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LITTER QUALITY AND THE TEMPERATURE SENSITIVITY OF DECOMPOSITION

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Abstract. The temperature sensitivity of litter decomposition will influence the rates of ecosystem carbon sequestration in a warmer world. A number of studies have shown that the temperature sensitivity of litter decomposition can vary depending on litter type and extent of decomposition. However, the underlying causes of this variation are not well understood. According to fundamental principles of enzyme kinetics, the temperature sensitivity of microbial decomposition should be inversely related to litter carbon quality. We tested the accuracy of this hypothesis by adding ground plant shoot and root material to soils incubated under controlled conditions and measuring the temperature sensitivities of decomposition at three time points throughout a 53-d incubation. As the overall quality of the litter organic C declined, litter decomposition became more sensitive to temperature. This was true regardless of whether differences in C quality were due to inherent differences in litter chemistry or due to differences in the extent of decomposition. The same pattern was observed when specific C compounds of varying quality were added to soil, suggesting that substrate C quality has a significant and predictable influence on the temperature sensitivity of microbial decomposition.

Key words: *CO_2; litter decomposition; mineralization; Q_{10}; respiration; soil carbon; temperature.*

INTRODUCTION

Microbial decomposition of plant biomass, the conversion of litter carbon to CO_2 by microbial respiration, is one of the major processes controlling terrestrial CO_2 fluxes and ecosystem carbon storage (Raich and Schlesinger 1992, Couteaux et al. 1995, Aerts 1997). Temperature is often the primary factor determining rates of litter decomposition (Meentemeyer 1978, Anderson 1991, Hobbie 1996) and decomposition rates are generally more sensitive to temperature than are rates of net primary production (Lloyd and Taylor 1994, Schimel et al. 1994, Kirschbaum 2000). Thus, the balance between ecosystem C fixation and decomposition may be altered under a warmer climate, potentially causing a dramatic increase in the flux of CO_2 from soils to the atmosphere (Townsend et al. 1992, Schimel 1995, Cox et al. 2000). However, the accuracy of any quantitative predictions of this flux is highly dependent on the assumed temperature sensitivity of decomposition (Couteaux et al. 1995, Holland et al. 1995, Jones et al. 2003). For example, a 25% increase in the assumed Q_{10} value (the factor by which a 10°C increase in temperature will increase the rate of decomposition) can increase the predicted net flux of C from boreal forest soils as much as 200% (Townsend et al. 1992).

Most ecosystem carbon models assume that the temperature sensitivity of decomposition is identical for all types of organic matter (VEMAP Members 1995, Burke et al. 2003). However, the Q_{10} of microbial decomposition can vary by up to 40% depending on the type of litter and the extent of litter decomposition (Howard and Howard 1979, Kirschbaum 1995, Katterer et al. 1998, Dalias et al. 2001). It is unclear why there is such a wide range in Q_{10} values and how the decomposition of different litter types will respond to changes in temperature. To accurately assess the impacts of future climate change on terrestrial C dynamics, we need to better understand the factors that control the temperature sensitivity of litter decomposition.

Bosatta and Ågren (1999) have hypothesized that the temperature sensitivity of litter decomposition is gov-

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erned by microbial enzyme kinetics and that the Q_{10} value measured at any specific point in time will be influenced by the quality of the litter C being consumed by microorganisms. They proposed that the enzymatic reactions required to metabolize structurally complex, low-quality C substrates should have a higher net activation energy than reactions metabolizing C substrates that are structurally simpler and of higher quality. As such, the temperature sensitivity of a reaction should be inversely proportional to the net activation energy of the reaction (Stryer 1995). As the net activation energy required for decomposition increases, the temperature sensitivity of decomposition should also increase, yielding an inverse relationship between litter C quality and the Q_{10} of decomposition (Bosatta and Ågren 1999, Ågren and Bosatta 2002, Mikan et al. 2002). This hypothesis, which we will refer to as the ''C quality–temperature'' hypothesis, has never been tested experimentally but it should apply to the decomposition of substrates that differ in their initial chemistry as well as substrates at different stages of decomposition.

