Organic Matter Decomposition: Interactions of Temperature, Moisture and Substrate Type

Major Paper by:

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Abstract

The decomposition of organic matter is a major biogeochemical process because of its effect on ecosystem productivity and its implications on climate change. Temperature and moisture are two variables that have a tremendous influence on microbial decomposition. Decomposition is also influenced by substrate type, in which higher quality substrates often have greater decomposition than lower quality substrates. Pine and hardwood litters, popsicle sticks, aspen and pine wood stakes were subjected to 4 temperature treatments (10ºC, 20ºC, 30ºC, and 40ºC) and 4 moisture content treatments (wet 23-28%, moist 15-20%, dry 3-7%, & fluxing between 3-7% and 23-28% saturation) over the course of 30 months, in order to determine the influence of temperature, moisture, and substrate type on decomposition. As a subset of the experiment soil respiration was recorded from one pvc collar with leaf litter and one without litter and was subjected to the same treatments. There were different responses with different substrates, but overall microbial decomposition was greatest at the highest temperatures. For the wood substrates the "moist" and "dry" moisture contents generally produced the highest mass losses. The pvc collar's highest soil respiration rates were with the "wet" moisture treatment. Temperature and moisture are both significant in decomposition, but the moisture relationship interaction with decomposition is much harder to understand.

Introduction

Decomposition of organic matter is an essential component of forest ecosystems in order to ensure the physical and chemical breakdown of organic materials and the mineralization of nutrients. Through the decomposition process, nutrients in organic materials are converted to forms which are available for uptake by vegetation. An accurate assessment of decomposition activity within a particular forest ecosystem is an essential part of a total assessment of the ecosystem's health and function because most forest ecosystems are self maintained through primary production and nutrient cycling (Baker et al. 2001). Baker et al. (2001) noted that "micro and macro invertebrate, bacterial, and fungal communities depend on these organic resources for food" and that the decomposition of organic materials into basic nutrient materials represents a "critical control on vegetation productivity".

The decomposition process consists of two stages, beginning with the breakdown of organic materials (leaf litters, wood, etc.) by detritivores into smaller pieces which can then be further reduced and mineralized in a second stage by soil microorganisms (mainly bacteria and fungi) which converts these small fractions into basic inorganic molecules, such as ammonium, phosphate, carbon dioxide, and water, which are available for uptake by plants. Detritivores and soil microorganisms are often referred to as secondary and primary decomposers, respectively. It is the primary decomposers that comprise a large majority of the decomposer biomass; however, the secondary decomposer activity can significantly stimulate the decomposition activity and effectiveness of the primary decomposers within forest ecosystems. Bacteria are the most abundant soil microbe followed by fungi. Their abundance in the soil and thus the speed with which organic materials are decomposed depends on many factors like nutrient availability, substrate type, oxygen, pH, temperature and moisture. Temperature and moisture has been shown by some researchers, in one way or another, to have a major effect on decomposition. The studies by Baker et. al. (2001), Meentemeyer (1978), Preston et al. (2000), and Swift et al. (1979) have shown how temperature and moisture influence organic matter decomposition, in that warmer temperatures and high moisture levels (including precipitation) result in higher rates of decomposition, faster litter turnover, and less organic matter accumulation. It should be noted however, that excessively low or high temperatures can decrease fungal and microbial activity. Likewise, excessive water (which can lead to anaerobic conditions) may result in less available oxygen, which hinders decomposition. Jurgensen et al. (2006) showed that of the two physical variables, temperature seemed to be the more important driver in decomposition. However, Woods and Raison (1983) suggested that moisture was a major factor in controlling decomposition, while Ibrahim et al (2010) suggested that a combination of the two was the most important factor controlling decomposition.

Decomposition is commonly studied using the litter bag method, which consists of enclosing plant material of known mass and chemical composition in a screened container so that the bags can be analyzed for loss of mass and/or changes in the chemical composition of the litter (Wieder and Lang, 1982). Wieder and Lang (1982) also noted the long history of this method, which dates to the 1930's. They also noted that a number of studies have examined drawbacks to this method of analysis decomposition, and also stated that "considerable variation occurs in the statistical procedures used to examine decomposition data," though it remains the most widely used experimental design" (Wieder and Lang, 1982). Ibrahim et al. (2010) employed self-contained "microcosms" which held the litter material being analyzed in their research, which consisted of plastic cylinders fitted with a lid and a bottom, a hole which allowed for the draining of excess water, into which "one kilogram of a previously prepared soil mixture" and the collected leaf litter for each species of tree being studied were placed (Ibrahim et al., 2010). Other substrates of known composition were traditionally used to compare decomposition of standardized substrates among different environmental conditions. In the study done by Baker et al. (2001), popsicle sticks were used to assess the organic matter decomposition, while Wang et al. (2007), Jurgensen et al. (2004); and Jurgensen et al. (2006) used standard wood stakes to compare decomposition in forest soils over a wide range of temperatures and moisture regimes. Fang and Moncrioff (2001) measured the release of CO_2 from soil at varying temps and moisture regimes to measure the activity of soil microorganisms in decomposing organic materials. Some studies have combined the use or all of these materials and methods to gain more knowledge of the effect of substrate quality on decomposition.

