CONTRASTING NUTRIENT DYNAMICS OF LITTER DECOMPOSITION
IN A DECIDUOUS FOREST AND POND ECOSYSTEM

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SES 2010

Abstract

Leaf litter decomposition is a crucial process in forest ecosystems, as well as in ponds surrounded by forest. Litter decomposition recycles nutrients and provides energy for detrital food chains. Rates and patterns of decomposition depend both on environmental factors and chemical characteristics of the initial litter. This study explores differences in mass loss, nitrogen and phosphorus content, lignin, and microbial extracellular cellulase between four litter species in a forest and a pond ecosystem. I incubated litter for 8, 16, 25, and 30 days in these two ecosystems to develop a time series for changes in mass, chemical content, and microbial enzyme production on litter. Of the litter species, red maple (Acer rubrum) lost the most mass after 30 days. There were few observed differences in litter decomposition processes between ecosystems during a 30-day timeframe. Observed changes in mass, nutrient content and cellulase depended much more on species than on location in this experiment. Relative rates of mass loss were somewhat inconsistent with expected rates based on chemical make-up of the different litter types and observed cellulase activity; sweet pepper bush (Clethra alnifolia) had slower decay rates than can be explained by the data from this study. Further investigation may shed light on why Clethra did not decay as predicted.

Keywords: Decomposition, immobilization, lignin, cellulase, pond, litter quality, Acer rubrum, Quercus velutina, Pinus strobus, Clethra alnifolia
Introduction

Small ponds in forested areas receive large volumes of allochthonous input in the form of leaf litter from surrounding trees. (Oertli 1993) This litter serves as an energy source for detrital pathways and provides nutrients to the ecosystem. Considering differences in temperature, moisture, and access to oxygen between forest soils and pond sediments, it seems likely that decomposition processes would differ between these ecosystems. Previous studies have contrasted decomposition processes between freshwater streams and forest soils, and shown faster decomposition rates and lower microbial exocellulase activity in stream sites (Linkins & Sinsabaugh 1990). However, less has been done to investigate decomposition in pond systems.

Another, well-studied factor controlling litter decomposition is initial litter composition (Mascha et al. 2010). Different species have differing decay rates, often dependent on initial nutrient content and relative amounts of labile and refractory carbon (Aber & Melillo 1991, Melillo 1982). Nutrient dynamics are especially important during early stages of decomposition before labile carbon is exhausted and microbes are limited by nutrients as opposed to energy (Aber & Melillo 1991). Litter with greater initial nitrogen content generally decomposes at a faster rate because it poses a smaller discrepancy in the C:N ratio between the litter and decomposer microbes, and so microbes will need to immobilize less nitrogen to process the litter (Aber & Melillo 1991). While it has not been studied as extensively, I predicted that a similar relationship may exist between phosphorus content and decay rate, especially in pond sediments where phosphorus is often limiting (Valiela 1995). With regards to carbon, lignin in litter can slow decomposition rate since it is more refractory than other forms of organic carbon in litter. Accordingly, lignin:N is a commonly used metric in predicting how quickly a type of litter material will decompose.
This study aims to examine the effects of environment and initial leaf composition on litter decay processes within a 30-day incubation period, using a litter bag experiment with four litter types in two distinct ecosystems (forest soil and freshwater pond sediment). The species I incubated were red maple (*Acer rubrum*), eastern black oak (*Quercus velutina*), eastern white pine (*Pinus strobus*), and sweet pepper bush (*Clethra alnifolia*). I assessed decomposition processes by measuring changes in mass, nitrogen content, phosphorus content, and cellulase on litter at four time points during the 30-day study. I also measured initial and final lignin content of the litter, and made invertebrate counts on the litter from the final collection.

My hypothesis with regards to mass loss was that litter types with high initial nutrient content and low lignin would decompose most rapidly. I also expected that litter would decompose faster in the pond ecosystem than in the forest. Linkins & Sinsabaugh (1990) have shown litter to decompose faster in freshwater streams than in forest soils, and other studies have demonstrated the importance of moisture availability on microbial activity and decomposition rates. I hypothesized that greater access to moisture might speed leaching and microbial processing of litter in our pond ecosystem.