We tested the ''C quality–temperature'' hypothesis in two independent experiments. In experiment 1, we measured the Q_{10} of decomposition for 24 different litter types that vary in chemical composition. We also measured how the Q_{10} of decomposition changes for individual litter types at different stages of decomposition since we would expect a decrease in the average quality of litter C over time (Berg 2000). Experiment 2 was designed as a more direct test of the proposed hypothesis; we individually added one of seven known C compounds of varying quality to replicates of a common soil and measured the temperature sensitivity of microbial respiration. The ''C quality–temperature'' hypothesis predicts that the decomposition of lower quality C substrates (more recalcitrant litter types, litter in advanced stages of decomposition, or specific carbon compounds of lower lability) will be more sensitive to changes in temperature than the decomposition of higher quality C substrates.

Methods

Experiment 1

We obtained aboveground and fine root biomass from six grass species grown under high and low N fertilization treatments (Appendix A) at Cedar Creek Natural History Area (CCNHA) in central Minnesota, USA and harvested in July after two and one-half growing seasons (Craine et al. 2002). Plant material was dried at 50°C, ground with a Udy cyclone mill (Seedburo Equipment, Chicago, Illinois, USA), and passed through a 1-mm mesh. Plant tissue chemistry was determined by sequentially digesting plant material into fractions that correspond with soluble cell contents, cellulose, hemicellulose, and lignin (Ryan et al. 1990) on a forage fiber analyzer (ANKOM 200, Macedon, New York, USA). Total litter C and N was partitioned into soluble and insoluble fractions by measuring C and N concentrations on material that had been extracted with a neutral detergent solution (Van Soest 1963). The C and N content of samples were measured using a Fisons NA1500 C/N analyzer (Fisons, Danvers, Massachusetts, USA).

The litter samples were mixed into a sandy, N-poor, grassland soil obtained from CCNHA the previous year. The soil is 90% sand with 1.4 g organic C/100 g soil and 0.1 g N/100 g soil. Before adding the litter, the soil was sieved to 2 mm, homogenized, and 100 g of dry mass equivalent soil was weighed into each of 25 150-mL glass jars, one jar for each biomass type plus the ''no litter'' control. The soil samples were moistened to 35% of water holding capacity (WHC), as described in Fierer and Schimel (2002). The wetted soils were equilibrated at 20°C for 10 d before the addition of litter material.

With the exception of the ''no litter'' control, the equivalent of 1 g of ash-free plant litter was added to each of the 100-g soil samples. The resulting soil–litter mixture contained 10 mg ash-free litter/g soil, which is equivalent to 4 mg litter C/g dry soil. After homogenizing all samples by hand, each sample was divided into 10 50-mL plastic centrifuge tubes, with each replicate tube containing ~10 g (dry mass equivalent) of the soil–litter mixture. Except for the brief periods of time during which the Q_{10} analyses were conducted, all 250 tubes were kept in a 20°C controlled temperature incubator during the course of the 2-mo incubation. Samples were weighed periodically to assure that soil water contents did not change during the incubation.

The rates of CO_2 production in the soil samples were measured two to three times each week. At each time point, CO_2 production rates were measured on one randomly selected subsample of each biomass type (and the ''no biomass'' control), giving a total of 25 individual measurements per time point. We used a static incubation procedure described in Fierer et al. (2003) to estimate CO_2 production rates.

Q_{10} assays were conducted at three time points over the course of the incubation, at 4, 23, and 53 d. Five replicate sample of each litter type were incubated simultaneously to determine Q_{10} values with one replicate sample per litter type and a ''no biomass'' control incubated at each of the five temperatures (10, 15, 20, 25, and 30°C). After a 1-h equilibration period at the target temperature, CO_2 accumulation in the headspace of each tube was measured over a 24-h period as described in Fierer et al. (2003). We subtracted the basal soil CO_2 production (represented by the control samples incubated at each of the five temperatures) from the CO_2 produced in the samples receiving litter to calculate the dependence of litter decomposition (in μg $C\text{-}CO_2 \cdot g\ soil^{-1} \cdot h^{-1}$) on soil temperature.

