Working Group Report
Meta-Analysis & SynthesiS – Leaf decOmposition in StreamS (MASS LOSS)
Submitted by Jennifer Follstad Shah, December 28, 2012

Title of proposal: Forecasting rates of stream leaf litter decomposition in response to inland climate change

Working group name: Meta-Analysis & SynthesiS-Leaf decOmposition in StreamS (MASS LOSS)

Meeting dates & locations: November 10-13, 2011 at Coweeta LTER (meeting 1), May 19, 2012 at the Society for Freshwater Science (SFS) 2012 Annual Meeting in Louisville, KY (meeting 2), September 12, 2012 at the LTER All Scientists Meeting in Estes Park, CO (meeting 3)

Working group participants & affiliations:

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Sherri Johnson	U.S. Forest Service & Oregon State University	AND
Walter Dodds	Kansas State University	KNZ

[1] Working group co-organizers

MASS LOSS participants who physically attended meeting 1 at the Coweeta LTER (two other individuals participated via Go To Meeting). (L to R) Jack Webster, Mark Gessner, Walter Dodds, Lydia Zeglin, John Kominoski, Jennifer Follstad Shah, David Manning, Amy Rosemond, Carri LeRoy, Natalie Griffiths, and Marcel Ardon. Participants posed for this picture at 11 am on 11/11/11.

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Summary: The Meta-Analysis & SynthesiS – Leaf decOmposition in StreamS (MASS LOSS) working group was funded by the LTER Network to assess the response of leaf litter breakdown to temperature, as well as other intrinsic (e.g., leaf chemistry) and extrinsic (e.g., water chemistry, macroinvertebrate density) factors in an effort to better understand the key drivers of leaf litter breakdown and how rates may change in the face of global change. The MASS LOSS working group met three times over the course of one year. In that time, the working group compiled a global database of leaf litter breakdown in streams and rivers. This database includes 300 studies and over 3500 records. The working group also conducted preliminary analyses that will be included in a manuscript to be submitted for publication in Spring 2013. This manuscript will include several novel findings: (1) microbially-mediated and total rates of leaf litter breakdown increase with rising temperature and have a similar activation energy, (2) leaf litter breakdown will likely increase between 10-18 % with a 3 °C increase in mean water temperature, (3) the response of leaf litter breakdown to rising temperature is not uniform across plant genera, (4) differences in the activation energy of leaf litter breakdown across genera is correlated with differences in leaf chemistry (i.e., leaf litter with higher quality, less recalcitrant litter decay most rapidly), and (5) leaf litter breakdown is not correlated with macroinvertebrate density on a global scale. We have identified several other research questions to be examined using the MASS LOSS database and intend to submit a number of additional manuscripts on these topics in 2013 and 2014.

Background: Recent work has shown that freshwater ecosystems play a significant role in the global carbon (C) cycle, potentially emitting 1.2 Pg C y^{-1} to the atmosphere [1, 2]. The majority of the CO_2 that is degassed from streams and rivers comes from the decomposition of allochthonous leaf litter inputs [3, 4]. The process of decomposition fuels aquatic food webs, helps to regulate surface water acidity, and links biogeochemical cycles [5, 6]. Mean annual water temperature for streams is rising in response to elevated air temperatures [7-12], but the response of leaf breakdown rates is unclear because temperature is one of myriad intrinsic and extrinsic factors controlling decomposition [13]. In the absence of other interacting factors, leaf breakdown rates should increase exponentially with temperature ranging from 0-30 ˚C based on the laws of thermodynamics (Fig. 1). Consensus on the main factors driving leaf breakdown in aquatic ecosystems has been slow to emerge [13] because we are currently lacking a synthesis that is, unlike previous syntheses [13-15] or critiques of methodology [16], quantitative in nature. Our study differs from previous broad-scale quantitative studies [i.e., 17, 18] because it will simultaneously consider the effects of both temperature and litter quality, as well as their interaction. Whereas previous studies [17, 18] transplanted between 1-10 species to multiple locales, we will consider data from studies using transplanted and native species. Finally, we will test whether increased temperature will result in no net change in leaf breakdown rate across broad scales due to covariation in temperature and metazoan densities, a prediction suggested by the findings of Boyero et al. [17] and Irons et al. [18] but yet to be directly tested.