Using data from an experiment that was previously conducted by other investigators (see below), the objectives of this study were: (1) to quantify the relative changes in decomposition of organic matter substrates under varying temperature and moisture regimes, using methods of mass-loss and CO_2 efflux; and (2) to examine the hypothesis that there is an optimal set of temperature and moisture regimes to support organic matter decomposition, within the normal environmental conditions of a managed forest in the southeastern US. Results of this analysis are intended to be useful to forest managers in understanding long-term trends in soil carbon losses in the southeast US.

Materials and Methods

Data for this study was collected between late November 2002 and May 2005 from the Santee Experimental Forest Site in Cordesville, South Carolina, which is located within the Francis Marion National Forest. The study was originally led by Dr. Carl Trettin (team leader for the site). Julie Arnold (research technician) conducted the experiment and collected most of the data. Though data was collected it was never completely analyzed. C. Trettin provided the data for analysis, in addition to valuable guidance on its interpretation.

Experimental design

Sandy 'A' horizon soils (80-90% sand) in the surface (0-30 cm) soil were utilized for this project. The preference was for sands, minimizing the fine (silt + clay) in the surface horizons; also, sandy solums were preferred to those with thick argillics or clayey subsoils. Potential soil series utilized, based on Berkeley County, SC soil survey included the sandy soils, Cainhoy, Chipley, Witherbee and sandy soils with loamy surfaces, which included Bonneau, Goldsboro, Lucy, Norfork, Ocilla, Pickney, and Seagate[1]. Drainage for these soils ranged from well to moderately well drained.

The substrates used in the experiment were typical of those used in studies similar to this one. Materials used in this study included wooden popsicle sticks (*Pine spp*.), 1 in. x 1 in. x 6 in wooden stakes of pine (*Pinus taeda)* and aspen *(Populous tremuloides)*, and leaf litter bags, each of which contained 5g of litter material of pine needles *(Pinus taeda)* and sycamore leaves *(Platanus occidentalis).* For the experiment, 2 popsicle sticks, 1 litter bag for each species, and 5 wood stakes of each species was included in a tray (24cm x 18cm) filled with 'A' horizon sandy soil 5cm deep. Three replicates were used for each temperature/moisture combination. A total of 96 popsicle sticks, 48 bags of pine litter and 48 bags of sycamore litter, and 240 pine stakes, and 240 aspen stakes were analyzed for the experiment.

[1] The Bonneau, Lucy, Ocilla, and Pickney had a fine sandy surface, which were the preferred soils in this group.

The pine and sycamore leaf litter were collected in the Santee Experimental Forest from a predominately pine forest stand with small populations of hardwood species. The litter was air dried at 60°C to remove moisture and obtain an initial weight. The litter bags were constructed of fiber glass window screening that was folded to create an enclosed 'bag'. At the end of the study all the litter bags were collected and the remaining litter was oven dried at 60°C to get a final weight.

The popsicles sticks were obtained commercially, and the pine and aspen wood stakes were provided from Michigan Tech and were previously dried and weighed. These stakes had the following quality criteria: straight grain, sapwood only, 6–10 rings, free of any defects, and "5% deviation of the mean density". The beginning weights for the popsicle sticks were written on aluminum tags attached to the sticks. The beginning weights were recorded and the collected popsicle sticks were air dried at 60°C. The air dried sticks were then weighed and the weights were recorded. The wood stakes were also oven dried after the experiment at 60°C and weighed after cleansing and attached soil and debris.

As a subset of the experiment, soil respiration from microbial activity was analyzed from PVC collars. Two PVC collars were placed in the trays along with the other substrates and set up with one containing just a sandy 'A' horizon soil and the other containing 66 g of ground sycamore *(Platanus occidentialis)* leaves mixed with an 'A' horizon sandy soil. Every month CO_2 was measured using the Licor photosynthesis system that was setup just above the PVC collars.

In this study the four substrates and the PVC collars were subjected to 4 temperature treatments (10ºC, 20ºC, 30ºC, and 40ºC) and 4 moisture content treatments (wet 23-28%, moist 15-20%, dry 3-7%, & fluctuated 3-7% to 23-28%) over the course of 30 months. These treatments were chosen to mimic the natural field conditions along an environmental gradient that reflects variations in temperature and precipitation, within a typical upland forest environment, in the Francis Marion National Forest. To control temperature four locations were used (a greenhouse, office, pole shed and cooler). Hobo™ temperature loggers monitored soil temperature and a Decagon™ soil moisture sensor was used to monitor moisture. The temperature logger and the moisture sensor were located 2cm deep in the trays and in the PVC collars. Twice per week soil moisture and temperature readings were recorded to determine if water needed to be added to the trays or if temperatures needed to be modified. The overall tray setup is depicted in Figure 1.

Analytic methods

Percentage mass loss from each tray for the popsicles sticks, leaf litter, and wood stakes was averaged to obtain the mean % mass loss for each replicate.

Mean percentage of cumulative mass loss was analyzed and compared using ANOVA (analysis of variance) in the SPSS statistical software and was further analyzed for normality using the Shapiro-Wilk test and then a multiple comparisons with the Bonferroni test in the same software. An ANOVA two way statistical test was used to test for differences in each substrate mass loss over a range of temperature and moisture conditions. The data for the individual substrates did not appear to be dramatically different from the normal distribution. Also, using the decomposition of all substrates, temperatures, and moistures were compared to each other with three-way ANOVA. The data was not normally distributed for the latter (p = <.001). The square roots of the means where used to achieve a normal distribution. A multiple comparison between the square roots of the means was performed with the Bonferroni test to test for specific differences in mass loss between substrates, temperature, and moisture.