Experiment 2

Homogenized CCNHA soil (5 g dry mass equivalent) of was weighed into 80 individual 50-mL plastic centrifuge tubes. The soil samples were adjusted to 35% of WHC and incubated for 25 d at 20°C. After this equilibration period, the samples were amended with 0.5 mL of solution containing one of seven different carbon compounds (Sigma-Aldrich, St. Louis, Missouri, USA) listed in Fig. 2. All of the solutions contained 120 mmol/L C and 7.5 mmol/L NH_4NO_3 (C:N ratio = 8) and were adjusted to pH 7 using either NaOH or HCl. Each C solution was added to 10 individual soil samples. Ten samples served as the ''no C'' controls and received only 0.5 mL of 7.5 mmol/L NH_4NO_3 (pH 7). Three days after the addition of the C substrates, two replicate samples per solution type were incubated simultaneously at 10, 15, 20, 25, and 30°C and the temperature dependence of C compound mineralization was determined using the methods described above. We averaged the CO_2 production rates for the two replicates and we assume that the rate of mineralization of each C compound is the rate of CO_2 production with the added compound minus the rate of CO_2 production in the ''no C'' control soils.

Data analyses

We used Eq. 1 (as in Lloyd and Taylor 1994) to describe the relationship between decomposition rates across the temperature range (10–30°C):

$$y_T = B \times e^{KT} \quad (1)$$

where y_T is the decomposition rate at any given temperature (in μg C-CO_2·g soil^{-1}·h^{-1}), T is temperature in °C, and B and k are the exponential fit parameters. Throughout this paper, we use Q_{10} instead of k to describe the temperature sensitivity of decomposition since Q_{10} values are more straightforward to interpret. Q_{10} is the average increase in respiration rates for a 10°C increase in temperature and is calculated as

$$Q_{10} = e^{10k}. \quad (2)$$

We consider substrate C quality to be equivalent to the relative rate of microbial respiration since we added the same amounts of litter C (experiment 1) or compound C (experiment 2) to each soil subsample. Therefore, we equate substrate C quality with B, the y-intercept of the first-order exponential equation relating decomposition rate to temperature. Other studies have described substrate C quality in a similar manner (Flanagan and Bunnell 1976, Bosatta and Ågren 1999, Mikan et al. 2002). The parameter B provides an index of the overall quality (the availability and the lability) of the C substrates that are being catabolized by decomposer organisms at a given point in time.

All statistical analyses were conducted using JMP 5.0 (SAS Institute, Cary, North Carolina, USA). We used a backwards stepwise regression model to examine the relationships between the various litter C and N fractions and the measured B and Q_{10} values.

RESULTS

Experiment 1

After 4, 23, and 53 d of incubation, there was a 13-, 9-, and sixfold variation in B and a 36%, 35%, and 35% variation in Q_{10}, respectively (Fig. 1). At each time point, litter C quality (B) was negatively correlated with Q_{10} across the temperature range (10–30°C). The strength of the correlation between B and Q_{10} was lowest at the initial time point (4 d) and increased as decomposition progressed over time (Table 1, Fig. 1). The relationships between B and Q_{10} differed for roots and leaves, but both showed inverse relationships at any given time point (Table 1). While the range in Q_{10} and B values was similar for both types of litter, root litter had lower values of B for a specific Q_{10} value (Fig. 1, inset).

As decomposition progressed over time, the relative quality of the catabolized C substrates tended to decrease, as evidenced by the decline in B values, while the temperature sensitivity of decomposition increased (Fig. 1, inset). With each successive determination (at 4, 23, and 53 d), B declined by 82% and 59%, respectively, while Q_{10} increased by 15% and 8% (Fig. 1, inset). Across all three time points, the slopes of the relationship between Q_{10} and B were similar for both litter types ($Q_{10} = 2.25B^{-0.09}$, $r^2 = 0.99$ and $Q_{10} = 2.11B^{-0.08}$, $r^2 = 0.98$, for root and shoot material, respectively).

In general, the quantity of the different C and N chemical fractions measured in each litter sample were poor predictors of either the B or the Q_{10} values measured at each time point (Appendix B). The ability to predict B and Q_{10} values from the chemical fraction pool sizes was only significant at certain time points and the overall explanatory power was relatively weak. No fraction was a significant predictor of Q_{10} at day 4 or 23. The total amount of litter C mineralized during the incubation period (0.4–2.3 mg C-CO_2/g dry soil, Appendix A) and the size of the soluble C pool (0.1–2.5 mg C/g dry soil, Appendix A) were significantly correlated across all litter samples ($P < 0.001$, $r^2 = 0.51$). Across all litter types, soluble C and soluble N explained 43% and 36% of the variation in total C respired over the entire incubation (total $r^2 = 0.80$) and cellulose explained only 21%.

