materials between plots suggested that fertilization does not alter the lignin content of recently dead roots and materials. This implies that although fertilization plays an important role in the initial phases of decomposition, when factors other than nutrients become limiting, such as carbon, lignin is responsible in controlling the rate of decomposition in the refractory phase.

The effect of nutrient availability on decomposition rate hypothesis is rejected in this study. The irresponsive k values in the live roots of the control plot may be explained by the higher concentration of ammonium already exist in the sediment (Figure 2). Although phosphate concentration is low in the control plot, phosphate is not generally a limiting factor in the marsh; therefore, did not affect the decomposition rate. The only increase in the k constant due to nutrient addition is observed in the live roots and rhizomes from the fertilized plot. It may be due to the low ammonium concentration in the pore water. Therefore, when $100\mu\text{M}$ of ammonium was added to live roots that are used to $12\mu\text{M}$ of ammonium, microbes can obtain nutrients more readily during decomposition (Figure 2).

Deviations in decomposition rate constant among live root materials, recently dead root materials and dead matter are observed as expected. The substantial drop in

decomposition rate in live roots during the initial stage is correspondent to the leaching phase, during which soluble substances leach for a month (Valiela et al., 1985). Since large amount of labile materials is available, microbes obtain nutrients readily for growth and this leads to higher k constant. However, as these nutrients are exhausted, microbes began to decompose organic matter to support growth; therefore, decay rate drops during the decomposer phase, which may be represented by the recently dead roots and rhizomes. In the recently dead roots and rhizomes, since most labile materials has been lost during the leaching phases, the decomposition of recalcitrant materials by microbes lead to a lower decomposition rate constant (Figure 11 (b) & (c)). However, since the dead materials are largely composed of relatively refractory material, the decomposition rate remains small and is two orders of magnitude lower than that of the live roots. This phase corresponds to the refractory phase (Valiela et al., 1985)

The relationship between litter quality and the decomposition rate constant is most obvious for the live roots and rhizomes. When the k constant is plotted against the C:N ratio, the live roots from the fertilized plot has a large k constant, whereas the high C:N ratio from the control plot has a small k constant (Figure 11). Within the live roots, the C:N ratio is found to be negatively related to decomposition rate. The reason is that higher nitrogen in the litter allows microbes to obtain nitrogen more efficiently. A similar trend is found between k and the lignin content. However, this relationship is true for all the litter type. It is probably because of lignin is a refractory materials. As roots senesce, lignin content increases proportionally. As a result, all litter types lie on the same straight line (Figure 13).

This study is an uncommon one in assessing the rate of decomposition under a laboratory set-up. Since no such experiment has been done previously, the uncertainties involved in this method led to the underestimating of the decomposition rate.

In the slurry experiment, the rates of belowground decomposition are largely underestimated. Although the rate of primary belowground production of $1400 \text{ g C m}^{-2} \text{ yr}^{-1}$ in both plots was criticized as an overestimate, the resulting decomposition rate should at least be in the same order as that from the slurry experiment. There are several possible reasons for the underestimation, including the potential oxic state of the slurry, the shallow depth of sediment studied, the uncertainty of using the infrared gas analyzer.

Under laboratory condition, I probably did not imitate the real anoxic situation in the salt marsh. Among the three litter types, the dense dead material is the closest in having an anoxic layer. Since both live and recently dead roots floated on water, considering the small amount of dead materials added, they were probably under oxic condition most of the time. According to a study of anoxic respiration in the salt marsh, sulfate reduction is considered as the most important pathway of anoxic respiration; loss of $1800 \text{ g org C m}^{-2} \text{ yr}^{-1}$ is estimated due to sulfate reduction (Howarth and Teal, 1979). Therefore, the estimates from this study are probably much lower than the real figure.