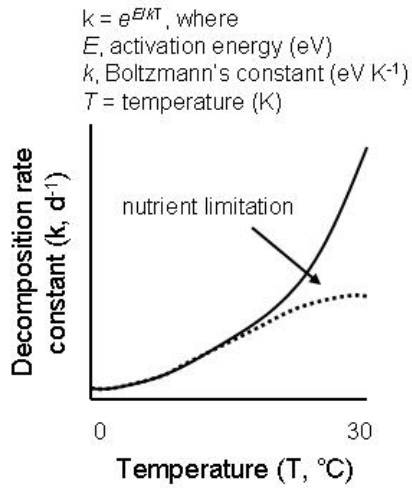

Figure 1. Expected temperature dependence of decomposition. Decomposition increases exponentially with temperature (solid line), as described by the Arrhenius equation ($k = e^{E/kT}$). The dashed line shows a scenario in which nutrient supply cannot support increased rates spurred by rising temperature, which may occur if foliar C:N and C:P ratios become elevated in response to climate change.

Research questions:

1. Based on the observed activation energies of aquatic leaf litter breakdown from Boyero et al. [17] and this study, how are rates predicted to change with increased mean water temperature on the order of 1-4 °C? Do metazoan densities decline with elevated temperature, thereby resulting in no net change in decomposition across broad scales despite increases in microbial processes?
2. How much variation in aquatic leaf litter breakdown is explained by water temperature as compared to other key intrinsic (e.g., leaf chemistry and structure) and extrinsic factors (e.g., stream nutrient concentrations, pH, hydrology, decomposer community structure) and their interactions? Are patterns similar to those observed in terrestrial ecosystems
3. If interactive effects exist (e.g., Fig. 1), can we use them to better predict how increased temperature combined with indirect effects of global environmental changes (e.g., changes in hydrology, leaf litter chemistry, riparian community composition and production) will alter C processing?

Meeting 1 – November 10-13, 2011 at Coweeta LTER: Prior to meeting 1, we identified five LTER databases on aquatic leaf litter decomposition through the LTER Data Portal and identified 636 papers on leaf litter decomposition in streams and rivers using an ISI Web of Science literature search on May 13, 2011. Of these 636 papers, 270 were selected for data extraction based on the following four criteria: the breakdown of (1) leaves (no leaf proxies such as cellulose sticks) was measured (2) in a natural stream (3) using leaf bag or nylon monofilament techniques and (4) each paper reported (a) leaf mass loss or decay coefficients, (b) temperature (min/max and/or mean) during the period of study, (c) leaf chemical traits (e.g., C, N, P, lignin, cellulose, tannin content) and/or macroinvertebrate abundance or biomass.

Prior to meeting 1, we extracted data from all but 37 of the 270 papers that met our criteria. In addition to the parameters listed as core criteria, we have extracted data related to the identity of leaves (clade, family, genus, species), physical description of study site (e.g., latitude/longitude, elevation, stream order, discharge, velocity, land use), methodology (e.g., study duration and number of sampling dates, technique used, mesh size, number of species studied in isolation or in mixed litter bags, experimental treatment [if any]), water chemistry, macroinvertebrate richness, microbial (bacteria and fungi) abundance, biomass, richness and production.

Eleven working group participants were physically present at meeting 1 and two working group participants joined the meeting via video conference. At this two-day meeting, working group participants reviewed preliminary analyses for the first paper we intend to publish, interpreted and discussed these results, identified next steps for the project, and volunteered for tasks.

Meeting 2 – May 19, 2012 at the Society for Freshwater Science (SFS) 2012 Annual Meeting in Louisville, KY: We amended our search in early 2012 to include papers published through December 2011. Prior to meeting 2, we contacted authors of 70 papers for unpublished information and successfully obtained the data for 51 papers (a 73% success rate). We completed data extraction from all by 37 of the 300 papers we identified as meeting our inclusion criteria. We began to standardize units of measure across parameters included in our database. We also began our quality assurance/quality control (QA/QC) process (1) to ensure that data was extracted properly and (2) to correct typos and incorrect unit conversions.

All working group participants attended meeting 3. At this one-day meeting, we again reviewed and discussed preliminary analyses for the first paper we intend to publish, interpreted and discussed these results, discussed challenges associated with data standardization and QA/QC, identified other research questions that could be addressed using our database, identified next steps for the project, and volunteered for tasks.