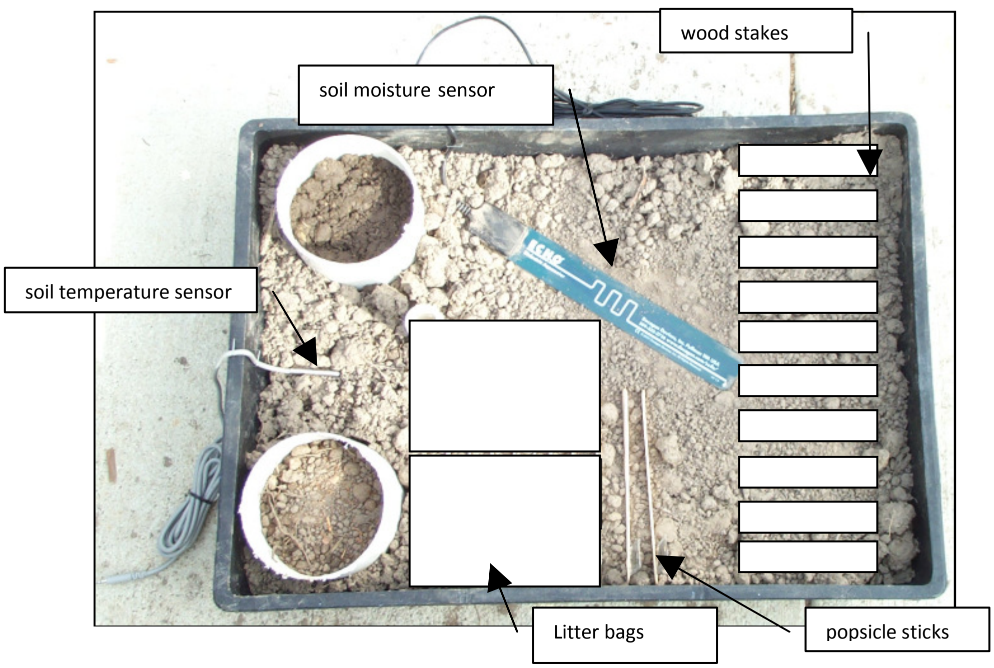


Figure 1. Photograph of experimental tray design, showing the relative locations of PVC collars, sensors, litter bags and wood stakes.

Results

Popsicle Sticks

After 30 months the decay of popsicle sticks was greater than any other substrate in the experiment (Figure 2). For most of the temperature and moisture combinations there seemed to be lower % mass loss of other substrates relative to the popsicle sticks. Average end of study mass losses of popsicle sticks ranged from 46.64% to 92.86%. From the ANOVA results in

Table 1, temperature ($p < 0.001$), but not moisture ($p = 0.119$) had a significant effect on the decomposition of popsicle sticks. The R^2 of 0.81 suggest that the relationship explained much of the variation. The interaction of the two also was not significant ($p = 0.467$). Of all the temperature treatments, the 40˚C appeared to have the most significant effect on the mass loss of the popsicle sticks. These results showed that the popsicles sticks responded positively to an increase in temperature.

Leaf Litter

The end of study mean % mass loss of pine and hardwood leaf litter was similar across the range of temperature and moisture conditions. The final percentage mass loss for hardwood and pine leaf litter ranged from 9% – 32%, with the lowest mass losses typically occurring at 10˚C. There were no significant differences among treatments or substrates, and these overall mass losses were generally much lower than those of the popsicle sticks.

As noted later in the Discussion section, it appears that experimental artifacts led to the litter bags being not truly representative of the targeted experimental treatments, and thus these litter bags were not further analyzed.

Figure 2. End-of-study mass loss for each substrate under the four temperature (10, 20, 30, and 40° C) and four moisture ("Wet", "Moist", "Flux", and "Dry") treatments.

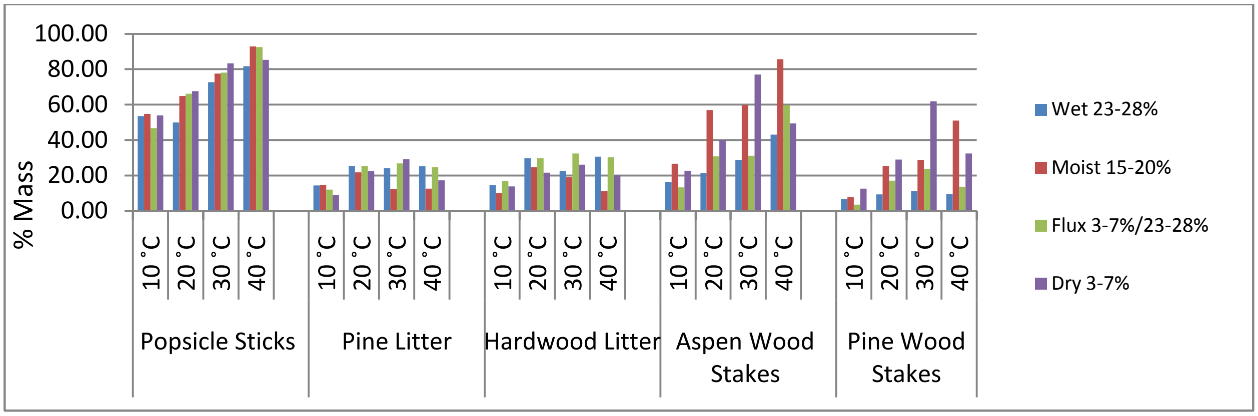


Table 1. ANOVA results for the effect of temperature and moisture treatments, and their interactions, for each of the three wood substrates, showing the F statistic, level of Significance, R^2 coefficient of determination, and degrees of freedom.