With regards to nutrients, I predicted that differing nutrient limitations in the ecosystems—forest soils tend to be nitrogen limited while freshwater systems are often phosphorus limited (Valiela 1995)—may cause different rates of nutrient immobilization as litter decomposed. Previous studies have shown that increases in exogenous nitrogen or phosphorus supply can increase immobilization rates of those nutrients (Melillo & Aber 1984). I expected to see similar results in this experiment with lesser nitrogen immobilization on land and lesser phosphorus immobilization in the pond.

Finally, I expected higher levels of cellulase to correspond with greater mass loss. This is because higher cellulase activity corresponds to more degradation of cellulose. Since cellulose is a more labile
form of carbon, its decay may be responsible for a significant portion of the mass lost during the 30-day study.

This study hopes to explore the dynamics of initial decomposition processes in forest soils and pond sediments. A greater understanding of these processes could allow us to predict when nutrients and energy will be made available to an ecosystem following autumn litterfall events, and may allow us to know in more detail the importance of allochthonous inputs into ponds.

Study Site

Beebe Woods (Figure 1) is a 397-acre protected forest in Falmouth, MA, which has been relatively undisturbed since a large fire in 1947 and is currently used primarily for recreation (Caljouw 2005). The tree species composition of the forest is fairly diverse, with mixed oak and pine species making up 70% of the forest cover, and other species such as red maple and American beech (Fagus grandifolia) common as well (Caljouw 2005). Sweet pepper bush is an abundant understory species near the Punch Bowl, my aquatic site. The Punch Bowl is a small, deep kettle-hole pond in Beebe woods surrounded mainly by forest, with the exception of a wetland area on one side of the pond.

Methods

I collected white pine, black oak, red maple, and sweet pepper bush litter from Beebe woods. I collected leaves from the top layer of litter so as to primarily use leaves fallen during this autumn. I air-dried all leaves before incubating them in litter bags, and oven-dried all litter at 50°C before conducting analyses. To compare the initial air-dry weights to final oven-dry weights, I weighed separate air-dried samples of litter and oven-dried them, to create an air-dry to oven-dry ratio for the initial leaves. This allowed me to calculate an initial oven-dry weight for the litter that I could compare to the final oven-
dry weight after incubation. Before measuring lignin, CHN content, and phosphorus content, I ground subsamples of litter using a Wiley Mill or WigLBug.

Litter Bag Incubation

I put 3-5 g of air-dried litter from each species in approximately 400 cm$^2$, 1 mm-mesh bags, sewn on three sides and closed on the fourth side using staples. Each species had four replicate bags for each of four time periods at each of two sites. I attached all bags to be collected at a given time from a given site on a single string to increase ease of collection. I arranged bags within a time period randomly along the string so as to minimize spatial bias. I buried terrestrial bags between the O and A soil horizons at a depth of approximately 4 cm following the methods of Linkins & Sinsabaugh (1990). I pinned aquatic bags to the surface of the pond sediment near shore using landscaping staples so that litter could interact with the sediment. Initially bags were weighted to mid-water, and were pinned down on the fourth day of incubation. Water at the aquatic sites was approximately 0.5-1.0 m deep. I deployed bags on November 3, and collected sets of bags 8, 16, 25, and 30 days after deployment.

After collection, I stored litter bags in individual plastic zip-top bags at 4°C until processing. To process bags, I took a subsample of leaf material for a cellulase assay. I removed soil and sediment from the remaining litter by brushing off leaves from the terrestrial site and by gently rinsing leaves from the aquatic site in tap water. Soil was more easily removed from terrestrial leaves by brushing, without the risk of leaching leaves by rinsing. Rinsing proved to be a more effective method of removing sediment from aquatic leaves than brushing, and leaching was not a concern since litter had been incubating underwater. Once sediment and soil were removed, I oven-dried litter at 50°C and weighed it to calculate a change in mass during incubation. After enzyme analysis, I dried and weighed the subsamples taken for enzyme assays, in order to obtain a total final mass for the incubated litter.