Meeting 3 – September 12, 2012 at the LTER All Scientists Meeting in Estes Park, CO: Prior to meeting 3, we completed data extraction. Data standardization and QA/QC were not completed until after the meeting (November 2012). Half of our working group participants (n = 7) attended meeting 3. At this one-day meeting, we determined how to address remaining challenges associated with data standardization and QA/QC, conducted exploratory analyses to ensure that the QA/QC process had been successful and to give us confidence in the database, and began drafting our first manuscript.

Final analyses for our first manuscript will be conducted in early 2013. The tentative title of this manuscript is *Leaf breakdown increases with elevated temperature and higher leaf litter quality but not macroinvertebrate abundance at the global scale*. We intend to submit this manuscript in Spring 2013. Ongoing analyses will be conducted for several other manuscripts to be submitted in 2013 and 2014. Tentative titles for these manuscripts are as follows:

- *Key intrinsic and extrinsic drivers of leaf breakdown world-wide*
- *Regional climate and biogeochemical variation explain patterns of organic matter breakdown throughout the United States*
- *Dissolved nutrients modulate the temperature dependence of leaf breakdown and stimulate higher loss rates: A global meta-analysis*
- *Global mapping of plant phylogentic traits and ecosystem functioning in streams*
- *Consumer functioning and magnitude vary throughout river networks: Location, location, location*
- *Variation in leaf stoichiometry alters leaf breakdown rate through time*
- *Effect of flow variation on leaf breakdown in streams: A global meta-analysis*
- *Disentangling the influences of land use on leaf breakdown in streams*

Results to date: The final database includes 300 studies and over 3500 individual records of leaf litter breakdown in streams and rivers worldwide (Fig. 2). This number includes rates in both control and experimental treatments, as well as for single species and mixed leaf litter studies.

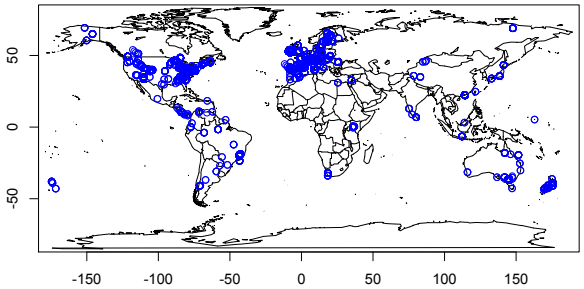

Figure 2. The global distribution of records of leaf litter breakdown included in the MASS LOSS database (n = 3583).

Our database includes 1193 records from control treatments at reference sites, which are predominantly (78%) forested streams in North America and Europe (Fig. 3).

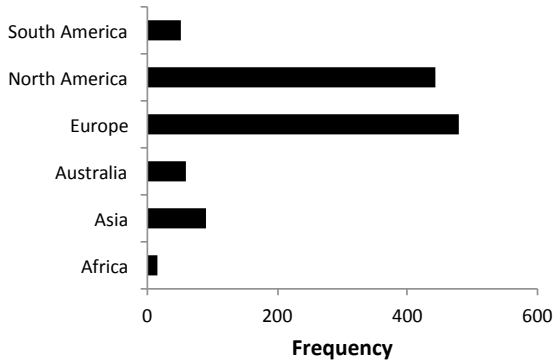

Figure 3. The continental distribution of records of leaf litter breakdown from control treatments at reference sites in the MASS LOSS database (n = 1193).

The database for control treatments at reference sites contains 172 species, 94 genera and 57 families of plants. Almost two-thirds (63%) of the records are from the 6 most common genera (Fig. 4).

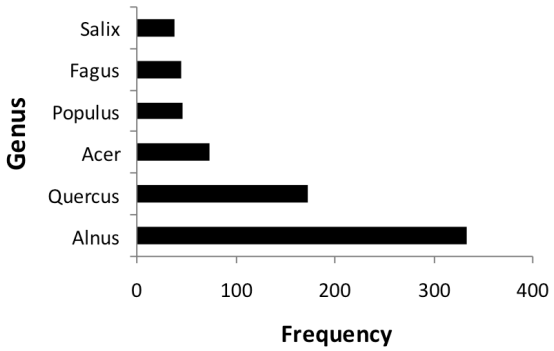

Figure 4. The distribution of records from control treatments at reference sites across the eight most common plant genera included in the MASS LOSS database (n = 1193).