	F	Sig.	R^2	Adjusted R^2	df
Popsicle Sticks			0.801	0.708	48
Temperature	37.975	0.000			
Moisture	2.106	0.119			
Temperature * Moisture	0.991	0.467			
Aspen Wood Stakes			0.820	0.736	48
Temperature	27.500	0.000			
Moisture	14.316	0.000			
Temperature * Moisture	2.305	0.040			
Pine Wood Stakes			0.775	0.670	48
Temperature	14.509	0.000			
Moisture	14.717	0.000			
Temperature * Moisture	2.521	0.026			

Wood Stakes

Mass losses ranged from13.33% to 85.62% for aspen and 3.54% to 61.87% for pine. There was a significant effect of temperature and moisture on the percent of mass remaining for both of the wood stakes (Table 1; $p<.001$). The interaction of temperature and moisture was also significant (Table 1; Aspen $p = .040$ and Pine $p = .026$). The aspen wood stakes experienced an overall greater mass loss than the pine wood stakes across the range of moisture and temperatures (Figure 2). The aspen wood stakes had somewhat lower mass loss than equivalent popsicle stick treatments, with the greatest losses generally occurring between the 20°C to 40°C temperatures, depending on substrate. When comparing temperature regimes, the aspen wood stakes generally increased in mass loss with increases in temperature across a range of moistures, although there was a relative decline under the “dry” moisture condition at the highest temperature (40°C). The pine stakes exhibited the same significant trend in higher mass loss with temperature, but the differences were not significant. For both the aspen and pine wood stakes the highest mass losses were at 30°C-“dry” and 40˚C-“moist” combination, while the lowest mass losses occurred under the 10°C-“wet” and 10°C-“flux” temperature-moisture treatments. When comparing moisture regimes the aspen generally had the highest loss at the “moist” moisture level (but it was not significant), while the pine had significantly higher losses at the “dry” and “moist” moisture levels).

Comparing all moistures, temperatures, and substrates

The mass loss of all substrates, moistures, and temperatures were compared to one another and all were found to have significant effects on mass loss, but their interaction (substrate x moisture x temperature) did not (Table 2). In comparing the moisture content overall (Table 3) the “moist” treatment was greater than, but not statistically significant different from the “dry”. The “moist” and “dry” both had greater overall mass losses than the “flux” and “wet”, the latter being equivalent in mass losses. In comparing the temperature treatments (Table 3), the 40˚C and 30˚C treatment had significantly higher mass losses than the two lower temperature treatments, with the 10°C treatment being significantly lower than all others. In comparing the substrates, the popsicle sticks had higher mass losses than aspen stakes, which in turn had higher losses than the pine stakes.

Table 2. Anova results for comparison of all substrates, moisture, and temperature treatments.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	680.574[a]	47	14.48	19.113	0.000
Intercept	5635.523	1	5635.523	7438.308	0.000
Substrates	393.571	2	196.786	259.737	0.000
Temp	142.974	3	47.658	62.904	0.000
Moist	65.047	3	21.682	28.619	0.000
Substrates * Temp	10.239	6	1.707	2.252	0.045
Substrates * Moist	22.952	6	3.825	5.049	0.000
Temp * Moist	29.259	9	3.251	4.291	0.000
Substrates * Temp * Moist	16.531	18	0.918	1.212	0.267
Error	72.733	96	0.758		
Total	6388.83	144			
Corrected Total	753.307	143			

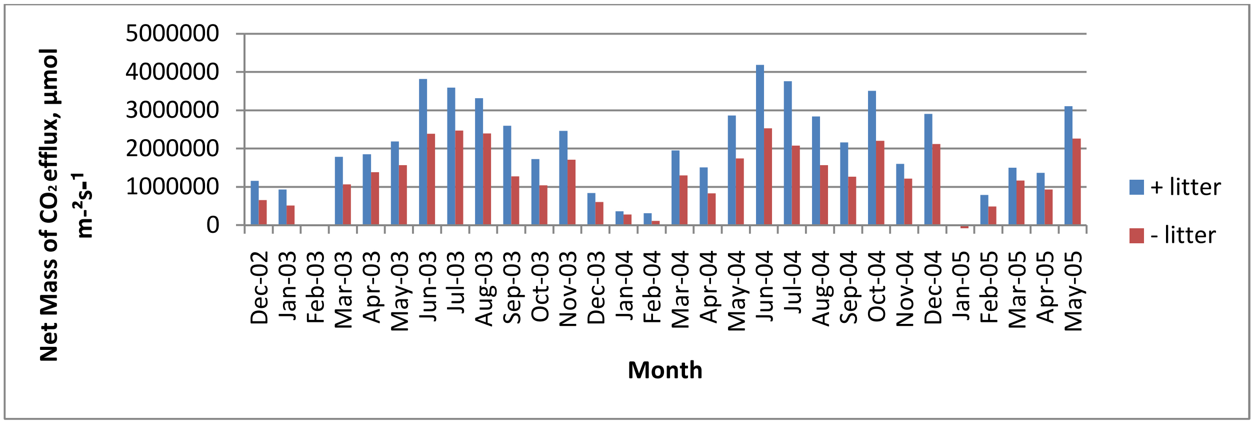
Table 3. Simple ranking from multiple comparisons of mass losses among treatments (temperature, moisture, and substrates) . An equal sign indicates no statistical difference was observed between the two adjacently ranked sites.

