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Determining Temperature-Normalized Decomposition Rates

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1 Introduction

Temperature is the most universal factor governing rates of processes ranging from chemical reactions (Arrhenius 1889) and metabolic activities (Robinson et al. 1983; Allison et al. 2010) to transformations of organic matter in ecosystems (Davidson and Janssens 2006; Graça et al. 2015). Attention to accounting for temperature effects on physiological and ecological processes has continuously grown, prompted in part by theoretical interest (Allen et al. 2005), comparative considerations of latitudinal patterns (Irons et al. 1994; Boyero et al. 2011; Follstad Shah et al. 2017), and the challenge of quantifying and forecasting the ecological consequences of climate warming on carbon and nutrient cycling (Davidson and Janssens 2006; Allison et al. 2010). This includes efforts devoted to assessing the influence of temperature on the decomposition of plant litter in both terrestrial (e.g., Fierer et al. 2005; Prescott 2010) and aquatic ecosystems (e.g., Petersen and Cummins 1974; Hietz 1992; Ferreira and Canhoto 2015).

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The process of plant litter decomposition has been typically described by first-order kinetics, where litter mass loss at any given point in time is assumed to be proportional to the litter mass present, independent of temperature (Chap. 6):

$$\frac{dm}{dt} = -k \cdot m \tag{60.1}$$

where m is the litter mass, t is time, and k is the decay rate coefficient. Dividing by m and integrating both sides of the equation over time t (i.e., from the initial time $t_0 = 0$ till t_n = elapsed time) results in the familiar negative exponential decay model:

$$\int_{t_n}^{t_0} \frac{1}{m} \frac{dm}{dt} dt = \int_{t_n}^{t_0} -k \cdot dt \tag{60.2}$$

$$\Rightarrow \ln\left(m\left(t\right)\right) - \ln\left(m_0\right) = -k \cdot \left(t_n - t_0\right) \tag{60.3}$$

$$\Rightarrow m_t = m_0 \cdot e^{-k \cdot t} \tag{60.4}$$

where $m_t = m(t)$ and $m_0 = m(t = 0)$. Although not entirely realistic, this model has proved extremely useful in practice, one of the key advantages being that decomposition can be assessed based on a single parameter, the exponential decay rate coefficient k.

In aquatic environments, temperature-normalized decay rate coefficients have been reported almost invariably by assuming a linear temperature dependency of the overall decay rate (Table 63.1). Thus, the standard first-order decay model expands to

$$\frac{dm}{dt} = -k_T \cdot \frac{T\left(t\right)}{T_R} \cdot m, \tag{60.5}$$

where temperature $T(t)$ varies with time and k_T is the temperature-normalized decay rate coefficient. The reference temperature of normalization (T_R) ensures that k_T has the same dimension as k in Eq. 60.4 without temperature normalization. Setting $T_R = 1$ °C results in the same numerical value of k_T as in the degree-day models commonly used in the literature. However, other reference temperatures could be used, with 10 °C being particularly convenient, not least for ease of comparison and consistency with other models of temperature dependencies (see below). A requirement to employ this model is that $T \geq 0$ °C to ensure positive overall decomposition rates. Equation 60.5 can be solved exactly as above:

$$\int_{t_n}^{t_0} \frac{1}{m} \frac{dm}{dt} dt = \int_{t_n}^{t_0} -k_T \cdot \frac{T\left(t\right)}{T_R} \cdot dt \tag{60.6}$$

$$\Rightarrow \ln\left(m(t)\right) - \ln\left(m_0\right) = -k_T \cdot \frac{1}{T_R} \cdot \int_{t_n}^{t_0} T(t) \cdot dt \tag{60.7}$$

$$\Rightarrow m_t = m_0 \cdot e^{-k_T \cdot \frac{1}{T_R} \cdot \int_{t_n}^{t_0} T(t) \cdot dt} \tag{60.8}$$

The integral remaining in the exponent is the thermal sum commonly referred to as degree days (e.g., Irons et al. 1994; Woodward et al. 2012). It can also be viewed as the average temperature ($\overline{T}$) during the considered period of decomposition times the duration of this period ($t_n - t_0$):

$$\int_{t_n}^{t_0} T(t) \cdot dt = \overline{T} \cdot \left(t_n - t_0\right) = \overline{T} \cdot t_n \tag{60.9}$$

when $t_0 = 0$. In cases where decomposition is very slow, a more convenient unit for thermal sums can be degree years (Hietz 1992; Prescott 2010).