Carbon and Nitrogen
I weighed 4-6 mg of finely ground litter (mesh size of at least 40 in a Wiley Mill, or WigLbug) and folded it into tin vials to be combusted and measured using a CHN elemental analyzer (Perkin-Elmer), which measured the fractions of carbon and nitrogen in the litter. I conducted CHN analysis on composites of two replicate bags, so there were two composite samples analyzed for each species at each site for each time period.

Phosphorus

The method for my phosphorus analysis was based on a protocol for measurement of total phosphorus in soils and sediments (Harwood et al. 1969). I measured approximately 0.1 g finely ground litter into glass scintillation vials etched with numbers for identification. To each vial I added 0.5 mL 50% weight by volume magnesium nitrate solution and allowed the litter to absorb the liquid. I then ashed the vials at 550ºC to remove organic material. I resuspended the remaining ash in 10 mL 1 N hydrochloric acid and shook the vials for 16 hours. I then diluted this solution 20x and measured phosphate concentrations colorometrically using a method adapted from Murphy and Riley (1962).

Lignin

My method for analyzing lignin was based on a protocol by Effland (1977). I measured approximately 400 mg coarsely ground litter (Wiley Mill, mesh size 20) and deposited it into the bottom of a BD 20 tube, taking care that no particles stuck to the walls of the tube. I added 3 mL 72% sulfuric acid to each tube and let them incubate in a 30ºC water bath for 1 hour. I then autoclaved the tubes for 1 hour at 120ºC and filtered each resulting mixture through a pre-ashed, pre-weighed Gooch filtering crucible (coarse frit). I rinsed the tubes with DI to remove all particles, and rinsed the residue remaining on the filters with DI. I then dried the filters at 50ºC for 36 hours and weighed the filters with dried material on them. I kept the filters in a dessicator until immediately prior to weighing to avoid mass gain from atmospheric moisture. After weighing, I ashed the filters at 450ºC for three hours and weighed
them to measure the amount of ash in the initial sample. The non-ash material left on the filters after acid digestion was considered lignin. I calculated lignin as a percent of the non-ash weight of the initial sample.

I conducted lignin analyses on samples of initial litter from each species, as well as one composite sample of litter from each species that had incubated for 30 days in the terrestrial and the aquatic site.

Cellulase Assay

I conducted a cellulase assay based on methods adapted by Jen Bowen (2003). I stored subsamples of litter from litterbags in scintillation vials at 4°C until I conducted the assays. I added 10 mL room temperature 0.2 M Sodium acetate buffered at pH 5 to each vial. I added 1 mL of 1mM enzyme substrate (4-methylumbelliferyl β-D-glucopyranoside), hereafter called MUF substrate. When the MUF substrate reacts with its target enzyme, it releases a MUF molecule which fluoresces and can be measured using a fluorometer (Turner Designs, Sunnyvale, CA). I removed a 1 mL aliquot from each vial immediately after MUF substrate addition and added it to 4mL 0.2 M glycine buffer (pH 10.5) to halt the enzymatic reaction. I took subsequent aliquots at approximately 40 and 90 minutes after the start of the reaction. I diluted the aliquot and glycine buffer mixture so that the fluorometer reading was below 4.0 uM, the point at which it begins to saturate. Multiple time points allowed me to calculate a rate of accumulation of MUF as the reaction proceeded. This served as an indicator for the amount of enzyme present since more enzyme will cause a greater rate of formation of product. The expected linear increase in MUF over time follows the assumption that the enzyme is saturated with substrate throughout the course of the reaction. For the purposes of analysis, I assume that there was no cellulase on the initial, air-dried litter.

Invertebrate Counts
I visually inspected litter and counted visible macroscopic invertebrates for the final series of bags, and identified them to the class level.

**Results**

**Change in Mass**

After 30 days, maple litter from both sites had lost the most mass of any species, losing 18.8% of its initial mass at the terrestrial site and 24.1% at the aquatic site (Figure 2). All other litter types with the exception of sweet pepper bush in the aquatic site had similar mass remaining after 30 days, averaging a 5.7% loss. Sweet pepper bush gained 6.3% of its original mass after 30 days in the aquatic site. Change in mass values for all sites, species, and time points are summarized in Figure 3.