Experiment 2

Among the seven known C substrates added to soils, Q_{10} was again inversely related to B (Fig. 2) and those substrates with the highest quality had the lowest sensitivity to temperature ($Q_{10} = 1.42B^{-0.16}$, $r^2 = 0.91$, type II regression). In general, the structural complexity of the C compound was inversely related to the value of B (Fig. 2). The compounds containing aromatic rings (catechol, tannic acid, p-hydroxybenzoic acid) had

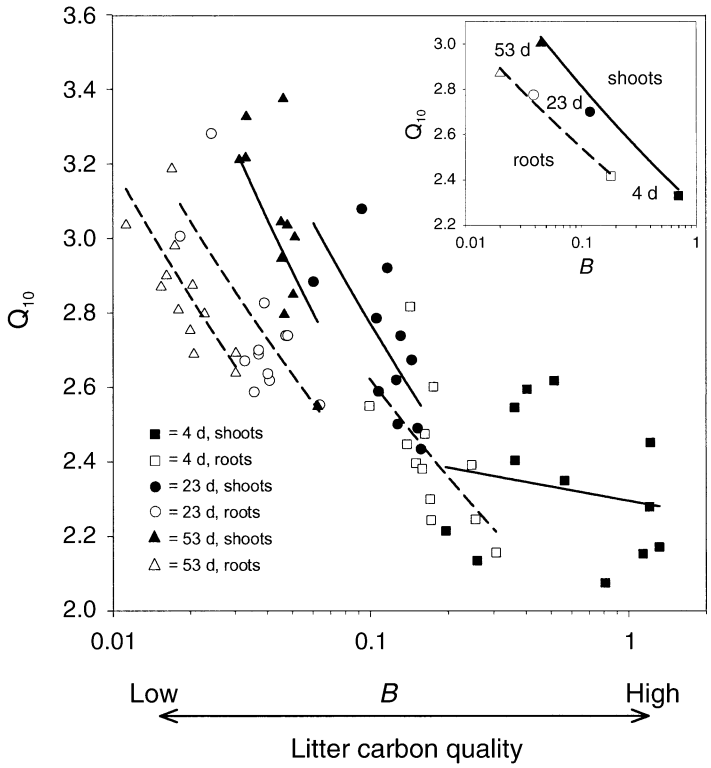

FIG. 1. The relationship between the parameter *B*, an index of litter carbon quality, and the Q_{10} of litter decomposition (10°–30°C). Units for the parameter *B* are μg C-CO_2·g^{-1} dry soil·h^{-1}. The inset graph shows averages for each time point. The three time points at which Q_{10} and *B* were measured are indicated by symbols: squares, 4 d; circles, 23 d; triangles, 53 d. Root and shoot litters are indicated by the open and filled symbols, respectively. The dashed and solid lines show the regression lines for root and shoot litters, respectively. Data were fit using the equation $Q_{10} = a \cdot B^k$.

lower B values than the structurally simple carboxylic acids (succinic acid, citric acid) and carbohydrates (glucose and lactose).

DISCUSSION

Overall, we observed strong inverse relationships between Q_{10} and *B* across different litter types (Fig. 1), litter in different stages of decomposition (Fig. 1, inset), and specific C compounds (Fig. 2). These results support the hypothesis that enzymatic reactions involved in the catabolism of structurally complex, low-quality, C substrates should have higher activation energies and temperature sensitivities than reactions metabolizing simpler, more labile, C substrates. Hobbie (1996) and O'Connell (1990) have also shown that the temperature sensitivity of decomposition is higher for low-quality litters than for litter types of higher quality. We must be careful when comparing the results of this study to studies examining the temperature sensitivity

TABLE 1. Regression lines describing the relationships between Q_{10} and carbon quality (*B*), as shown in Fig. 1.

Time point	Litter type	*a*	*x*	r^2
Day 4	leaf	2.29	−0.02	0.04
	root	1.85	−0.15	0.40*
Day 23	leaf	1.81	−0.18	0.45***
	root	1.63	−0.16	0.52***
Day 53	leaf	1.22	−0.29	0.57***
	root	1.59	−0.15	0.55***

Notes: Data were fit using the equation $Q_{10} = a \cdot B^x$. For each litter type at each time point, $N = 12$.
* $P < 0.05$; *** $P < 0.001$.