The same basic rationale can be used when an exponential instead of a linear dependency between temperature and decomposition rate is assumed. Accordingly,

$$\frac{dm}{dt} = -k_{\exp} \cdot e^{c(T(t) - T_R)} \cdot m \tag{60.10}$$

where $k_{\exp}$ is the temperature-normalized decay rate coefficient at the reference temperature T_R (e.g., 10 °C as above) and c is a parameter that describes the sensitivity of the temperature response. If temperature during decomposition equals the reference temperature (i.e., $T(t) = T_R$), the exponent becomes 0, and since $e^0 = 1$, Eq. 60.10 becomes Eq. 60.5 with $k_{\exp} = k$. In other words, $k_{\exp}$ is the decay rate coefficient at the reference temperature. Note that the overall decomposition rate (*dm*/*dt*) decreases with decreasing temperature but does not cease at the freezing point, in contrast to the model assuming a linear temperature dependence (Eq. 60.5). Solving Eq. 63.10 results in the same kind of relationship as in Eqs. 60.4 and 60.8, the only difference being the way in which the influence of temperature is accounted for:

$$m_t = m_0 \cdot e^{-k_{\exp} \cdot \int_{t_0}^{t_n} e^{c(T(t) - T_R)} dt} \tag{60.11}$$

A common approach when considering such exponential temperature relationships with decay rate is to apply Q_{10} values, where Q_{10} indicates by which factor a process rate coefficient is increased when temperature is raised by 10 °C. This approach is standard in modeling soil organic matter turnover (e.g., Davidson et al. 2006) but has rarely been used in litter decomposition studies in aquatic environments (but see Hietz 1992). Q_{10} is often found or assumed to be about 2, meaning that process rates double when temperature increases by 10 °C. However, values of up to 3 are not uncommon and values <2 and >3 have also been observed. Just like in Eqs. 60.10

and 60.11, the Q_{10} approach assumes an exponential relationship between temperature and decomposition rate. As a result, Q_{10} values can be readily converted to the constant c, and vice versa, according to

$$Q_{10} = e^{c \cdot 10\,°\mathrm{C}} \tag{60.12}$$

$$\Rightarrow c = \frac{\ln(Q_{10})}{10\,°\mathrm{C}} \tag{60.13}$$

A Q_{10} of 2.0 thus corresponds to a c of 0.069 °C^{-1}, a Q_{10} of 2.5 corresponds to a c of 0.092 °C^{-1}, and a Q_{10} of 3 is equivalent to a c of 0.110 °C^{-1}. Consequently, Eq. 60.11 can be rewritten as:

$$m_t = m_0 \cdot e^{-k_{\exp} \cdot \int_{t0}^{tn} Q_{10}^{\frac{(T(t)-T_R)}{10\,°\mathrm{C}}} dt} \tag{60.14}$$

This chapter describes procedures to analyze temperature-dependent litter decomposition, assuming both a linear and an exponential relationship between temperature and decomposition rate. Selected rate coefficients (k and k_T) from assessments made in various streams are presented in Table 60.1. All are based on the assumption that the temperature effect is linear. Similar examples based on exponential relationships have not been published for streams and rarely for other freshwater environments (Hietz 1992).

