The effect of shredder species, shredder richness, and leaf diversity on decomposition rates

BIOS 35501-01: Introduction to UNDERC

Kate Kirbie: kkirbi01@saintmarys.edu

Advisor: Christopher Patrick

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Abstract

Shredders are important macroinvertebrates that break down leaf litter in waterways and produce food for collectors (gathering and filtering insects). The rate of the decomposition of the leaf litter by the shredders is dependent on multiple factors, one of these being the leaf species and leaf species richness in a leaf pack. Leaf species richness has been shown to both positively and negatively affect the decomposition rate but the interaction between shredder richness, shredder species identity, and leaf species identity has not been tested. Five different leaf species (speckled alder, quaking aspen, American basswood, sugar maple, and pin oak) were crossed with four shredder treatments (*Pycnopsyche guttifer*, *Caecidotea*, and *Hyallela azteca*, and a mix of the three). Mesocosms with 0.5 g of the leaf material a sealed bag of 0.5 g of leaf material and shredder treatments were run in artificial streams for 26 days. I hypothesized that there would be more leaf mass consumed in multispecies treatments across leaf species identity and therefore a negative relationship between log response ratio (LRR, the interaction between shredders) and decomposition rate. I also predicted caddisflies would decompose more leaf material independent of leaf type, while American basswood would decompose the fastest independent of shredder treatment. Results showed more leaf mass was consumed in mixed species treatments than in the average individual treatment but no relationship was seen between the LRR and decomposition rate. Unlike hypothesized, no shredder significantly dominated the decomposition. As expected the control leaves decomposed at different rates, but surprisingly, speckled alder decomposed significantly slower than pin oak.

Introduction

Shredders are macroinvertebrates that decompose leaf litter in streams and rivers (Cummins *et al*. 1973). The litter consumed is larger than 1mm in diameter and is termed course particulate organic matter (CPOM) (Vannote *et al*. 1980). Through defecation of consumed leaf material and the breakup of non-consumed food, these macroinvertebrates produce fine particulate organic matter (FPOM), particles smaller than 1mm in diameter (Webster and Benfield 1986). FPOM provides substrate for bacteria and fungi to grow. This material is fed on by collectors (gathering and filtering insects) (Cummins *et al*. 1973; Wallace and Webster 1996; Jonsson and Malmqvist 2005). The digestion of leaves by shredders also prevents buildup of dead vegetation downstream (Wallace and Webster 1996).

The speed at which the shredders process leaves depends on the type of shredder, type of leaf, and the temperature of the water (Cummins *et al*. 1973). Abelho (2009) predicted intrinsic factors like leaf chemistry and toughness have a larger impact on decomposition rates than other extrinsic variables. Leaves with low carbon to nitrogen or carbon to phosphorus ratios, low levels of secondary metabolites, and low levels of lignin usually increased in decomposition rate (Srivastava *et al*. 2009; Madritch and Cardinale 2007). Decomposition rates can also depend on the type of leaves mixed together in a pack. Swan and Palmer (2006) found that when presented with a solitary unpalatable species of leaf more mass was consumed than when presented in a pack of more palatable species. The outliers in this group likely come from external factors, like mixing compounds from adjacent leaves or differing levels of microbial growths (Swan and Palmer 2006).

Although increased shredder species richness increases the rate at which detritus decomposes, it is suggested that a very high species richness level has little additional impact compared to a moderate richness level (Jonsson and Malmqvist 2005; Srivastava *et al.* 2009). While shredders often positively interact with each other, increasing decomposition rates through facilitation there are examples of interspecific competition being an important process as well (Creed *et al*. 2009, Patrick and Fernandez unpublished). As Srivastava *et al*. (2009) suggested there is a great need to understand how decomposition rates change with shredder diversity.

To understand the effects of shredder richness and leaf richness on decomposition, Srivastava *et al.* conducted a meta-analysis of decomposition experiments (2009).The effect of species richness was measured by calculating the LRR, the log of the average amount decomposed in single species treatments divided into the mixed species treatment. The conclusions in this review came from a meta-analysis of articles with data of multiple detritivores (fungi, macroinvertebrates, and bacteria). Some of the results came from studies (Cardinale *et al.* 2002, Johnsson and Malmqvist 2003, and Cardinale and Palmer 2002) where no leaves or shredders were actually used (Cardinale *et al.* 2002, Cardinale and Palmer 2002). On average, the log response ratio (LRR), of the mixed leaf species treatments was no different from zero, a result of experiments either yielding synergistic or antagonistic effects of richness (Srivastava *et al.* 2009).

While the results of the meta-analysis are interesting, none of the articles included in the analysis manipulated both leaf richness and detritivore richness. Furthermore, I question whether the results of experiments involving manipulations of bacteria and fungi can be compared to manipulations of shredders since the latter experiments must have included bacteria and fungi as well. While Srivastava *et al.* (2009) demonstrated that leaf species richness alone does not appear to matter, they have not demonstrated if there is an interaction between leaf species identity and shredder richness.