Factor	Mass Loss Rankings*
Popsicle Sticks	
Temperature	40˚C = 30˚C > 20˚C > 10˚C
Aspen Wood Stakes	
Temperature	40˚C = 30˚C = 20˚C > 10˚C
Moisture	Moist = Dry = Flux = Wet
Pine Wood Stakes	
Temperature	40˚C = 30˚C = 20˚C > 10˚C
Moisture	Dry = Moist > Flux = Wet
Overall	
Temperature	40˚C = 30˚C > 20˚C > 10˚C
Moisture	Moist = Dry > Flux = Wet
Substrates	Popsicle Sticks > Aspen WS > Pine WS

CO_2 efflux

Overall, CO_2 efflux from soil was strongly influenced by season (Fig. 3), with the highest of net mass efflux observed during June and July when soil temperatures were presumably at their highest for the entire year. This supports Fang and Moncrieff (2001) assertion that the efflux of soil carbon is highly sensitive to changes in surface temperature. In contrast the lowest months of CO_2 efflux were January and February. Due to an equipment malfunction a few readings for the 10˚C treatment were not recorded.

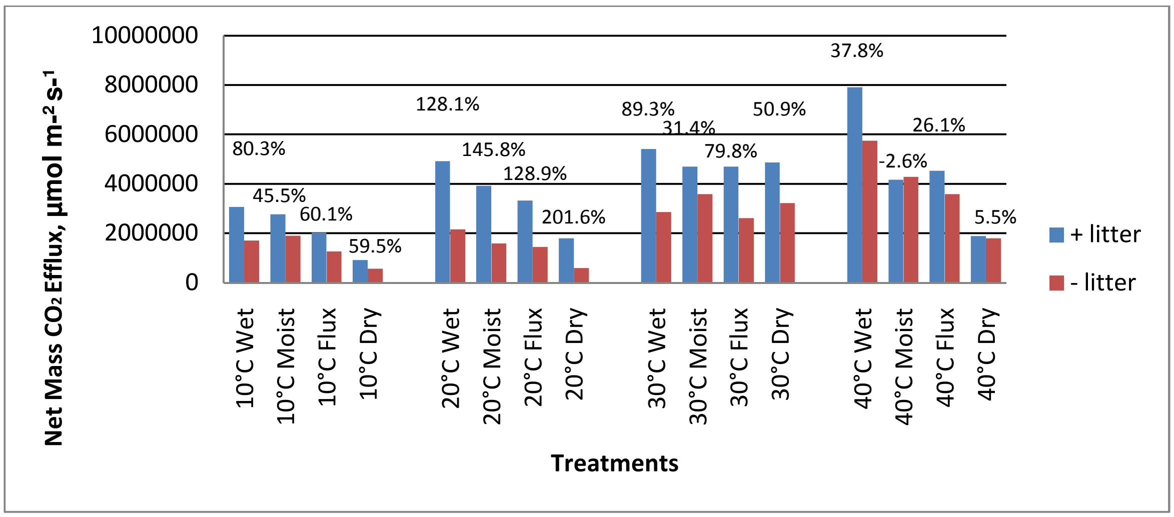
Figure 3. Seasonal trends in monthly net mass accumulation of CO2 efflux from PVC collars with and without litter, aggregating all moisture/temperature treatments.



Regardless of temperature, the "wet" treatment content generally produced the largest CO_2 efflux from PVC collars with litter added and overall for this part of the experiment. In the collars without litter added, soil CO_2 efflux was the largest at the "moist" and "wet" treatments across the range of temperatures. In the PVC collar with litter added, the 30˚C treatment produced the highest net mass efflux, but there was surprisingly little variation in respect to moisture. The PVC collar with leaf litter also experienced the same trend at 30˚C. This may suggest that microbial decomposition is stable at 30˚C. In addition across a range of temperatures there seemed to be a general decline with dryness in all the temperature classes except the 30˚C (although in there was a small incremental rise from moist to flux at 40˚C).

It seems that microbial activity is highest when moisture conditions are wet (with respect to field conditions) and generally warm. Also cool/cold temperatures with dry moisture contents or hot and dry moisture contents are not favorable to microbial decomposition. In addition, it seems that a hot and wet temperature (40˚C series, wet moisture content) have the highest mass CO_2 efflux.

Figure 4. Net mass of CO_2 efflux from PVC collars with and without litter for each of the treatments over the course of the study. Also included is percentage increases of CO_2 efflux with leaf litter added.