Table 60.1 Range of standard (k) and temperature-normalized decay rates (k_T) in streams

Leaf material	Environment	k (day^{-1})	k_T (day^{-1})[a]	Reference
10 species	Costa Rica, latitude 10°N	0.0200–0.5586	0.008–0.280	1
10 species	Michigan, USA, latitude 46°N	0.0036–0.0684	0.004–0.040	1
10 species	Alaska, USA, latitude 65°N	0.0013–0.0259	0.052–0.852	1
Quercus robur	95 European streams, latitude 40–60°N, coarse-mesh bag	0.0019–0.0687	0.005–0.141	2
Quercus robur	95 European streams, latitude 40–60°N, fine-mesh bag	0.0016–0.0588	0.004–0.116	2
Alnus glutinosa	98 European streams, latitude 40–60°N, coarse-mesh bag	0.0045–0.2137	0.012–0.259	2
Alnus glutinosa	98 European streams, latitude 40–60°N, fine-mesh bag	0.0043–0.0468	0.007–0.146	2
Alnus glutinosa	4 alpine floodplain streams, coarse-mesh bag	0.0039–0.0305	0.024–0.181	3
Alnus glutinosa	4 alpine floodplain streams, fine-mesh bag	0.0029–0.0036	0.014–0.108	3

[a]Reference temperature T_R = 10 °C

1 = Irons et al. (1994), 2 = Woodward et al. (2012), 3 = Gessner et al. (1998)

2 Equipment, Materials, and Software

- Leaf litter, litter bags, drying oven, etc. to run decomposition experiment (see Chap. 6).
- Temperature data logger, calibrated and programmed to record data at hourly intervals during the expected duration of the decomposition study.
- Spreadsheet such as Excel and optionally statistical or mathematical software such as R or Matlab.

3 Procedures

3.1 Data Acquisition

1. Run a litter decomposition experiment in the field or laboratory or in mesocosms to determine litter mass remaining after at least five different time periods, spaced sufficiently to ensure that between 60% and 80% of the initial litter mass has been lost at the last collection date.
2. Before starting the experiment, program a calibrated temperature logger to record temperature at hourly intervals, deploy the data logger at the experimental site, ensuring that it is protected from direct sunlight or other heat sources.
3. Periodically collect replicate litter samples and determine the percent litter mass remaining.
4. At the final sampling date, also retrieve the logger and import the temperature data into a spreadsheet.

3.2 Linear Temperature Relationship

1. Calculate the thermal sums (degree days) reached by each of the sampling dates.
2. Construct a data sheet for regression analysis showing in separate columns the sample identifiers, elapsed time, thermal sums, percent litter mass remaining, and the natural logarithm of percent litter mass remaining (Online Appendix 1).
3. Run an ordinary least-squares regression analysis or, often superior, a nonlinear regression analysis using thermal sums divided by T_R = 10 °C as independent variable and, as dependent variable, the natural logarithm of percent litter mass remaining (least-squares regression; as illustrated in Online Appendix 1) or percent mass remaining (nonlinear curve-fitting, using statistical or mathematical software).
4. Ensure that the estimated initial litter mass is reasonably close to the theoretical value of 100%; otherwise consider fixing the intercept at 100% with the data

points for $t_n = 0$ omitted from the regression analysis in that case, or refrain from fitting the observational data to the model.

3.3 Exponential Temperature Relationship

1. Set an *a priori* value for the constant c in Eqs. 60.10 and 60.11 (e.g., $c = 0.069$ °C^{-1} for $Q_{10} = 2$) as well as a reference temperature T_R (e.g., 1 or 10 °C).
2. Calculate daily mean values of the temperature terms $e^{c\cdot(T - T_R))}$.
3. Compute the thermal integral reached by each of the sampling dates by summing the daily mean temperature terms from the start of the experiment to each of the sampling dates; these sums need to be multiplied by 1 day to be the formally correct integrals, although this does not change the numerical value.
4. As for the linear temperature relationship above, construct a data sheet for regression analysis showing in separate columns the sample identifiers, elapsed time, thermal integrals, percent litter mass remaining, and the natural logarithm of percent litter mass remaining (Online Appendix 1).
5. Run an ordinary least-squares regression analysis or, often preferable, a nonlinear regression analysis, using the thermal integrals as independent variable and, as dependent variable, the natural logarithm of percent litter mass remaining (least-squares regression; as illustrated in Online Appendix 1) or percent mass remaining (nonlinear curve-fitting; using statistical or mathematical software)
6. Repeat the calculations and regression analysis by testing different values for c, ranging, for example, from 0.0405 °C^{-1} ($Q_{10} = 1.5$) to 0.1099 °C^{-1} ($Q_{10} = 3.0$) to determine, by iteration, the best fitting parameter set m_0, k_{exp}, and c, as indicated by the highest coefficient of determination (r^2).
7. Ensure that the estimated initial litter mass is reasonably close to the theoretical value of 100%; otherwise, consider fixing the intercept at 100% with the data points for $t_n = 0$ omitted from the regression analysis in that case, or refrain from fitting the observational data to the model.
8. Alternatively, run regression analyses directly based on the relationship of Eq. 60.11 to fit m_0, k_{exp}, and c simultaneously, which requires mathematical or statistical software with a fitting function capable of integration or summation (Online Appendix 2).