I examined the collected data from the review to determine if there was a relationship between leaf species identity and shredder interactions. By performing a regression I found that of the studies where the same species of shredders were used, there was a strong negative relationship ($F_{1,1}$ =98.444, p=0.064,r^2 = .99) between the intrinsic rate of decay (k) and the LRR of shredder richness (Figure 1).

Based on the research reviewed by Srivastava *et al*. (2009) and this understanding of the interaction between shredders and detritus it seems possible that leaf species does play an important role in controlling decomposition rates. The data presented above is suggestive of this relationship; however, testing this relationship directly is necessary. Therefore, the main purpose of this study is to look at how the decomposition rate of leaf species can change the role of shredder species richness in affecting decomposition rates. The null hypothesis is that a change in shredder species, shredder richness, and leaf species will have no effect on decomposition rates. Multiple hypotheses stem from this study's goal:

1) I hypothesize that there will be a greater amount of leaf mass consumed in the multispecies treatment compared to an average of the individual treatments. Different types of shredders are better at decomposing varying parts of leaves because one shredder consuming part of the leaf material can allow others to more easily decompose other parts of the leaf material (Heard 1994).
2) I expect a negative relationship between the amount of decomposed leaf litter and the LRR, as we saw after reviewing the papers compiled from Srivastava *et al.* (2009). The leaves that are harder to decompose and have more leaf mass left may need more shredder richness to assist in the decomposition of the leaves. While leaves that decompose faster may be easier for solitary shredders to consume, decreasing the LRR.

3) I predict that caddisflies will decompose all leaves faster than the other shredders because they have been shown to be decomposing leaf litter faster. There is little information to show the differing levels of decomposition rates between amphipods and isopods. Therefore I expect these two types of organisms to decompose material at the same rate when biomass of the individuals is compared to leaf material consumed.
4) I anticipate that different species of leaves will decompose at different rates. Webster and Benfield (1986) found that leaves from trees in the Tiliaceae family, some now in Malvaceae (American basswood), decomposed the fastest. Trees in the Betulaceae family (speckled alder) decomposed slower than that in Tiliaceae but at a similar rate to those in the Salicaceae family (quaking aspen) and Aceraceae family, some now in Sapindaceae (sugar maple). But all of these species of leaves decomposed faster than those from the family Fagaceae (pin oak).

Materials and Methods

Senesced leaves from *Alnus incana* (speckled alder), *Populus tremuloides* (quaking aspen), *Tilia americana* (American basswood), *Acer saccharum* (sugar maple), and *Quercus palustris* (pin oak) were collected. Collection took place in the October of 2010 on the UNDERC (University of Notre Dame Environmental Research Center) property during leaf abscission. I chose these species of leaves as they are common in the forests of the Upper Peninsula of Michigan and they comprise a gradient of intrinsic rates of decay (Webster and Benfield 1986).

The experiment was performed in individual mesocosms. Each mesocosm was made of a plastic cup ($130 cm^3$ in volume), with the bottom removed and replaced with 500 µm mesh fabric. Each mesocosm held 0.5 g of senesced loose leaf material. This allowed the macroinvertebrates to freely consume leaf detritus. I also placed a sealed bag composed of 63 μm mesh in the mesocosm which also held 0.5 g of leaves, inhibiting shredders from entering the bag. I used this bag to later measure microbially driven leaf decay.

I caught *Pycnopsyche guttifer* (caddisflies), *Caecidotea* (isopods), and *Hyalella azteca* (amphipods) in two different locations at the UNDERC field site and one location in the Ottawa National Forest. These detritivore species were chosen based on their abundance on the UNDERC property. Although caught in different locations, it is common for these shredders to live in the same site.

Mesocosms contained two levels of species richness. I housed each species of macroinvertebrate alone in a separate mesocosm. The number of shredders used was based on a shredder biomass: amphipod treatments had 75 *Hyalella azteca*, caddisfly treatments had 3 *Pycnopsyche guttifer,* and isopod treatments had 6 *Caecidotea*. A fourth mesocosm housed all three species but contained the same total biomass: 25 *Hyallela azteca*, 2 *Caecidotea,* and 1 *Pycnopsyche guttifer*. I crossed these four shredder treatments with the five individual leaf types and used five replicates, totaling 100 mesocosms. The mesocosm was placed in a closed loop artificial stream continuously filled with 10 percent filtered water from a local lake and 90 percent well water. The streams were aerated by means of the turbulent flow and I covered the streams with shade cloth to limit periphyton growth. Mesocosms were blocked across the individual streams with 12-13 per stream (Figure 2).

After 26 days leaves were dried at 60°C and ashed at 550°C. They were weighed to determine dry weight lost and ash free dry mass (AFDM). The AFDM was subtracted from the original 0.5 g to determine amount consumed. Nitrogen and carbon values of these species were determined using a Costech elemental analyzer at the University of Notre Dame Center for

Environmental Science and Technology. I also used the phosphorus and lignin values reported by Berg and McClaugherty (1989) to better judge differences in the species of leaves. To measure leaf toughness, results from a penetrometer were used.