Geographic coverage of the dominant genera differs (data not shown). The majority of studies on *Alnus* have occurred in Europe, while the majority of studies on *Acer*, *Salix*, and *Populus* have occurred in North America. The majority of studies on *Quercus* are almost evenly split between Europe and North America.

Research question 1: What is the activation energy of decomposition (for coarse vs. fine mesh bags; across and within genera)? Do metazoan densities decline with increased temperature?

Fine (< 1 mm) and coarse (≥ 1mm) mesh bags are used in leaf breakdown studies to isolate the effects of microbially-mediated decomposition from breakdown attributed to microbes plus macroinvertebrates, respectively. Boyero et al. [17] found breakdown within fine mesh bags to have a strong temperature dependence (i.e., activation energy of 0.46 ± 0.21 eV) that was close to the value predicted by metabolic theory (~ 0.6 eV), but there was no relationship between temperature and decomposition in coarse mesh bags. This difference was attributed to variation in macroinvertebrate density as one moves from the tropics to northern latitudes. In contrast to Boyero et al. [17], we found no difference in the temperature dependence of breakdown in fine (0.44 ± 0.09 eV, $r^2 = 0.12$, $p < 0.001$, n = 181, 95% CI: 0.26 to 0.62 eV) vs. coarse (0.33 ± 0.04 eV, $r^2 = 0.07$, $p < 0.001$, n = 929, 95% CI: 0.26 to 0.41 eV) mesh bags (Fig. 5). However, as found by Boyero et al. [17], we found that breakdown in coarse mesh bags is weaker than predicted (i.e., eV < 0.65) by metabolic theory. Our results suggest microbially-mediated and total leaf breakdown will increase, on average, 18% and 10%, respectively, with a 3 °C rise in mean water temperature (Fig. 5). Once we have compiled elevation data for all of our study sites from an independent database (by end of January 2013), we will re-analyze these regressions after correcting for the effects of latitude and elevation.

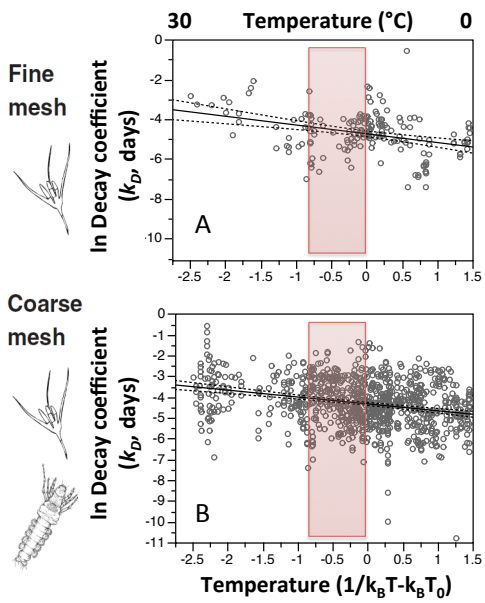

Figure 5. Microbially-mediated (fine mesh bags, A) and total (coarse mesh bags, B) leaf litter breakdown (k_D) responses to temperature. The temperature dependence of leaf litter breakdown is similar in both cases (0.44 ± 0.09 eV, $r^2 = 0.12$, $p < 0.001$, n = 181, 95% CI: 0.26 to 0.62 eV in A; 0.33 ± 0.04 eV, $r^2 = 0.07$, $p < 0.001$, n = 929, 95% CI: 0.26 to 0.41 eV in B), X-axes are normalized so the intercepts reflect k_D at 10 °C (T_0), where k_B is the Boltzmann's constant (8.62 x 10^{-5} eV/K) and T is ambient temperature in K. The red boxes indicate 18% (A) and 10 % (B) increases in k_D with a rise of 3 °C.

Data on macroinvertebrate abundance was available for a subset of our database. We found no relationship between the mean density of macroinvertebrates (#/leaf pack) and leaf breakdown for the studies with these data (Fig. 6). Nor did we find any relationship between the mean density of macroinvertebrates (#/leaf pack) and the residuals of our temperature-leaf breakdown in coarse mesh bags analysis (Fig. 6). We also found no trend between macroinvertebrate density and latitude, as suggested by Boyero et al. [17] and Irons et al. [18].