4 Final Remarks

The linear or exponential temperature dependencies are only valid within a narrow range. This is particularly important in streams (and possibly other cold environments) where temperature optima of aquatic hyphomycetes, the main microbial decomposers of leaf litter, are low (Suberkropp 1984; Chauvet and Suberkropp 1998; Dang et al. 2009). Therefore, caution is needed when applying either linear or exponential temperature relationships to litter decomposition rates when ambient temperatures notably exceed 20 °C.

Types of temperature relationships other than linear or exponential can be modelled in the same way as outlined above. However, with more complex models (e.g., Dang et al. 2009), it may not be convenient to solve the equations and thus calculate decay rate coefficients, k, in a spreadsheet. Instead, the use of mathematical or statistical software such as R, Matlab, or others is recommended.

Several studies on litter decomposition have resorted to the Metabolic Theory of Ecology (Allen et al. 2005) to assess the influence of temperature on litter decomposition rates (Boyero et al. 2011; Follstad Shah et al. 2017), where the temperature dependence follows the Arrhenius law. Accordingly, the decay rate coefficient is expressed as a function of the inverse of absolute temperature (T_{abs}) in Kelvin and the Boltzmann constant, $B = 8.617 \cdot 10^{-5}$ eV K^{-1}, with the activation energy, E_A, being the fitted proportionality constant with a predicted value of 0.65 eV. Thus:

$$k = k_{\mathrm{Arr}} \cdot e^{-\frac{E_A}{B}\left(\frac{1}{T_{\mathrm{abs}}} - \frac{1}{T_{R,\mathrm{abs}}}\right)} \tag{60.15}$$

where k_{Arr} is the temperature-normalized decay rate coefficient for Arrhenius' law at the reference temperature $T_{R,\mathrm{abs}}$. The term $1/T_{R,\mathrm{abs}}$ is introduced to ensure that, similar to Eq. 60.11, k_{Arr} becomes k when decomposition occurs at the reference temperature, expressed here in degrees Kelvin. In essence, this approach uses yet another function for the temperature dependence of the decay rate coefficient. However, in the temperature range relevant for litter decomposition in natural environments, the temperature dependence of the function of Eq. 60.15 with $E_A \sim 0.65$ eV is very similar to the exponential (or Q_{10}) temperature dependence described above.

References

Allen, A. P., Gillooly, J. F., & Brown, J. H. (2005). Linking the global carbon cycle to individual metabolism. *Functional Ecology, 19*, 202–213.

Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience, 3*, 336–340.

Arrhenius, S. (1889). Über die Reaktionsgeschwindigkeit bei der Inversion von Rohrzucker durch Säuren. *Zeitschrift für Physikalische Chemie, 4*, 226–248.