The data was first normalized by log transforming it. An independent regression analysis was run to relate the LRR of shredder species richness to the intrinsic rate of decay of each leaf species. I also compared LRR to various leaf traits including the percent lignin, C, N, and P. The decomposition rates of individual shredders were compared to each other across leaf types using multiple ANOVAs. All analyses were performed using SYSTAT.

Results

When comparing the overall amounts consumed by individual species and that of the mixed treatments in an ANOVA the mixed treatments lost significantly more leaf mass than the single species treatments ($F_{1,98}$=3.936, p=0.050, Figure 4). ANOVAs looking at the difference in decomposition rate between mixed and individual shredder species on each individual leaf species showed American basswood was the only leaf species to differ in decomposition rate ($F_{1,18}$=4.463, p=0.0489). There was no significant difference between mixed and individual treatments of speckled alder ($F_{1,18}$=0.925, p=.349), quaking aspen ($F_{1,18}$=0.279, p=0.604), sugar maple ($F_{1,18}$=0.708, p=0.411), or pin oak ($F_{1,18}$=1.543, p=0.230). Results from a regression show no significant correlation between the total leaf mass leached from the control bags and the LRR (Figure 3).

Overall there was no difference in the amount decomposed across individual shredder species, seen in an ANOVA looking at individual shredder species, decomposition was dependent on leaf species (Figure 5). Individual ANOVAs also showed shredders did not decompose speckled alder ($F_{2,12}$=0.885, p=0.438), American basswood ($F_{2,12}$=3.308, p=0.072), sugar maple ($F_{2,12}$=0.024, p=0.977), or pin oak leaves at significantly different rates ($F_{2,12}$=1.336, p=0.299), but shredders did decompose quaking aspen at a significantly different rate. ($F_{2,12}$=5.553, p=0.020). A Tukey post-hoc test showed caddisflies decomposed the quaking aspen leaves significantly faster than the amphipods (p=0.017) but there was no significant difference between any other shredder and leaf combinations (Table 1).

An ANOVA also showed that the leaf material in the control bags had a significantly different mass decomposed ($F_{4,95}$=78.813, p =0.000, Figure 6). A Tukey post-hoc test showed all leaves decomposed at significantly different rates from each other (Table 2) with the exception of quaking aspen and sugar maple (p=0.999).There was overall no significant difference between the mass lost in the control bags compared to that of the mesocosm ($F_{1,198}$=0.360, p=0.549, Table 3)

Discussion

Species richness

As hypothesized, overall more leaf mass was consumed in the mixed species treatments than compared to that of the average individual treatments, but when broken down into the amount consumed by mixed and individual shredders in each leaf treatment the only leaf that showed this significant difference was American basswood. Although American basswood has been shown to decompose quickly, the assistance from other shredders in the mixed treatment allowed the leaves to decompose significantly faster. Speckled alder appears to have decomposed faster in the individual treatments likely due to the large rate of decomposition from the caddisfly treatments. Further analysis should examine different levels of species richness and use different shredder species.

Log response ratio

My hypothesis that there would be a negative relationship between the LRR and the amount of decomposed leaf mass was not supported by my analyses. After reviewing the paper by Srivastava *et al*. (2009) a negative relationship seemed highly likely, but this relationship was not seen (Figure 3). Therefore results show a limited collaboration by shredders across all leaves. American basswood is known to decompose quickly and had a high LRR. On the other hand, according to Webster and Benfield (1986), pin oak decomposes the slowest of the five leaves, yet the oak had the second highest LRR. In my study, quaking aspen decomposed at a medium rate and had a negative LRR, showing a negative interaction between the shredders in the aspen treatments. Clearly other factors, affecting the aspen alone, cause the shredders to not be as productive in feeding. Aspen has a lower amount of nitrogen (Figure 7) which could cause competition for the food source, but this competition is not seen intraspecifically. Sugar maple also has the lowest amount of nitrogen and has only the second lowest LRR. Multiple factors must combine to change the interspecific interactions.

Shredder species

Unlike hypothesized, no shredder significantly lead the decomposition, although there appears to be a trend showing caddisflies decomposed more of the leaf material. Caddisflies did decompose significantly more quaking aspen leaf litter than the amphipods. Previous work has shown caddisflies take the lead in decomposition but there has been no true understanding for why this occurs.

Leaf species

As anticipated, the leaves in the control bags did decompose at different rates (Figure 5). A report from Webster and Benfield (1986) suggested that American basswood would decompose the fastest; quaking aspen, sugar maple and speckled alder, should decompose in a medium range, and pin oak should decompose the slowest. My data supports this except for the decomposition order of pin oak and speckled alder. American basswood decomposed fastest, then quaking aspen and sugar maple, then pin oak. The slowest to decompose was speckled alder. This trend may correspond to the amount of lignin present in the leaves (Figure 8). According to Berg and McClaugherty (1989), speckled alder contained the most amount of lignin, next to pin oak, a type of red oak. Both sugar maple and quaking aspen had lower levels of lignin, allowing them to naturally decompose faster.