Discussion

Leaf Litter artifacts

Analysis was discontinued on the leaf litter experiment, as the mass losses from the litter bags was found to be much lower that would be expected (relative to other components of the overall experiment). In retrospect, it appears that the primary reason the litter bags had lower mass loss than the popsicle sticks (and other substrates) may be due to their enclosure in bags which were placed on a window screen above the soil. This prevented direct contact with the soil, and soil microorganisms that are the primary drivers of decomposition. This placement may have also led to the pine and sycamore leaves to have dried out more than the popsicle sticks. Though there was a soil moisture sensor, it only monitored moisture below the soil surface and did not account for moisture on top of the surface. In addition, typically leaf litter studies occur in situ on forest floors. However, given the experimental location of the trays (i.e., removed from the forest), new leaf litter was not able to accumulate on top of the bags, which otherwise could be an aid in decomposition.

The litter bag results also showed much lower mass losses compared to similar studies. Choonsig (2003) noted that after 869 days about 52% and 59% of mass loss was recorded for oak litter and mixed hardwood litter species respectively. The Baker et al. (2001) study in Coosawhatchee, SC revealed that approximately 84.2%and 82.2% mass loss from its mixture of oak and sweetgum leaf litter. Mun (2009) reported leaf litter mass loss of 50.6% from Q. mongolica, a 44.5% for Q. variabilis, and 58.1% for P. densiflora after 30 to 33 months. Given that the litter bag experiment was one component of a larger experimental design, it was determined that the potential artifacts induced by the original experimental design were too problematic to warrant further analysis, relative to the goals of my paper.

Controls on decomposition

A major goal of this experiment was to examine the effects of temperature and moisture on substrate decomposition. With the exception of the popsicle sticks, both temperature and moisture had a significant effect on decomposition of all the substrates in the experiment. Also, the popsicle sticks exhibited the greatest sensitivity among any other substrate in the experiment, in regards to temperature. Given that the leaf litter was the higher quality substrate it was expected that it would exhibit the greatest sensitivity among both temperature and moisture, but as noted above, problems with the original experimental setup of the bags led to inconclusive results.

The quality of wood - or more appropriately the quantity of cellulose and lignin in wood - is important, with lignin a particularly important consideration in decomposition studies. One source (Ragauskas, 2010) measured percent lignin and percent cellulose in aspen at 18.2% and 50.2%, and loblolly pine at 28.6% and 44.5%, respectively. While not directly measured, it may be that the aspen wood stakes had greater mass losses because of the lower amount of lignin present. Slow rates of decomposition are often associated with the secondary decomposition organic matter that is high in lignin and cellulose, after more labile fractions are eliminated.

The interaction of moisture and temperature had a significant effect on decomposition. For the most part decomposition increased with temperature to a certain point, which was expected. However, the analysis of the moisture treatments produced unexpected results. In the wood substrates the “moist” and “dry” treatments were responsible for the most mass losses most of the time, and the “wet” treatment was responsible for the lowest mass losses across a range of temperatures. Usually the lack of water is a limiting factor in soil microbial population growth, but this did not appear to always be the case in this experiment. It appears that the soil microbes present did not favor the wet environment for decomposing the wood substrates. Generally, a moisture content of 23%-28% is not enough to cause anaerobic conditions and reduce microbial populations. An explanation for the unexpected results is that maybe soil conditions were too wet and inhibited growth for the soil microbes, when compared to the other moisture treatments. A more likely explanation is that maybe other factors (such as pH, soil type, etc.) could be interacting with moisture regimes to produce confounding results. Because the original experiment was conducted some years before, by other investigators, it is difficult to discern the most plausible explanation.

There were more studies to compare decomposition of wood stakes than the popsicle sticks. In a study done on the Priest River Experimental Forest in northern Idaho (Collins, n.d.) aspen wood stake mass loss was recorded at around 40%, 55%, and <80% and pine wood stake mass loss was <24%, 39%, and<70% across of range of uncut forest, cut forest without compaction, and cut forest with compaction and organic matter removal respectively. The study lasted 2.5 years. It was inferred that the sites that experience the highest soil temperatures had the greatest mass loss overall. Also sites with the highest compaction experience decreased water holding capacities. The González et al. (2008) study of aspen wood stakes had approximately 96% mass loss on a tropical forest sites after two years. After four years approximately 17% and 11% percent of mass loss was recorded on a boreal and temperate forest sites. They found no significant direct effect of moisture on the percent mass remaining. The percent of mass remaining was significantly greater in dry than in moist forest sites in boreal and temperate locations, but the opposite was found in the tropical forests. Overall González et al. (2008) found that decay rates were higher in wet/warm climates than in cold/dry climates for aspen wood stakes.

When considering decomposition of coarse woody debris the literature available has produced conflicting results when considering moisture as a main driver. In a coarse woody debris experiment in a mixed conifer forest, Harmon et al. (1991) found that excess moisture (through precipitation) can reduce aeration for the primary decomposers, which in turn can reduce decomposition. Marra and Edmonds (1996) found that saturated conditions did not control seasonal variations and the decay of coarse woody debris on a clearcut forest in Washington state. In addition, González et al. (2008) found that both percent mass remaining and the decay rate constant were significantly and negatively correlated with annual precipitation. Decay for aspen stakes was much higher in the dry than in the moist sites in the tropical forests.
Thus, the results of this study and others support the idea that moisture is important, but can be difficult to quantify due to multiple interactions with other ecosystem processes.