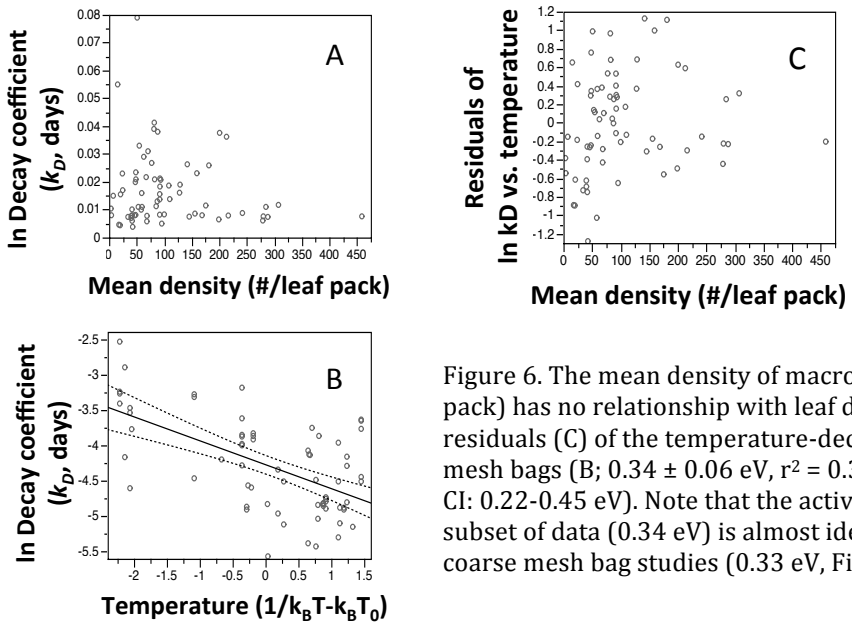

Figure 6. The mean density of macroinvertebrates (#/leaf pack) has no relationship with leaf decay (A) or with the residuals (C) of the temperature-decay relationship for coarse mesh bags (B; 0.34 ± 0.06 eV, $r^2 = 0.34$, $p < 0.001$, n = 69, 95% CI: 0.22-0.45 eV). Note that the activation energy for this subset of data (0.34 eV) is almost identical to the value across coarse mesh bag studies (0.33 eV, Fig. 5B).

The temperature dependence of leaf breakdown varied across the 8 most common genera included in our database (Table 1). Activation energy was greatest for *Fagus*, lowest for *Quercus* and statistically similar to 0.65 eV for *Acer, Liquidambar, Liriodendron*, and *Salix* (Table 1). Similar to Boyero et al. [17], the activation energy for *Alnus* was weaker (0.33 eV, 95% CI: 0.21-0.45 eV) than predicted by metabolic theory. Temperature-breakdown relationships were significant ($p < 0.01$) for all genera but *Quercus, Populus*, and *Salix* (Table 1).

Table 1. Variation in the temperature dependence of leaf litter breakdown across the 8 most common plant genera in the MASS LOSS database. Group differences are significant at $p < 0.05$.

					95% CI		
Genus	**n**	**r^2**	**p**	**eV***	**high**	**low**	**Group**
Acer	74	0.23	<0.001	0.47	0.67	0.27	B
Alnus	333	0.08	<0.001	0.33	0.45	0.21	BC
Fagus	48	0.41	<0.001	1.17	1.58	0.75	A
Liquidambar	30	0.25	0.005	0.55	0.92	0.18	B
Liriodendron	33	0.38	<0.001	0.77	1.13	0.41	AB
Populus	47	0.004	0.669	0.05	0.31	-0.20	CD
Quercus	174	0.006	0.293	0.08	0.24	-0.07	D
Salix	38	0.04	0.225	0.31	0.82	-0.20	BC

*Across coarse & fine mesh bags

Variation in the temperature dependence of leaf breakdown across genera is positively correlated with the cellulose ($r^2 = 0.49$) and N:P ($r^2 = 0.40$) content of leaf litter and negatively correlated with

the mean recalcitrance index ($r^2 = 0.41$), which is defined as the lignin/(lignin + cellulose) ratio (Fig. 7). In short, higher quality, less recalcitrant litter decays most rapidly.