Moreover, this study only included the top 20cm in the decomposition rate calculation. Although much fewer live and recently dead roots and rhizomes were observed beyond 20cm, the anoxic decomposition of dead materials could be very large considering the mass of this compartment. The same study of Howarth and Teal (1979) on sulfate reduction finds significant amount of organic carbon loss through sulfate reduction beyond 20cm. Due to the importance of sulfate as an electron acceptor, the anoxic layer should be maintained if similar slurry experiments are to be conducted under laboratory conditions. Sampling deeper core may account for the reality better. The uncertainty involved in the using the infrared gas analyzer to measure CO_2 on overlying water may have affected the result. Since most samples have air-water layer, the equilibrium between carbon dioxide and bicarbonate may have disturbed and caused inaccurate results.

Furthermore, the sample sizes in this study are small due to the time constraint, which does not allow statistical analysis. It is also necessary to sample from more than one fertilized plot and control plot in order to get a representative sample.

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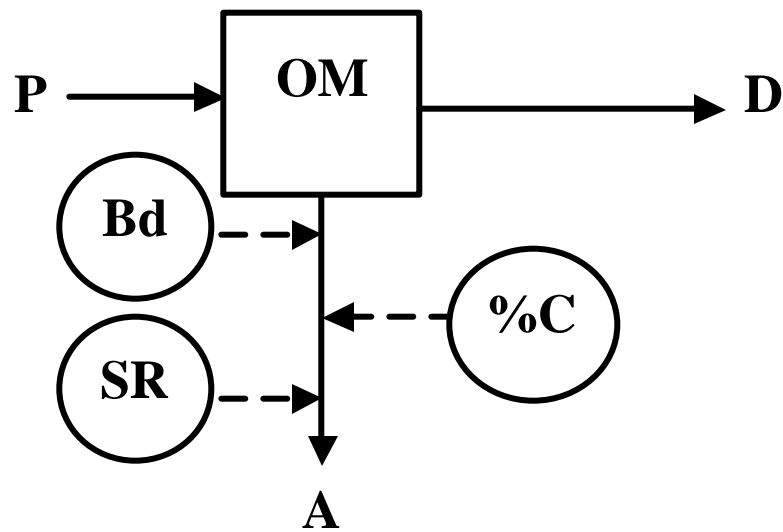


Figure 1: A mass-balance approach is used to estimate the rate of belowground decomposition (a steady state of OM is assumed). OM = organic matter storage; P = rate of primary belowground production; D = rate of belowground decomposition; A = rate of organic matter accumulation; Bd = bulk density; SR = sea-level rise; %C = percent carbon in the sediment.

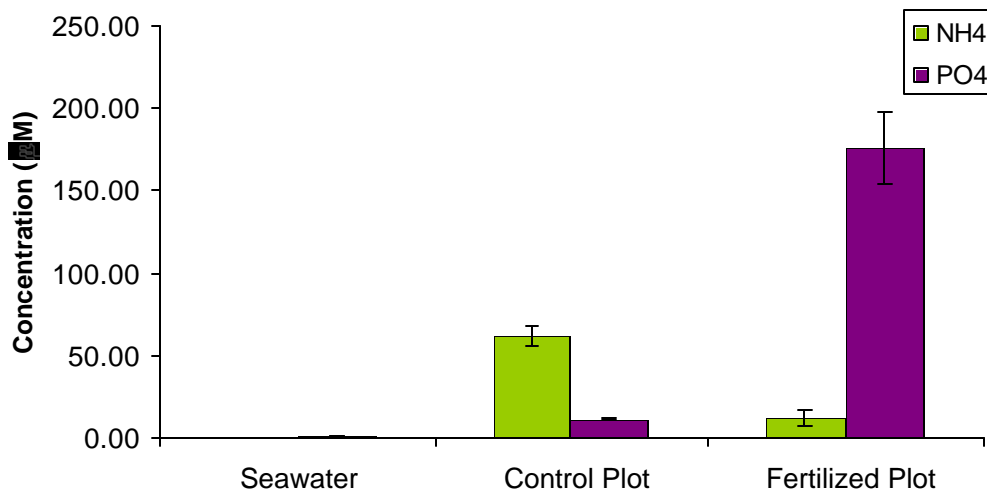


Figure 2: Ammonium and phosphate concentration in seawater and porewater samples from the control and fertilized plot of Great Sippewissett salt marsh.