Confounding variables

While not directly studied, the size of the wood substrates may have led to results indicating highest decomposition rates of popsicle sticks. The popsicles sticks were much smaller in size than the wood stakes. A decrease in size of the substrate will generally be associated with an increase in the amount of surface area exposed in relation to volume. This difference may be one of the reasons the popsicle sticks exhibited the largest mass loss in the experiment. The popsicle sticks are a generally low quality substrate, which may have impeded their rapid degradation early on in the study; however it was clear that at the end of the study decay increased dramatically. Additionally, the popsicle sticks were buried in the soil, allowing for direct contact to soil microorganisms. Taken together, multiple factors (size, substrate quality, and burial in soil) could have led to results showing popsicle sticks having the highest decomposition rate of all of the substrates.

In comparison, Baker et al. (2001) study % mass loss for popsicles sticks after 1.5 years was 61.3% for a relatively dry floodplain site on the Coosawhatchie River in South Carolina, while in an often inundated floodplain site in SC % mass loss was 90.6% after the same time. Percentage mass loss rates for the inundated floodplain were similar to the 40°C losses in this study across a range of moisture conditions.

Another variable that this experiment did not account for was soil organisms. Soil macro and micro fauna are important determinants of decomposition. The fast decay of organic matter, on the tropical sites in the González et al. (2008) study was explained by the high activity of fungi in the wood and the abundance of wood borrowing insects and termites. Fungi are often considered a main contributor to the breakdown of recalcitrant materials. Whitford et al. (1981) produced evidence that termites are capable of manipulating a site's microclimate and fragmentation of litter in arid ecosystems, resulting in faster decomposition rates. In some instances biotic controls on wood decay may be most important predictors of wood decay, especially in tropical or subtropical climates.

CO_2 Efflux

It is no secret that carbon efflux is strongly influence by season, but it was surprising considering seasonal effects were supposed to be masked in the experimental design. This suggests that seasonal variations may have had a slight effect on the results in the experiment. Also, the moisture contents that lead to the most decomposition in the wood stakes portion of the experiment were different from this portion. In the soil respiration subset the wet moisture content generally was responsible for the highest efflux and the dry moisture content was generally responsible for the lowest efflux across a range of temperatures. It is generally understood that high moisture levels can increase decay and high temperatures have been known to increase microbial respiration. This well known response was demonstrated in this part of the experiment. However, the sharp contrast compared to the results from the mass loss of wood substrates was unexpected. The PVC collars (with and without leaf litter) exhibited a different response, in regards to decomposition, from the wood stakes. Other factors not investigated may have interfered with soil microbial populations and conditions in the soil environment.

The experiment also provided further evidence that adding organic matter to soil is beneficial with respect to increases in the activity of soil microrganisms. As seen in Figure 4, there were increases (mostly large) in CO2 efflux from collars that received the added leaf litter, compared to those without supplements.

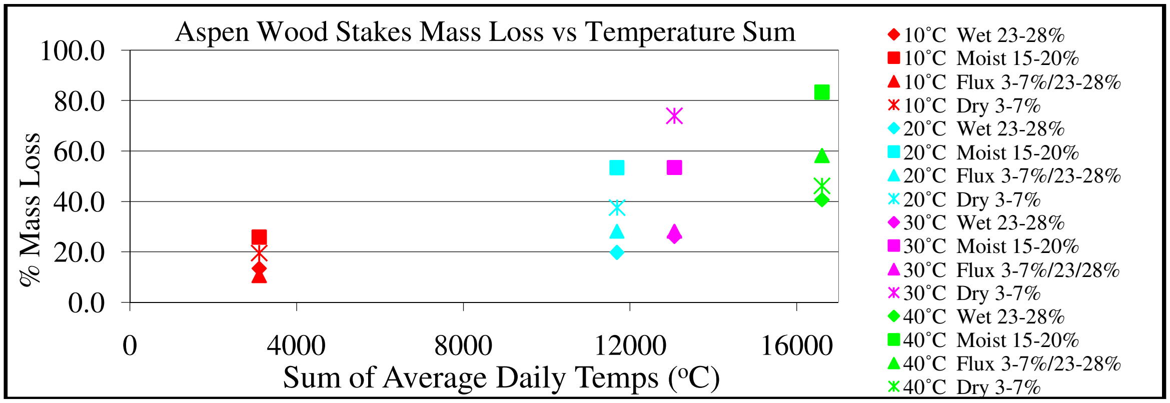
Optimal temperature and moisture regime

There did not seem to be a distinct temperature and moisture combination that is responsible for the highest decomposition. However, it appears the 40°C and "moist" treatment combination generally produced the highest, or near highest, decomposition rates for the wood substrates, while the 40°C and "wet" treatment combination led to the highest soil respiration rates.

Determining a single optimal moisture content for decomposition is difficult (more so than temperature) because the relationship between soil moisture and microbial processes varies depending on soil moisture-retention, porosity, the concentration of organic matter, pH, and soil depth. Usually microbial growth will occur up until there is a lack of oxygen due to water saturation, which can impede or interfere with a microbe's ability to respire.

While this study and others indicate there is a better defined relationship between temperature and decomposition rates (compared to moisture content), it is likewise somewhat difficult to determine an optimal temperature for the decomposition because of microbial species composition, and their associated temperature optima, vary among ecosystems and their climates. Nevertheless, the decomposition of non-woody and woody materials is usually accelerated by rising temperatures, as seen in results for our and other studies (see Introduction). Microbial activity is generally expected to increase rapidly up to a temperature of about 30˚C. An optimal temperature for microbial activity is considered between 35˚C and 45˚C, but there are cases when rates above 40˚C generally decrease rates (Paul, 2001). Some of the results for this study seem to agree with previous research where there were occasional declines in mass loss for environmental combinations from 30˚C and 40˚C. It was clear however that the higher temperatures contributed to the higher decay rates.