**Carbon and Nitrogen**

Percent nitrogen in litter increased steadily over the 30 day incubation period (Figure 3). The rate of increase was greatest with the maple litter in the aquatic site, and least with the pine litter in both sites (Table 1). Oak and sweet pepper bush had the highest initial nitrogen content, with 0.65% and 0.63% nitrogen respectively. Maple had 0.48%, and pine had 0.41% initial nitrogen. There were no patterns of difference in nitrogen dynamics between terrestrial and aquatic sites.

Percent carbon increased for all litter types in the terrestrial site, and decreased for all types in the aquatic site with the exception of pine (Figure 4). The terrestrial bags show a slow but fairly steady increase, while the aquatic bags show a pattern of a dip at the first or second time period, followed by a peak at the third time point, and a steeper decrease by the fourth time point (Figure 4). The greatest average rate of decrease in percent carbon over the 30 days was in the aquatic sweet pepper bush litter, and the greatest average rate of increase was in the terrestrial pine litter (Table 2). Pine litter had the
highest initial percent carbon (51.1%), followed by oak (48.9%), maple (47.5%) and sweet pepper bush (44.0%).

C:N ratios of all litters decreased over time (Figure 5). Pine had the highest initial C:N (146) followed by maple (117), oak (88.2), and sweet pepper bush (81.2).

Phosphorus

Sweet pepper bush had the highest initial phosphorus content, with 500 ppm phosphorus. Oak had 451 ppm, maple had 338 ppm, and pine had 266 ppm phosphorus. All litter types showed an increase in phosphorus over 30 days with the exception of aquatic oak litter, which showed a decrease, and the pine litters, which remained fairly constant (Figure 6). Most litter types did not see an increase in phosphorus until the third time point for terrestrial litter, or the fourth time point for the aquatic litter. There were no significant differences in phosphorus content between terrestrial and aquatic incubations of each litter species after 30 days, with the exception of oak which increased from 451 to 497 ppm in the terrestrial litter and a decreased from 451 to 328 ppm in aquatic litter.

Lignin

Lignin percent was initially lowest in the sweet pepper bush litter, and highest in pine litter (Figure 7). Lignin percent increased over the 30-day incubation period for all litter types. There were no clear differences between terrestrial and aquatic ecosystems in terms of lignin percentage after 30 days.

Pine had the highest initial lignin:N ratio (114) and sweet pepper bush had the lowest (21.7); maple and oak had comparable lignin:N (59.6 and 60.1, respectively)(Figure 8). I saw no substantial changes in Lignin:N ratio over 30 days, with the exception of sweet pepper bush, which increased its lignin:N ratio (Figure).

Cellulase Assay
Cellulase activity on litter increased over the 30-day incubation period for all litter types (Figure 9). Sweet pepper bush had the greatest cellulase activity by time period 4, and pine and oak had the least. There were no significant differences in cellulase between terrestrial and aquatic litters.

Figure 10 shows a negative linear correlation between initial lignin content and cellulase activity after 30 days with a correlation coefficient of 0.85.

Invertebrate Counts

Invertebrates were abundant on aquatic litter and nearly absent on terrestrial litter. Since I found very few invertebrates on the terrestrial litter, I do not include those results in this paper. A summary of the number of oligocheates I found on aquatic litter for the 30-day time point can be found in figure 11. There were no statistically significant differences between species in terms of number of oligocheates per gram of dry litter.

Discussion

From this study I found that maple litter decomposes the fastest in 30 days of the litter types I incubated, in both the terrestrial and aquatic sites (Figure 2). This isn’t what I might expect in light of the data I collected on nutrient content, lignin, and cellulase activity on the litter. In regards to nitrogen and phosphorus, microbes must immobilize these elements from their surroundings since litter is nutrient-poor relative to the amounts required by microbes (Aber & Melillo 1991). Therefore, I would expect litter types with greater starting concentrations of nitrogen and/or phosphorus to decompose faster (Aber & Melillo 1991). In this study, oak and sweet pepper bush had the greatest percentage nitrogen (Figure 3), and sweet pepper bush had the most phosphorus (Figure 6). Since maple decomposed faster than other species with greater initial nutrient concentrations, it appears that nutrient concentration is not the only chemical factor controlling mass loss within this 30-day experiment. The percent nitrogen
does increase on the litter over the course of 30 days, suggesting that net immobilization occurs during this time.