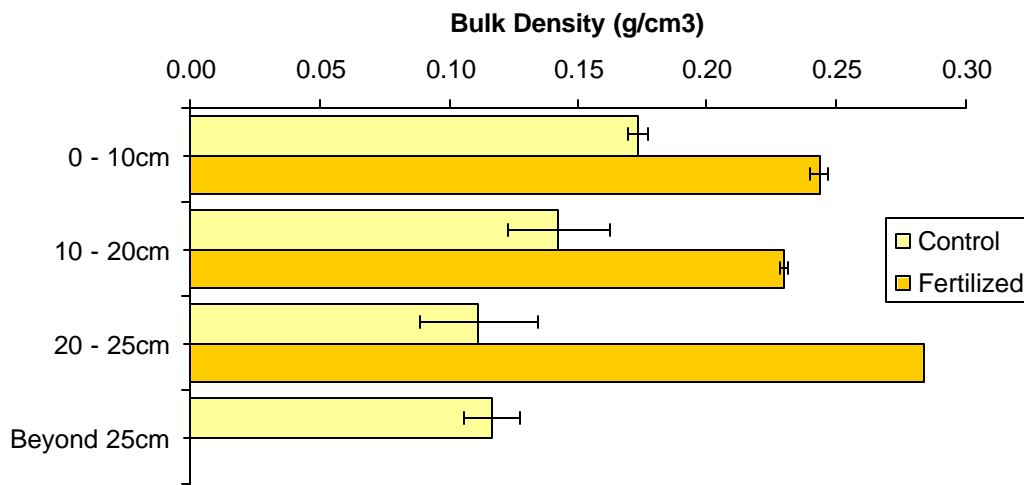


Figure 3: Bulk density (g cm⁻³) in the control and fertilized plot.

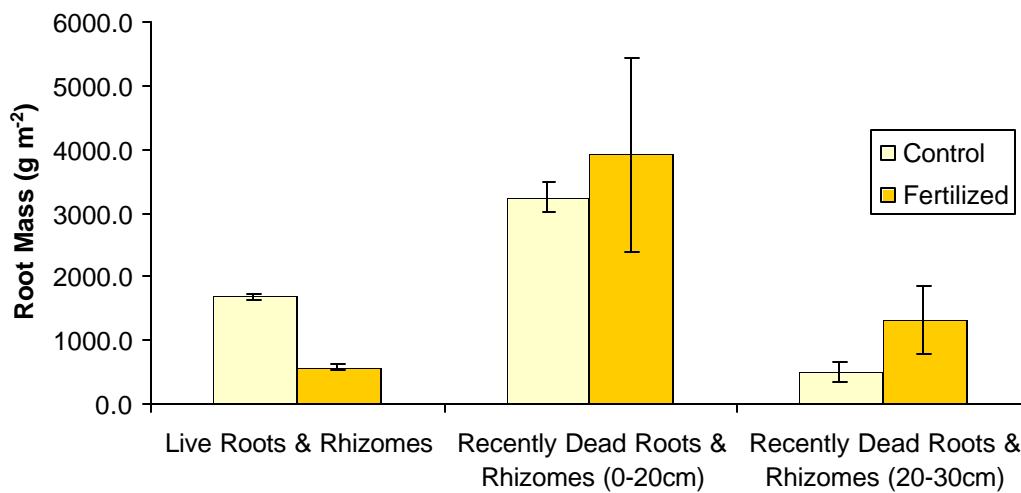


Figure 4: Mass (g m⁻²) of live and recently dead roots and rhizomes in the control and fertilized plot.