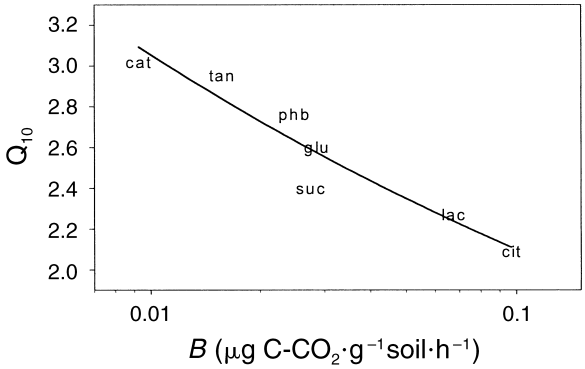

FIG. 2. The Q_{10} of microbial respiration (10°–30°C) vs. organic C quality (*B*) for seven organic C compounds added to the soil. Abbreviations are: cat, catechol; tan, tannic acid; phb, p-hydroxybenzoic acid; suc, succinate; glu, glucose; lac, lactose; cit, citric acid.

of soil organic matter (SOM) decomposition. We explicitly examined litter decomposition; the dynamics of SOM decomposition are likely to be quite different with factors such as physical protection (Thornley and Cannell 2001), potentially obscuring any relationship between Q_{10} and C quality. Nevertheless, Mikan et al. (2002), studying tundra soils, and Fierer et al. (2003), studying mineral soils from the profile of a semiarid Mollisol, have both observed an inverse relationship between the temperature sensitivity of microbial respiration and SOM quality (as estimated by a parameter identical to *B*).

The results of two recent studies suggest that the decomposition of low-quality organic matter is relatively insensitive to temperature (Liski et al. 1999, Giardina and Ryan 2000). Liski et al. (1999) used a modeling approach to predict the temperature sensitivity of decomposition and Giardina and Ryan (2000) based their conclusions on data from long-term (one year) soil incubations and land conversion studies. The fact that these studies examined soil organic C, not litter C, pools prevent us from directly comparing the results. However, it should be noted that the Liski et al. (1999) and Giardina and Ryan (2000) studies do not account for variations in the size and movement of organic C among pools of different qualities within a whole soil (see comments by Ågren [2000] and Davidson et al. [2000]). The balance of multiple organic C pools with different qualities has the potential to greatly affect the temperature sensitivity of soil respiration, yet there is a paucity of experimental data directly addressing the effects of temperature on different soil and litter C pools (Burke et al. 2003). In this study, we attempt to address this issue by using controlled additions of a defined substrate (litter) to evaluate how changes in organic C quality may alter the short-term temperature sensitivity of decomposition.

The range of Q_{10} values observed in this study (Fig. 1) is similar to that reported for other types of litter and organic soils (Howard and Howard 1979, Kirschbaum 1995, Katterer et al. 1998, Niklinska et al. 1999, Reichstein et al. 2000). However, since the methodologies used to calculate Q_{10} values can vary significantly across studies, it is important to exercise caution when directly comparing Q_{10} values reported in the literature. Lab-based estimations of the temperature sensitivity of decomposition are highly dependent on the length of time that samples are incubated. In this study, we used short-term (24-h) laboratory incubations to estimate the Q_{10} values for litter decomposition. One advantage of this method is that the samples are kept at a constant temperature before the Q_{10} assay, eliminating any confounding effects of temperature history on the estimation of Q_{10}. In addition, substrate availability will not change appreciably over the course of these short-term assays so our calculated Q_{10} values represent the temperature sensitivity of decomposition at a specific point in time. Due to substrate depletion, longer assay times may lead to an underestimation of Q_{10} values (Reichstein et al. 2000, Burke et al. 2003), potentially obscuring any relationship between Q_{10} and organic C quality. If Q_{10} values are estimated by integrating CO_2 production over a prolonged period of time, Q_{10} values will always approach 1; once the C substrates are exhausted, decomposition will have no apparent temperature sensitivity.