In terms of carbon percentage, I saw a dip in percent carbon in the aquatic bags in the first two time periods. Since leaching has been shown to play an important role in the loss of dissolved organic carbon (DOC) from litter within the initial stages of decomposition (Hansson et al. 2010), this may explain the loss of percent carbon. However, this doesn’t translate to a greater loss in mass in the aquatic bags. Another possibility is an error in methods, since I were using a different, less effective method of removing inorganic sediment from aquatic leaves (brushing as opposed to rinsing) for the first time period. This may cause percent carbon to appear to dip during this time period due to increased inorganic sediment on the leaves. Still, the greater losses of carbon we see in the aquatic bags suggests that DOC is being removed, likely through leaching. And yet, this loss of DOC is not reflected in greater mass loss in the aquatic bags. C:N ratio of litter decreased fairly uniformly over thirty days, which logically follows the observed increases in nitrogen and decreases (or minimal increases) in carbon.

There is net mineralization or no change in percent phosphorus in all litters besides the aquatic oak litter. Additionally, phosphorus content of litter did not vary between sites within a given litter type except with oak. The difference between oak terrestrial and aquatic leaves is something I might have expected due to phosphorus limitation in our pond ecosystem. This would limit the amount of phosphorus that microbes could immobilize, and therefore I expected a greater increase in terrestrial phosphorus than aquatic, which I observed. However, this does not hold true for our other species, so it is possible that the difference with oak is simply due to chance.

Percent lignin in litter increases over the 30-day incubation. One reason for this is that other, more labile compounds in the litter are preferentially broken by microbes, increasing the relative
amount of the lignin which is left behind. Also, in processing other compounds, microbes often convert them to more “lignified” compounds. This phenomenon has been shown to increase the absolute amount of lignin in the litter during early stages of decay (Aber & Melillo 1991, Ishikawa et al. 2007). The change in percent lignin is greatest with the sweet pepper bush litter, which suggests that it has seen the most microbial processing and/or loss of labile compounds. The lignin:N ratio would also suggest that sweet pepper bush should decompose the fastest, following the hypothesis that litters with lower lignin:N have faster decay rates (Aber & Melillo 1991). However, this is not reflected in the amount of mass lost by sweet pepper bush during the litter bag incubations.

One possible explanation for slowed decomposition in the relatively nutrient-rich, lignin-poor sweet pepper bush litter is anti-herbivory compounds such as tannins, which have been shown to retard decomposition (Aber & Melillo 1991). If this were the case, I would expect to see a relative lack of microbial extracellular enzymes on sweet pepper bush litter, since the anti-herbivory compounds would slow microbial activity or prevent these enzymes from being effective. In fact, sweet pepper bush has the highest increase in cellulase activity over 30 days, which suggests that microbes are actively breaking down cellulose in sweet pepper bush litter and not being hindered by anti-herbivory compounds. I have yet to develop another feasible hypothesis for the observed pattern of mass loss in sweet pepper bush.

Cellulase activity increases over the 30 day incubation period for all litter types in both sites. This suggests that microbes are colonizing the litter, growing, and digesting continually more cellulase over this time period. This data is consistent with other studies which show a peak in cellulase activity within the first 50-100 days of litter decomposition (Linkins & Sinsabaugh 1990). The amount of cellulase activity I measured on litter correlates to the initial lignin content of the litter in a negative linear relationship (Figure 10). This may be because litter types with greater amounts of lignin have less cellulose, and so microbes produce correspondingly less cellulase. This also may be caused by a
phenomenon in which cellulose is tightly bound to lignin and is therefore less accessible the more lignin is present in the initial litter (Aber & Melillo 1991 as cited in Forbes & Reardon). With the exception of sweet pepper bush, cellulase activity is generally predictive of decay rate, with maple having more cellulase than oak and pine. This suggests that microbial activities are responsible for mass losses in litter, and that some other factor is affecting mass loss for sweet pepper bush.