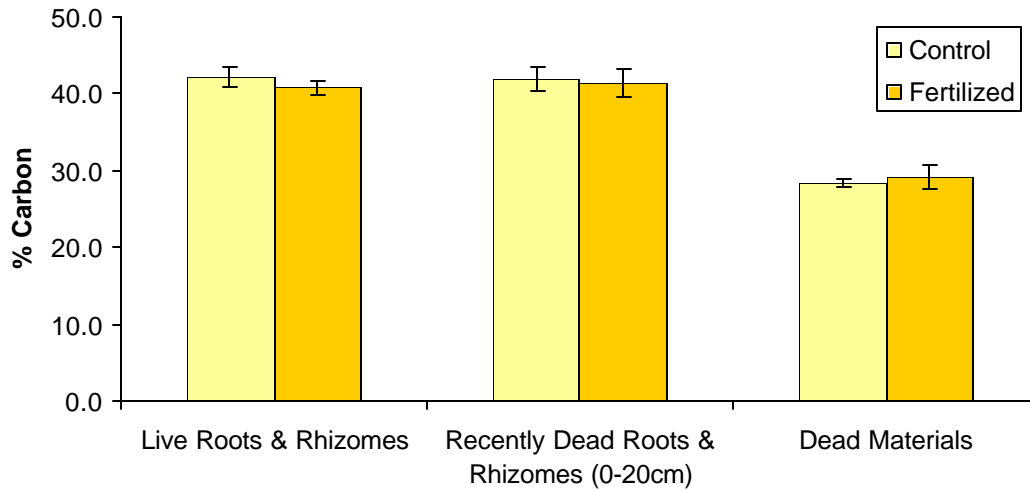


Figure 5: Percent carbon of different litter types of *S. alterniflora* in the control and fertilized plots.

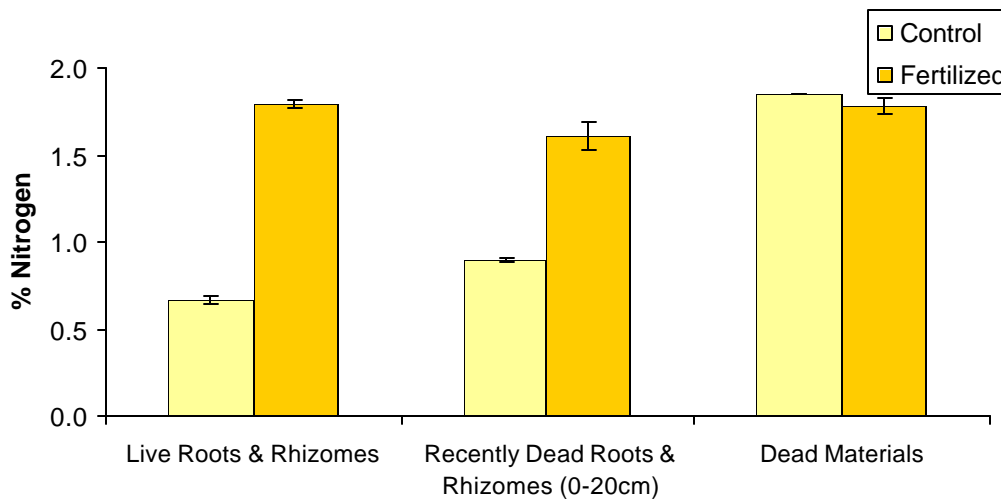


Figure 6: Percent nitrogen of different litter types of *S. alterniflora* in the control and fertilized plots.

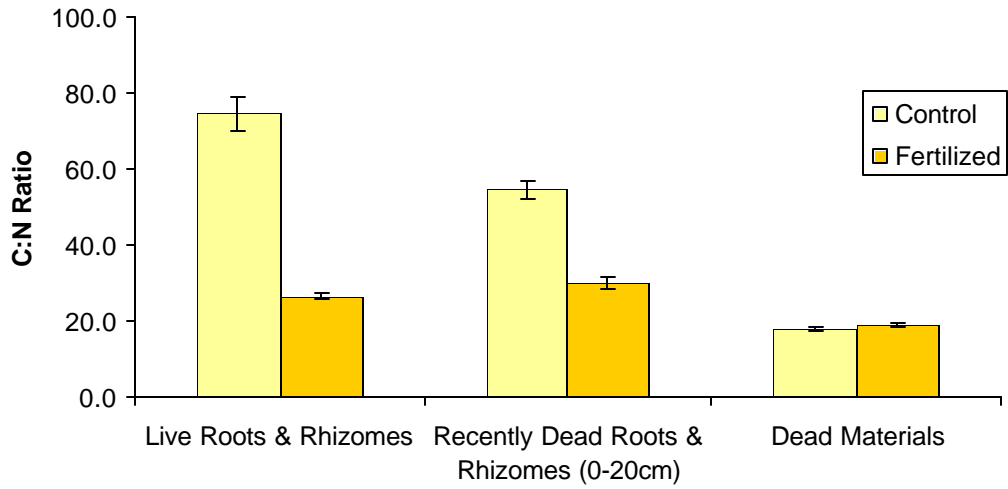


Figure 7: Carbon to nitrogen ratios of different litter types of *S. alterniflora* in the control and fertilized plots.