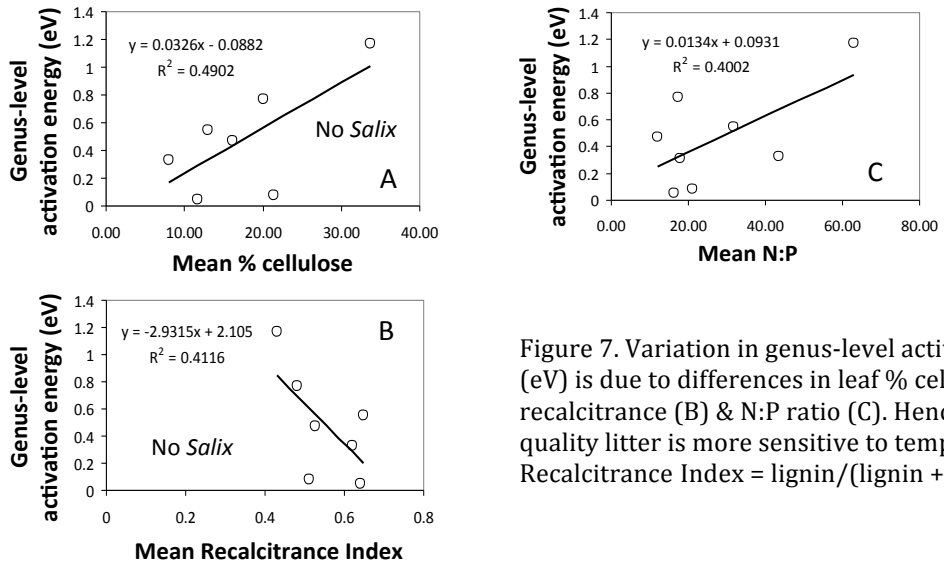

Figure 7. Variation in genus-level activation energy (eV) is due to differences in leaf % cellulose (A), recalcitrance (B) & N:P ratio (C). Hence, higher quality litter is more sensitive to temperature. Recalcitrance Index = lignin/(lignin + cellulose).

Research question 2: How much variation in aquatic leaf litter breakdown is explained by water temperature as compared to other key intrinsic and extrinsic factors? Are patterns similar to those observed in terrestrial ecosystems?

Temperature explained only about one-tenth of the variation in leaf breakdown rates across our dataset (Fig. 5) and about one-third of the variation for the subset of our dataset that also had measures of macroinvertebrate density (Fig. 6). Analyses conducted prior to meeting 1 showed that several other intrinsic and extrinsic variables were correlated with leaf litter breakdown including stream order ($r = 0.12$, $p = 0.001$), dissolved oxygen ($r = 0.27$, $p < 0.001$), and leaf chemistry (lignin ($r = -0.39$, $p < 0.001$), tannins ($r = -0.33$, $p = 0.02$), phenolics ($r = -0.28$, $p = 0.003$) and leaf C:N ($r = -0.17$, $p = 0.01$)). We will conduct Random Forest modeling to determine which variables best predict decay rates. We will assess whether the results of this modeling conforms to existing conceptual models of leaf breakdown [e.g., 19]. We also will test these conceptual models by running structural equation modeling.

We will also assess the role of location on leaf litter breakdown. Spatial autocorrelation and river network analyses will be used to test, respectively, whether decay rates are more similar within vs. across geographic regions and within vs. across stream orders.

Finally, we will compare results from all analyses to results reported from quantitative syntheses of terrestrial leaf litter decomposition [20-22].

Research question 3: If interactive effects exist (e.g., Fig. 1), can we use them to better predict how increased temperature combined with indirect effects of global environmental changes (e.g., changes in hydrology, leaf litter chemistry, riparian community composition and production) will alter C processing?

Temperature-leaf litter breakdown relationships indicate that breakdown rates will increase approximately 10-18 % with a 3 °C increase in mean water temperature (Fig. 5). This suggest that streams and rivers will store less C, unless there is a concomitant increase in the amount of autocthonous C produced in-stream or allocthonous C imported to streams and rivers from terrestrial sources.

We have not yet identified the key intrinsic and extrinsic factors controlling leaf breakdown rates, nor their interaction with temperature, so we cannot yet fully answer research question 3. This will be an area of ongoing investigation.

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