Experimental design

The bag in each mesocosm was intended to be the control for each treatment. Unfortunately the leaves did not act the same way in the mesocosm as in the control bag. Although there was more leaf material decomposed in the speckled alder mesocosm, compared to the control, there was no significant difference from the control in other leaf treatments (Figure 9). The final leaf mass in the mesocosm should have been lower than the leaf mass in the bag, but this was not found in sugar maple or pin oak treatments. Here the decomposition rate appeared higher. I expect there was not enough material leaching out of the control bags due to the size of the mesh bag material. The leaves in the bag also felt like they were covered in mucus, indicating that decaying material had not dispersed out of the mesh bag.

Conclusion

Shredders are important to the health of many waterways and consumers. To correctly study these organisms, there needs to be an understanding of their ability to decompose and what affects the decomposition of the leaf litter they consume. This study showed there was significantly more leaf mass consumed by treatments of higher shredder species richness than individual species. Yet there was no significant relationship between the LRR and the decomposition rate, as the review by Srivastava *et al.* (2009) showed looking at all shredders, fungi and bacteria. Unlike hypothesized, no shredder significantly led the decomposition of leaves, although caddisflies appeared to decompose more. Most leaves decomposed at rates similar to that recorded by Webster and Benfield (1986), but speckled alder decomposed significantly slower than pin oak. This could be due to the amount of lignin found in the leaves. Results could also have been altered resulting from the type of mesh bag the controls in which the leaves were held. These results should be taken into account as further studies are performed observing shredders and leaf decomposition.

Acknowledgements

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Tables

Table 1. P-value results of the Tukey comparing the amount decomposed of each leaf species by each shredder species.

shredder 1	shredder 2	AL	AS	B	M	O
A	C	0.842	0.017	0.590	1.000	0.274
A	I	0.732	0.511	0.386	0.979	0.603
C	I	0.409	0.122	0.476	0.982	0.800

A=amphipod, C=caddisfly, I=isopod, AL=speckled alder, AS=quaking aspen, B=American basswood, M=sugar maple, O=pin oak

Table 2. Results of the Tukey comparing the different leaf species in control bags.

Leaf sp. 1	Leaf sp. 2	p-Value
AL	AS	0.000
AL	B	0.000
AL	M	0.000
AL	O	0.000
AS	B	0.000
AS	M	0.999
AS	O	0.015
B	M	0.000
B	O	0.000
M	O	0.007

AL= speckled alder, AS=quaking aspen, B=American basswood, M=sugar maple, O=pin oak

Table 3. Results of individual ANOVAs comparing the amount decomposed of each leaf species in the mesocosm compared to that in the bag.

Leaf species	p-value	F-ratio
Speckled Alder	0.549	0.360
Quaking Aspen	0.754	0.100
American Basswood	0.792	0.071
Sugar Maple	0.122	2.504
Pin Oak	0.095	2.936

Figures

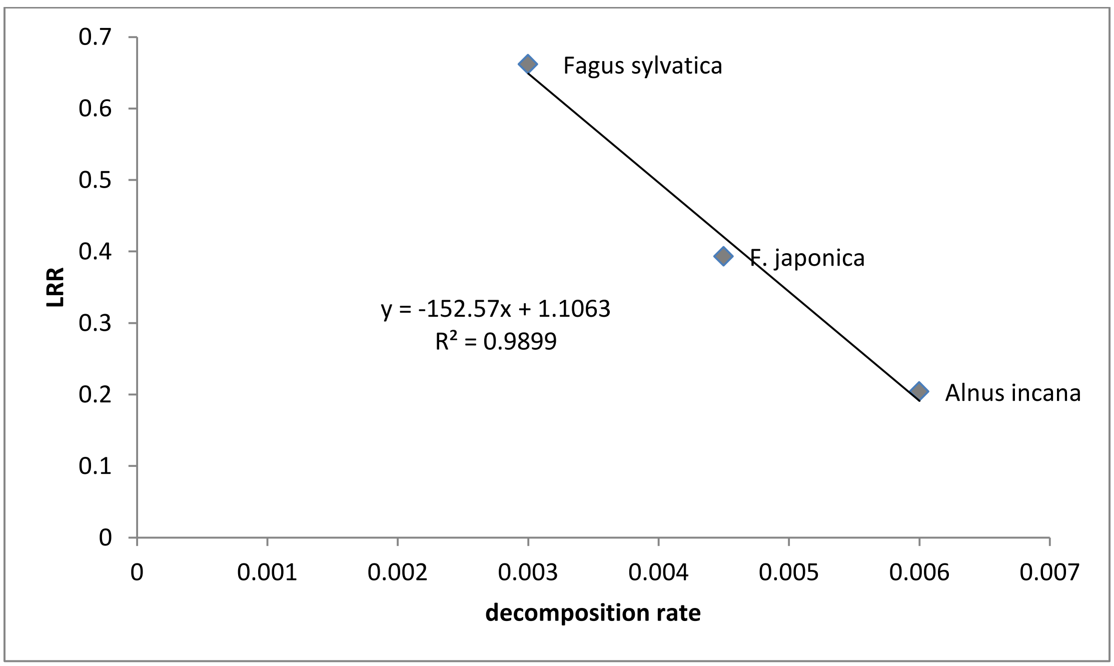

Figure 2. The LRR of three different species of leaves compared to their decomposition rates based on decomposition by *Nemurella picteti*. Data comes from Srivastava *et al*. (2009).