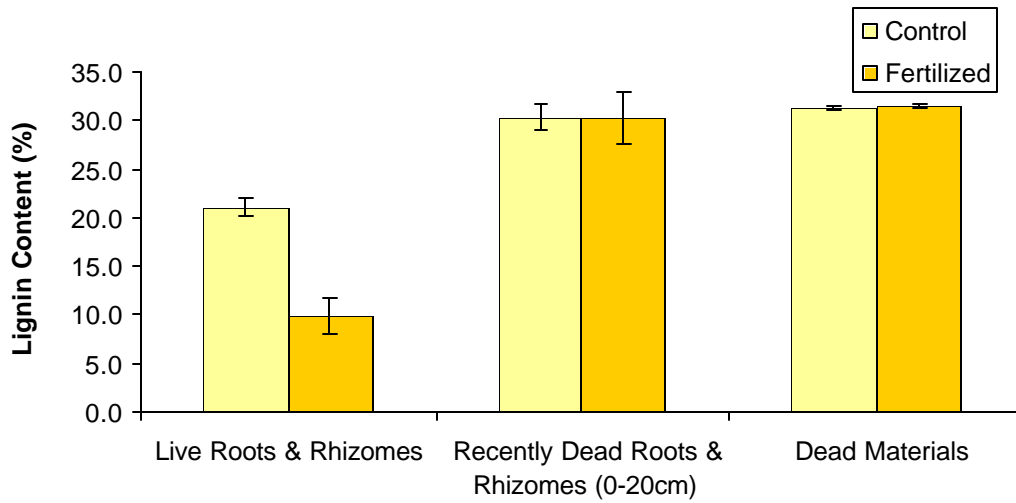


Figure 8: Percent lignin of different litter types of *S. alterniflora* in the control and fertilized plots.