In terms of invertebrates, the 1mm mesh size of our bags seemed to exclude most terrestrial shredders. There were communities of oligocheates in the pond ecosystem litter bags, although it is unclear whether these worms eat and shred the detritus or simply use it as a substrate to live on. The worms formed casings which were abundant on the litter, and so it is possible that the litter serves primarily as a surface to build these homes. This idea is supported by the lack of difference in mass loss between ecosystems—the activities of detritivores have been shown to increase litter decomposition rate, and I saw no differences in mass loss between ecosystems. I found no statistically significant differences in the number of oligocheates per gram of dry litter between litter species. I conclude that oligocheate populations may have contributed to litter processing in aquatic systems, but that this difference is not reflected in the mass loss data and so further study is needed to understand these interactions.

One striking aspect of our results is the similarity in results between ecosystems. Although oligocheate populations were present on aquatic bags, and despite greater carbon losses in the aquatic bags, these differences did not translate to differences in mass, nutrient content, or cellulase activity between the two ecosystems. Terrestrial and aquatic litters lost mass, immobilized nitrogen and phosphorus, and fostered microbial activity at the same rates and in the same patterns across both ecosystems. This suggests that, despite the obvious differences between a pond and forest, this
variation in environment does not play a large role in determining decomposition rates and patterns during the first 30 days following leaf fall. Instead, initial leaf species governed decomposition patterns.

This result contrasts with the Linkins & Sinsabaugh (1990) study in which litter decomposition and cellulase activity differed between terrestrial and aquatic ecosystems. There are several factors that could explain the discrepancy in mass loss. In the streams where Linkins & Sinsabaugh conducted their study, the water is likely more turbulent than in the Punch Bowl, meaning more access to oxygen in the stream sediments than in a pond. This could account for slower decomposition rates in the Punch Bowl, as could high tannin levels which may slow decomposition (Aber & Melillo 1991). Additionally, there was regular rainfall during the time of incubation, which minimized differences in moisture availability between the terrestrial and aquatic bags. Lack of turbulence could also explain the similarities in exocellulase between ecosystems in this study, where Linkins & Sinsabaugh saw less exocellulase in aquatic litter. It is possible that exocellulase does not diffuse as rapidly in still pond water as in a moving stream, which could explain the similar cellulase concentrations measured in both sites.

Conclusions

We conclude that litter composition is the main factor controlling decomposition in the first 30 days, and that in these ecosystems, environments are not as indicative of decay rates and nutrient dynamics in this timeframe. There are some deviations from correlations I would expect to see between litter characteristics and observed decay rate. This is particularly true in the case of sweet pepper bush, which doesn’t decay as quickly as I might predict based on nutrient, lignin, and cellulase measurements. In all, maple litter degrades the fastest of these litter types during a 30-day incubation period.

Acknowledgements

Special thanks to Linda Deegan, Jerry Melillo, Rich McHorney, David S. Johnson, Will Daniels, and Stefanie Strebel for help designing and executing this project, and interpreting its results. Thank you to Ken Foreman, SES, MBL and the Ecosystems Center for making this project possible.
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Table 1. Rates of change of percent nitrogen in litter over 30 days, expressed as change in % nitrogen per day. Calculated from the slope of the best-fit line to the data from each series.

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Table 2. Rates of change of percent carbon in litter over 30 days, expressed as change in % carbon per day. Calculated from the slope of the best-fit line to the data from each series.

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Figure 1. Map of Beebe Woods in Falmouth, MA, including terrestrial and aquatic sites for this study.
Figure 2. Change in percent remaining organic matter by species and site over time.
Figure 3. Percent nitrogen in litter by species and site over time.
Figure 4. Percent carbon in litter by species and site over time.
Figure 5. C:N Ratio by species and site over time.
Figure 6. Phosphorus content of litter by species and site over time.
Figure 7. Initial and final percent lignin in litter in terrestrial and aquatic ecosystems.
Figure 8. Initial and final Lignin:N ratio of litter in terrestrial and aquatic ecosystems.
Figure 9. Cellulase activity as measured by a rate of MUF formation (µmol g\(^{-1}\) dry litter min\(^{-1}\)) over a 90-120 minute assay, plotted against time of incubation.
Figure 10. Initial percent lignin of litter plotted against MUF formation (umol g⁻¹ dry litter min⁻¹) for 30-day bags.
Figure 11. Number of oligocheates found on aquatic litter from time period four, per gram of dry litter.