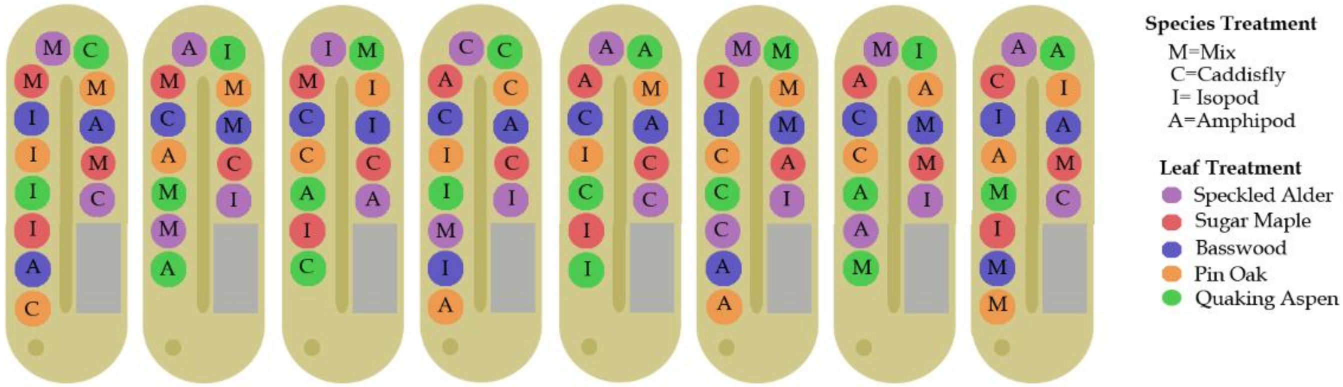

Figure 1. Diagram of leaf and shredder treatment distribution in the artificial stream.

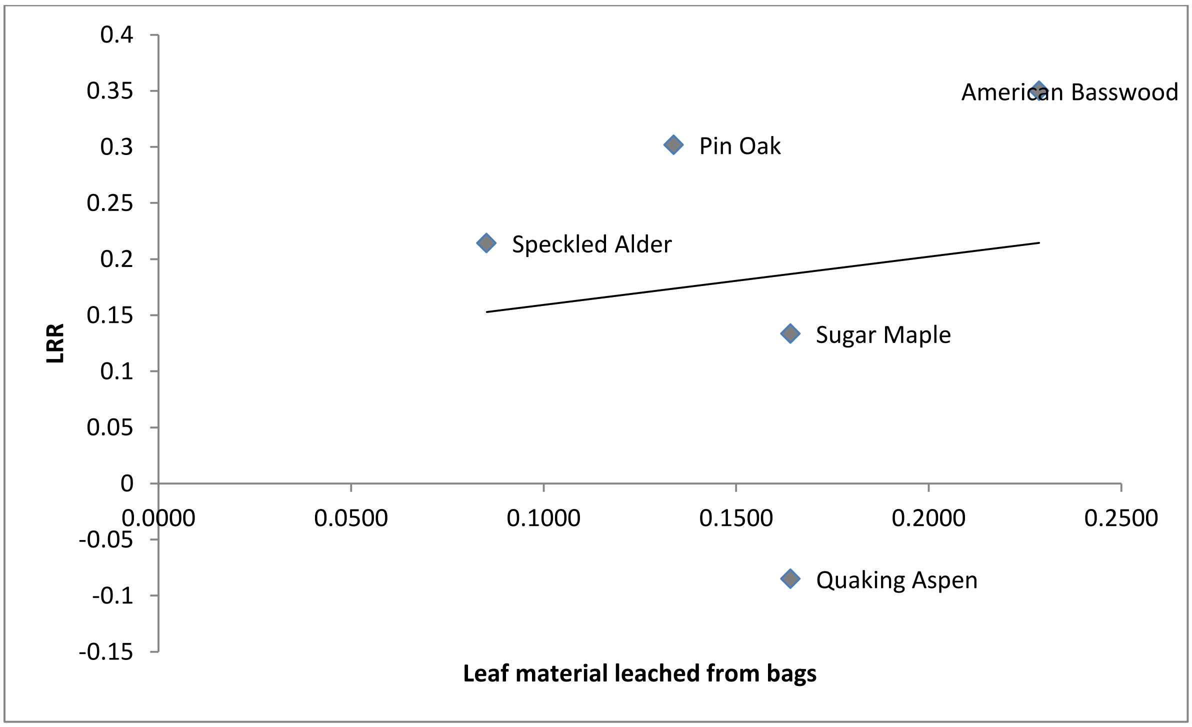

Figure 3. The LRR compared to the amount of leaf material leached from the control bags based on leaf species. R^2= 0.000; $F_{1,3}$=0.005; p=0.946