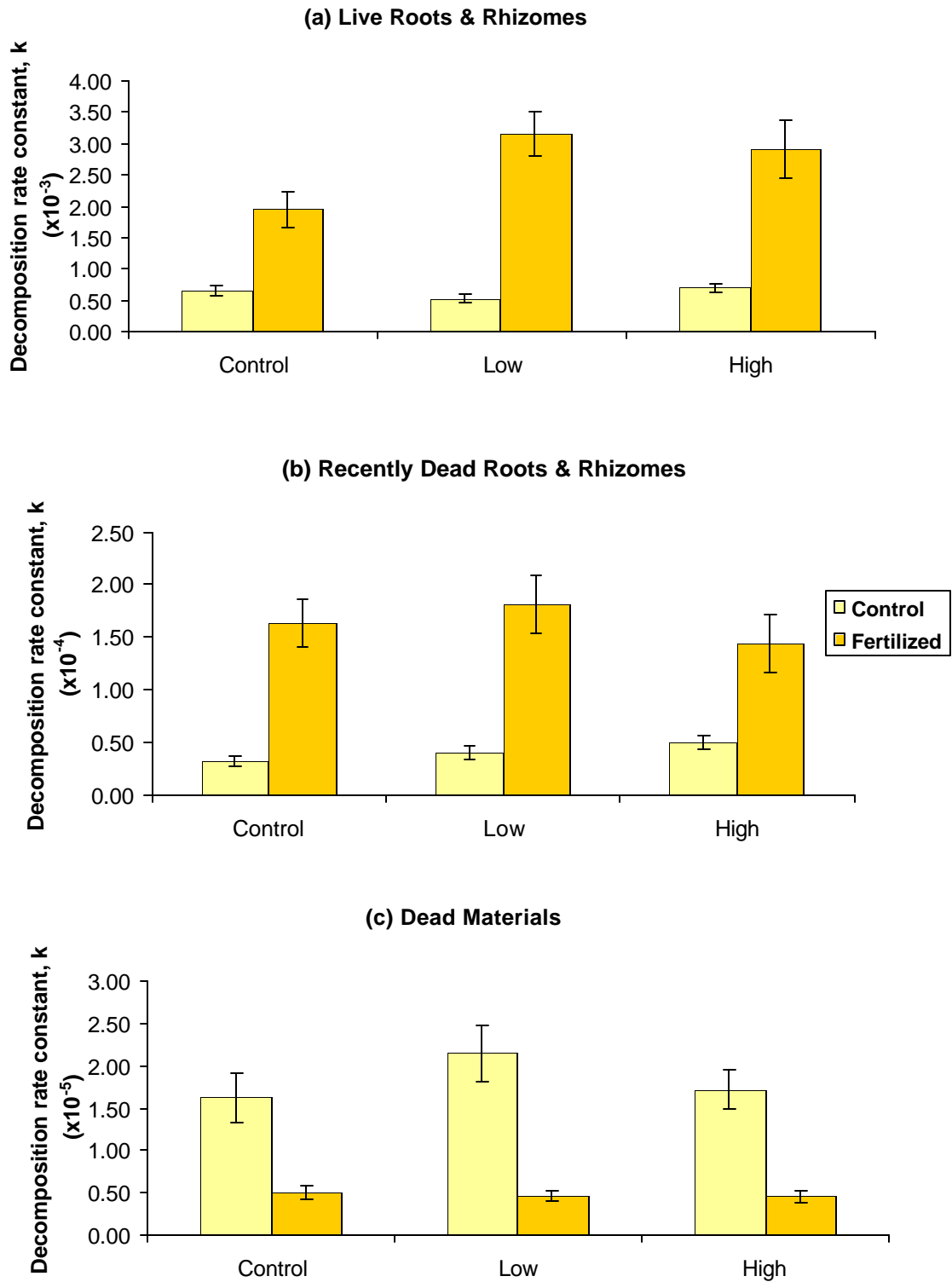


Figure 11 (a)- (c): The decomposition rate constant, k , of different litter types from the control and the fertilized plots under different nutrient treatments.

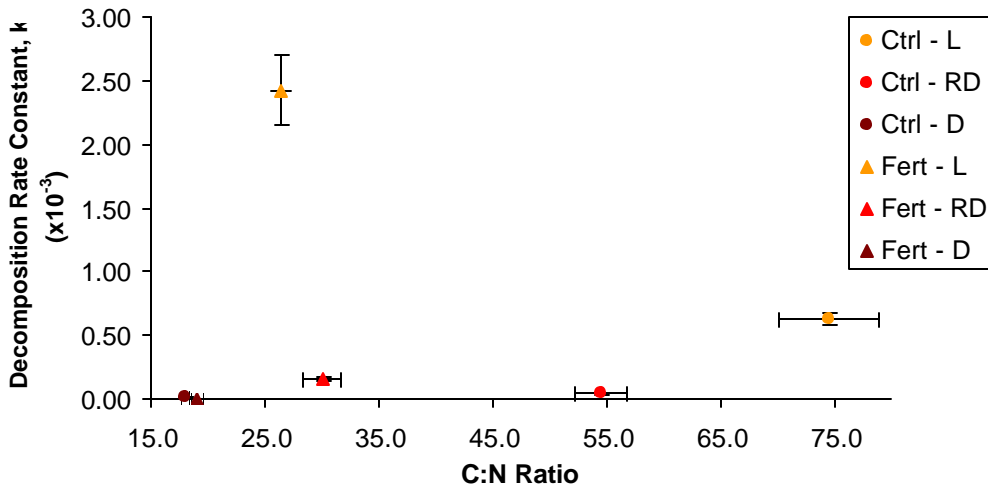


Figure 12: Relationships between the decomposition rate constant, k, and C:N ratio of different belowground litter types in the control and fertilized plots.