Since we added fresh litter to soil, there is a potential for a ''priming effect,'' the stimulation of soil organic C mineralization due to the addition of labile substrates (Kuzyakov et al. 2000). While we were not able to distinguish between soil-derived CO_2 and litter-derived CO_2, we do not expect the ''priming effect'' to influence the observed relationship between C quality and the temperature sensitivity of litter decomposition. The respiration rate of the ''control'' (no litter added) soil averaged 0.03 μg $C\text{-}CO_2 \cdot g\ soil^{-1} \cdot h^{-1}$ across the incubation period compared to an average rate of 1.4 μg $C\text{-}CO_2 \cdot g\ soil^{-1} \cdot h^{-1}$ for soil with litter added. The rate of CO_2 production from the ''control'' soil was, at most, only 10% of the CO_2 production measured from soils with litter added. This was true across the entire incubation period and across all temperatures. Even if the priming effect were to cause a doubling in the basal respiration rate, a priming effect of incredible magnitude (see references within Kuzyakov et al. 2000), the overall pattern relating *B* to Q_{10} would remain largely unchanged.

The variation in the initial pool sizes of the various litter chemical fractions could not adequately explain the observed variation in substrate C quality, as measured using the parameter *B* (Appendix B). The majority of the C respired over this relatively short incubation period (53 d) was likely derived from the soluble fraction. Other studies have shown a similar pattern: CO_2 production during the early stages of litter decomposition is largely regulated by the size of the soluble fraction and only in the later stages of decomposition do microorganisms catabolize significant quantities of insoluble litter fractions (Berg 2000, Sall et al. 2003). Since most of the respired C appeared to come from the soluble fraction, Q_{10} and *B* values should be most dependent on the quality of the soluble pools, not the relative sizes of the various chemical fractions (hemicellulose, cellulose, lignin) that would remain largely unmineralized over the course of the incubation. Conventional fractionation methods are useful for predicting litter decomposition rates over longer time periods (Meentemeyer 1978, Hobbie 1996, Joffre et al. 2001, Silver and Miya 2001), but they are not necessarily useful for predicting the relative quality of the C substrates catabolized by microorganisms at specific points in time, which is more accurately estimated from the relative rate of microbial respiration. The relationships between *B*, Q_{10}, and litter chemistry highlight the difficulties inherent in defining the quality of complex

C substrates where C quality is determined by both the relative sizes and the relative labilities of a range of different C pools. Additional research is required before we can accurately parameterize C quality at discrete points during the decomposition process.

While our data suggest that C quality has a significant influence on the temperature sensitivity of decomposition, a number of other factors may contribute to the observed variability in Q_{10} values. For example, the degree of nutrient limitation to microbial enzyme production may affect the observed Q_{10} values (Fierer et al. 2003), particularly in the early stages of decomposition when the microbial biomass is likely to be highly N and/or P limited (Berg and Matzner 1997). Although no significant relationships between Q_{10} values and litter N concentrations were observed in this study (data not shown), interactions between Q_{10} and microbial nutrient limitation may contribute to the weak relationships observed between Q_{10} and *B* at the early stages of decomposition (Fig. 1, Table 1). The composition of the decomposer microbial communities (Latter and Heal 1971, Balser 2000) and the degree of physical protection of carbon substrates (Thornley and Cannell 2001) may also affect the observed temperature sensitivity of decomposition in natural settings.

There has been much discussion of the temperature sensitivity of decomposition and there is some debate in the literature about the factors that regulate that relationship. We address one specific factor, the relationship between C quality (net activation energy of decomposition) and temperature sensitivity. While we only examined the early stages of decomposition, this study suggests that the temperature sensitivity of microbial decomposition can be related to basic principles of reaction kinetics. As predicted, the quality of the organic C substrates consumed by microorganisms is inversely related to the observed Q_{10} of litter decomposition. In all likelihood, C quality is not the sole factor influencing the temperature sensitivity of litter decomposition, and in natural systems, the relationship between the temperature sensitivity of decomposition and C quality may be obscured by complex interactions between temperature and a range of other factors that can influence the rate of decomposition. However, by establishing that there is a predictable relationship between C quality and temperature sensitivity, this work should provide a starting point for field-based studies examining the controls on the temperature sensitivity of decomposition.

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APPENDIX A

A table listing the characteristics of the 24 different litter types used in the experiment is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-015-A1.

APPENDIX B

A table showing parameter estimates, proportion of the total model variation explained by factors, and significance levels for the backwards stepwise regression models is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-015-A2.