Figure 5. Example of relationship between cumulative degree-days (above 4°C) and mass loss per treatment location at the end of the study for the aspen wood stakes substrate. Each symbol corresponds to a specific combination of temperature and moisture effects, as defined earlier.



As indicated above and in the Introduction, most literature states that soil temperature generally has the most important effect on soil decomposition. Accumulated temperature sum methods may work the best in predicting decomposition, especially when soil moisture is not considered to be limiting. Figure 5 shows an example of this cumulative predictor of decomposition for the aspen wood substrate in the experiment. The figures indicate the general trend of a positive correlation between cumulative degree days and mass loss. For understanding future trends in woody debris decomposition, this suggests that use of daily temperature sums may be an adequate, simple, predictor of expected decomposition under future climate trends.

CO_2 and Climate Change

Microbial-mediated decomposition converts organic carbon to CO_2, and is one of the major processes controlling global terrestrial CO_2 budgets. The analysis of the decomposition of organic matter is thus important not only at local or regional scale as it relates to the health of an ecosystem, but also on a global level because of the effect of decomposition on carbon levels in the soil and the atmospheric pools. The release of CO_2 by soil microbes can have a profound effect on the global carbon balance, because soils contain the largest carbon pool in terrestrial ecosystems (Zhang et al. 2011), especially those forested ones. Also, soil respiration is a major pathway for carbon transfer to the atmosphere (Ryan and Law, 2005), so small changes in the soil respiration rates could have a significant impact on the atmospheric CO_2 budget.

In recent years there has been increasing interests on the importance of the global carbon cycle and potential feedbacks to climate change, with CO_2 acting as a "greenhouse" gas which tends to trap heat in the lower atmosphere and increase global temperatures. One of the biggest concerns is that raising temperatures may cause soil microbes to decompose soil organic matter at a faster rate, thus releasing more carbon into the atmosphere and thereby reduce soil organic carbon storage. This acceleration of CO_2 releases would thus become part of a positive feedback loop, further increasing temperatures and subsequent respiration rates. This becomes particularly important when considering that soil contains approximately two or three times more carbon than the atmosphere (Davidson et al. 2000). On the other hand, elevated CO_2 can increase plant productivity and litter production (through and increase in photosynthetic rates and plant biomass) and thereby lead to an increase in soil organic carbon. Hence, climate change (including increasing CO_2 concentration) can have two opposing effects on global soil-carbon stocks. While it was clear that the effects of warming and increasing CO_2 would partly cancel each other, the net overall effect depends critically on the exact quantification of the two processes (Kirschbaum, 2006). In addition, it is also important to take moisture into consideration when evaluating short-term carbon responses to changes in temperature. Results (Figure 4) indicated that the greatest soil respiration (in each temperature class) was achieved with the wet and moist treatments. Also, Illeris et al. (2004) showed that ecosystem production and ecosystem respiration consistently were highest in the wet monoliths and lowest in the dry monoliths. Although moisture is important, temperature is still considered to be the most limiting, and degree-day indices of decomposition (Figure 5) may be one useful tool in projecting relative trends under scenarios of future climate change.

Conclusions

Methods

Although the experiment was designed and performed by colleagues, analysis of the results and comparisons with other studies provided some insights into the methods of comparing decomposition rates under varying conditions. In assessing organic matter decomposition, litter bags are one of the most widely used techniques. It is especially considered a valuable method in comparative studies covering the early stages of decomposition. To analyze short term decomposition, it can be a useful method, when prepared correctly. To achieve more realistic results in future studies, litter bags should be placed on either on top of the soil surface or below the duff layer within a forest setting. The wood stakes were effective indicators of relative rates of decomposition, especially when comparing the quality of different wood types and can be useful in measuring long term decomposition. The popsicle sticks yield the highest percentage losses, but are not widely used in other studies. Measuring soil respiration seems to be the most direct measure of decomposition because the activity of soil microbes, performing the breaking down of materials, is being directly sampled. However, the method requires significant investments of time and instrumentation costs, and thus mass-loss approaches continue to be used for comparisons among ecosystems.

The experiment seemed to highlight the popsicle sticks as a great indicator of temperature sensitivity. This substrate was also a cheap and easier to prepare than the other substrates or methods. However many studies have a nutrient analysis component that is highly useful in determining if a substrate decomposition was influenced by a substrate that is high in macronutrients.

Controls on decomposition

The results suggest that high temperatures are a principal driver in organic matter decomposition. Moisture is also important, but there is uncertainty of which moisture content leads to the greatest decomposition. While this study did not aim to provide novel types of data and analysis in understanding the multiple controls on organic matter decomposition, the analysis of an existing experiment provided additional information that supports our understanding of decomposition processes in forests of the southeastern United States. For projecting long-term patterns of CO_2 release with decomposition under various future climate scenarios, we inferred that the relationship between cumulative degree-days and decomposition may be useful, and summary results from this study provide support for such relative predictions of carbon decomposition trends.

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