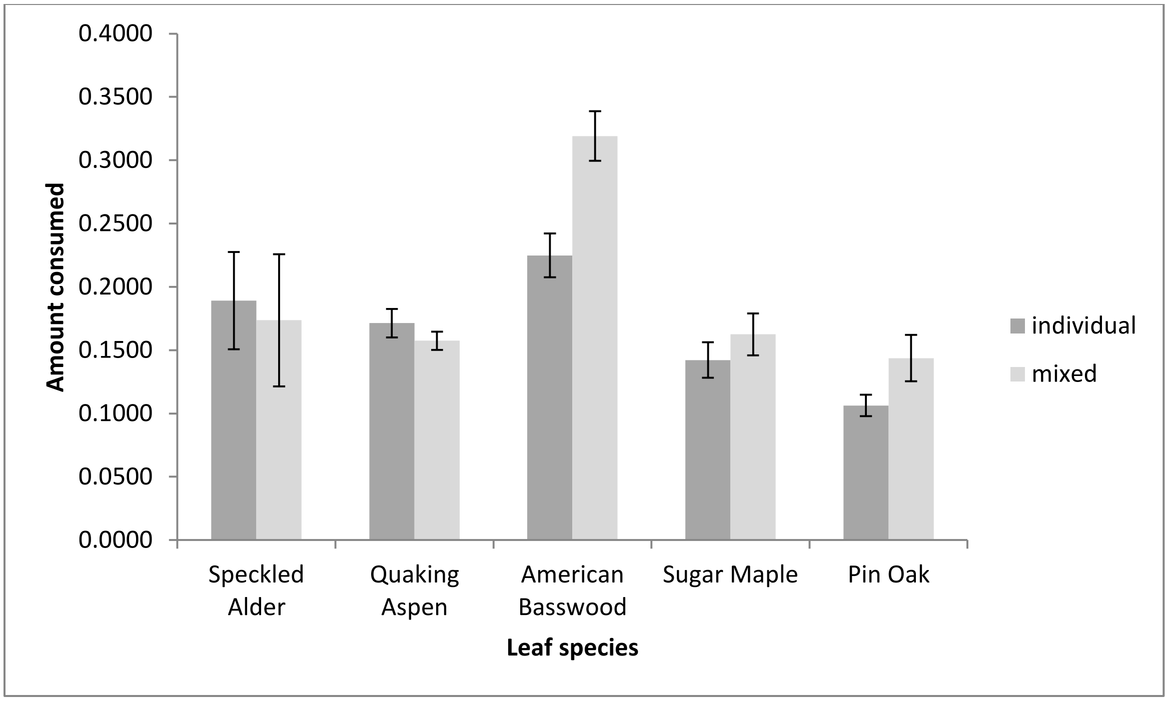

Figure 4. The amount of leaf litter consumed by the combination of all individual species shredder treatments compared to the mixed treatments. $F_{1,98}$=3.936, p=0.050

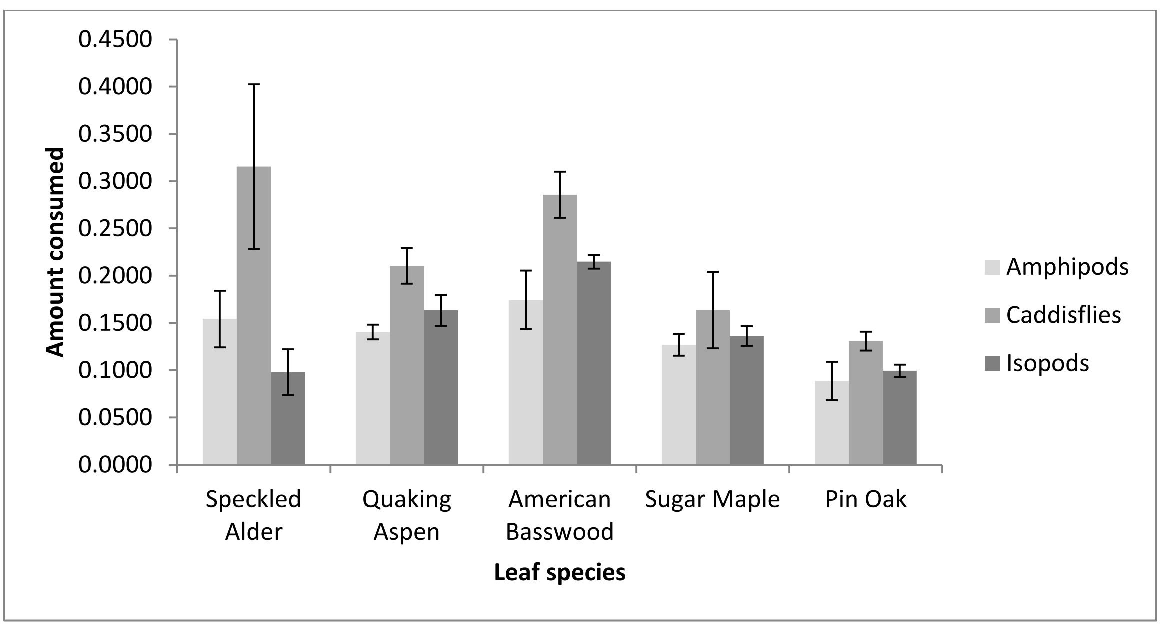

Figure 5. The amount of leaf litter consumed in the individual treatments in each leaf species treatment. Amphipods: $F_{4,20}$=1.596; p=0.214, caddisflies: $F_{4,20}$=0.879; p=0.494, isopods: $F_{4,20}$=10.438; p=0.000.