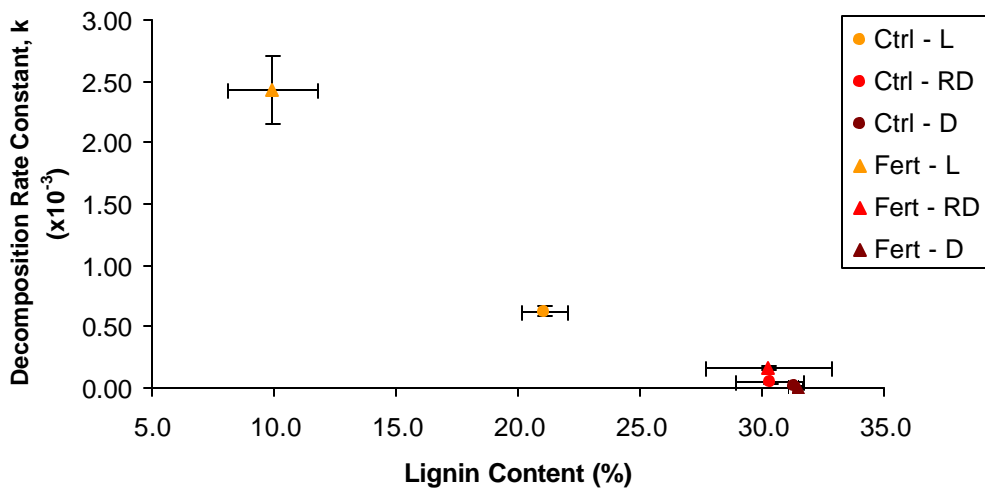


Figure 13: Relationships between the decomposition rate constant, k, and lignin content of different belowground litter types in the control and fertilized plots.

Table 1: The decomposition rate constant, k, and the corresponding standard errors for different belowground litter types of *S. alterniflora* in the control and fertilized plots of Great Sippewissett salt marsh.

| | Control | | Fertilized | |
|--------------------------------|--------------------------|------------|--------------------------|------------|
| | k ($\times 10^{-3}$) | \pm S.E. | k ($\times 10^{-3}$) | \pm S.E. |
| Live Roots & Rhizomes | 0.6253 | 0.0442 | 2.4237 | 0.275 |
| Recently Dead Roots & Rhizomes | 0.0408 | 0.0039 | 0.1626 | 0.0148 |
| Dead Materials | 0.0183 | 0.0018 | 0.0047 | 0.0004 |

Table 2: Rate of decomposition estimated from the slurry experiment in this study. The weighed k is calculated from Eq. (2). Annual decomposition is estimated assuming constant daily decomposition throughout 365 days at 21°C.

| | Control | Fertilized |
|--|-----------------------|-----------------------|
| Total mass of OM (g C m^{-2}) | 9156.89 | 11929.18 |
| Weighed k (d^{-1}) | 6.88×10^{-5} | 7.33×10^{-5} |
| Rate of decomposition ($\text{g C m}^{-2} \text{d}^{-1}$) | 0.63 | 0.87 |
| Rate of decomposition ($\text{g C m}^{-2} \text{yr}^{-1}$) | 229.83 | 319.33 |

Table 3: A mass-balance approach to determine the rate of belowground decomposition. A simple diagram of this model is shown in Figure 1.

¹Estimations from Valiela et al. (1976); ²Personal communication with Chuck Hopkinson.

| | Control | Fertilized |
|--|---------|------------|
| Rate of belowground production ¹ ($\text{g C m}^{-2} \text{yr}^{-1}$) | 1399.2 | 1326.0 |
| Sea-level rise ² (cm yr^{-1}) | 0.24 | 0.24 |
| Bulk density (g cm^{-3}) | 0.16 | 0.24 |
| Percent carbon of the sediment (%) | 28.95 | 25.22 |
| Rate of OM accumulation ($\text{g C m}^{-2} \text{yr}^{-1}$) | 109.88 | 143.15 |
| Rate of belowground decomposition ($\text{g C m}^{-2} \text{yr}^{-1}$) | 1289.32 | 1182.85 |