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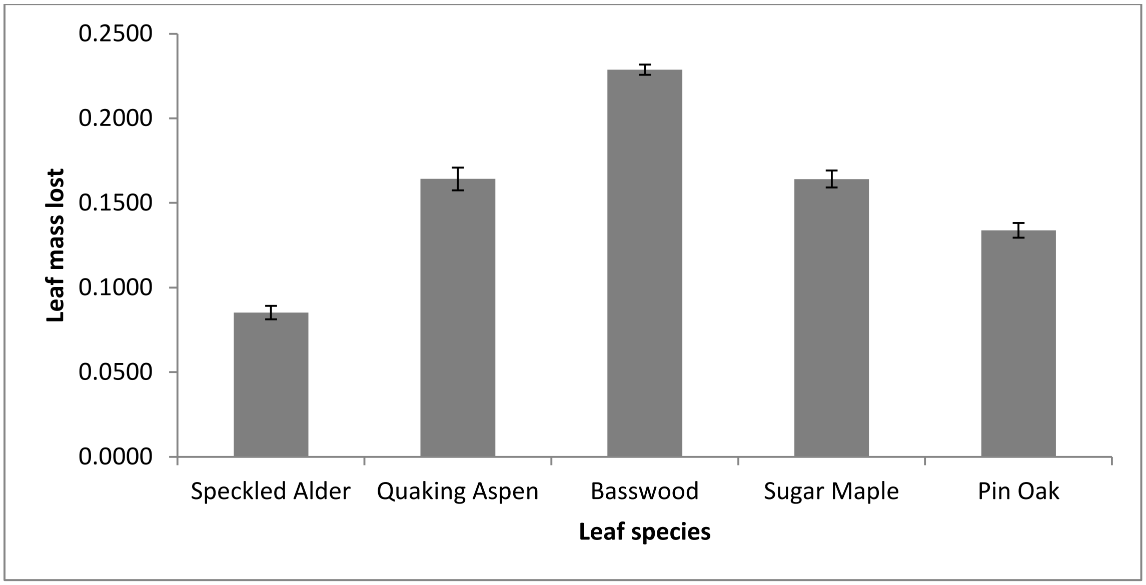

Figure 6. The leaf mass lost from the control bags in each different leaf species treatment.

$F_{4,95}$=78.813, p =0.000

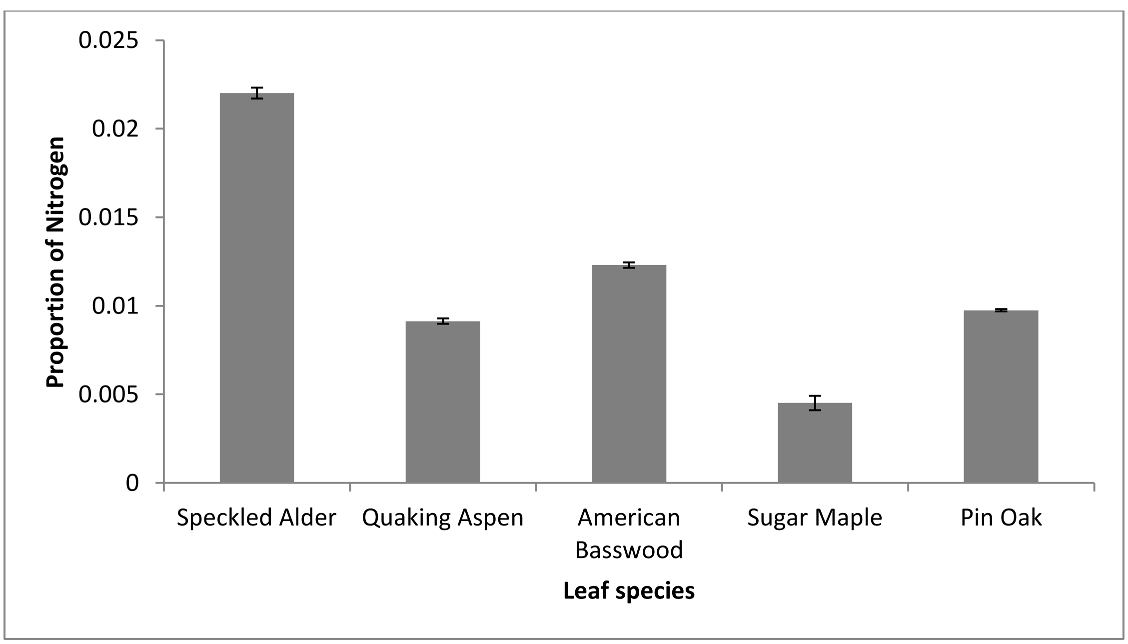

Figure 7. The proportion of nitrogen to other compounds for different leaf species.

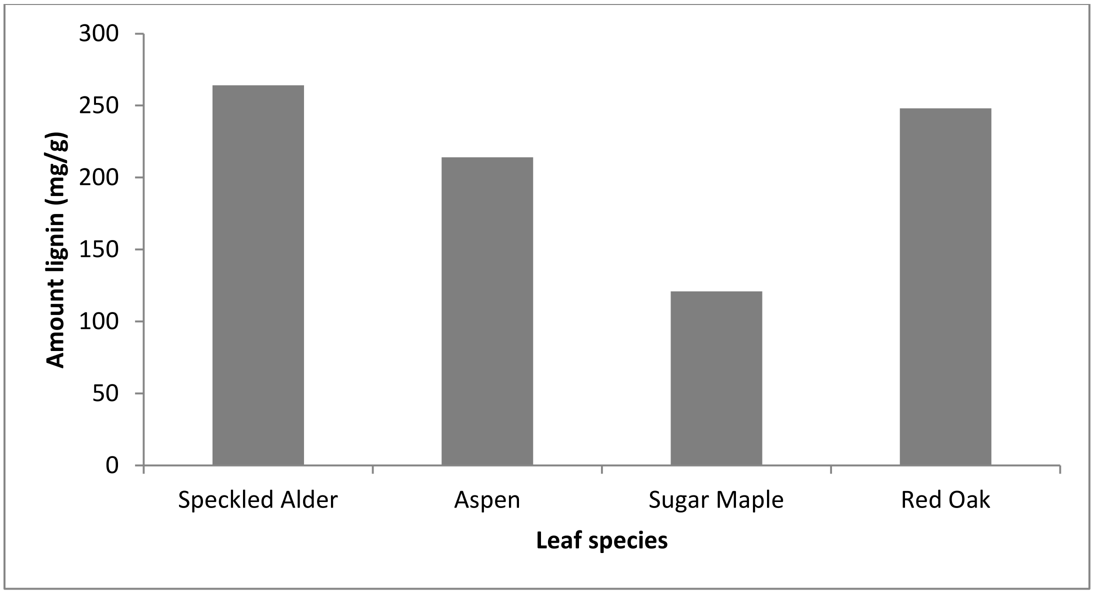

Figure 8. The amount of lignin in four different species of leaves. Data taken from Berg and McClaugherty (1989)

*Basswood data not available

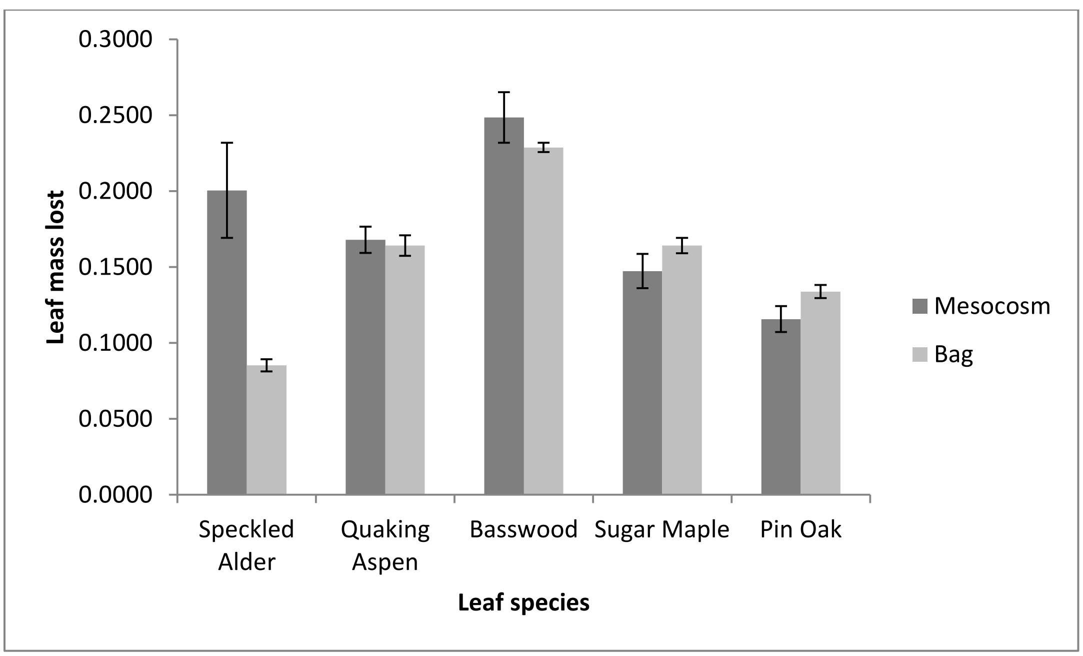

Figure 9. The leaf mass lost from the control bags and in the mesocosm containing each different leaf species treatment. $F_{1,198}=0.360$, $p=0.549$