Boyero, L., Pearson, R. G., Gessner, M. O., Barmuta, L. A., Ferreira, V., Graça, M. A. S., Dudgeon, D., Boulton, A. J., Callisto, M., Chauvet, E., Helson, J. E., Bruder, A., Albariño, R. J., Yule, C. M., Arunachalam, M., Davies, J. N., Figueroa, R., Flecker, A. S., Ramírez, A., Death, R. G., Iwata, T., Mathooko, J. M., Mathuriau, C., Gonçalves, J. F., Jr., Moretti, M. S., Jinggut, T., Lamothe, S., M'Erimba, C., Ratnarajah, L., Schindler, M. H., Castela, J., Buria, L. M., Cornejo, A., Villanueva, V. D., & West, D. C. (2011). A global experiment suggests climate warming will not accelerate litter decomposition in streams but might reduce carbon sequestration. *Ecology Letters, 14*, 289–294.

Chauvet, E., & Suberkropp, K. (1998). Temperature and sporulation of aquatic hyphomycetes. *Applied and Environmental Microbiology, 64*, 1522–1525.

Dang, C. K., Schindler, M., Chauvet, E., & Gessner, M. O. (2009). Temperature oscillation coupled with fungal community shifts can modulate warming effects on litter decomposition. *Ecology, 90*, 122–131.

Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature, 440*, 165–173.

Davidson, E. A., Janssens, I. A., & Luo, Y. (2006). On the variability of respiration in terrestrial ecosystems: Moving beyond Q_{10}. *Global Change Biology, 12*, 154–164.

Ferreira, V., & Canhoto, C. (2015). Future increase in temperature may stimulate litter decomposition in temperate mountain streams: Evidence from a stream manipulation experiment. *Freshwater Biology, 60*, 881–892.

Fierer, N., Craine, J. M., McLaughlan, K., & Schimel, J. P. (2005). Litter quality and the temperature sensitivity of decomposition. *Ecology, 86*, 320–326.

Follstad Shah, J. J., Kominoski, J. S., Ardón, M., Dodds, W. K., Gessner, M. O., Griffiths, N. A., Hawkins, C. P., Johnson, S. L., Lecerf, A., LeRoy, C. J., Manning, D. W. P., Rosemond, A. D., Sinsabaugh, R. L., Swan, C. M., Webster, J. R., & Zeglin, L. H. (2017). Global synthesis of the temperature sensitivity of leaf litter breakdown in streams and rivers. *Global Change Biology, 23*, 3064–3075.

Gessner, M. O., Robinson, C. T., & Ward, J. V. (1998). Leaf breakdown in streams of an alpine glacial floodplain: Dynamics of fungi and nutrients. *Journal of the North American Benthological Society, 17*, 403–419.

Graça, M. A. S., Ferreira, V., Canhoto, C., Encalada, A. C., Guerrero-Bolaño, F., Wantzen, K. M., & Boyero, L. (2015). A conceptual model of litter breakdown in low order streams. *International Review of Hydrobiology, 100*, 1–12.

Hietz, P. (1992). Decomposition and nutrient dynamics of reed (*Phragmites australis* (Cav.) Trin. ex Steud.) litter in Lake Neusiedl, Austria. *Aquatic Botany, 43*, 211–230.

Irons, J. G., III, Oswood, M. W., Stout, R. J., & Pringle, C. M. (1994). Latitudinal patterns in leaf litter breakdown: Is temperature really important? *Freshwater Biology, 32*, 401–411.

Petersen, R. C., & Cummins, K. W. (1974). Leaf processing in a woodland stream. *Freshwater Biology, 4*, 343–368.

Prescott, C. E. (2010). Litter decomposition: What controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry, 101*, 133–149.

Robinson, W. R., Peters, R. H., & Zimmermann, J. (1983). The effects of body size and temperature on metabolic rate of organisms. *Canadian Journal of Zoology, 61*, 281–288.

Suberkropp, K. (1984). Effect of temperature on seasonal occurrence of aquatic hyphomycetes. *Transactions of the British Mycological Society, 82*, 53–62.

Woodward, G., Gessner, M. O., Giller, P. S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B. G., Tiegs, S. D., Cariss, H., Dobson, M., Elosegi, A., Ferreira, V., Graça, M. A. S., Fleituch, T., Lacoursière, J. O., Nistorescu, M., Pozo, J., Risnoveanu, G., Schindler, M., Vadineanu, A., Vought, L. B.-M., & Chauvet, E. (2012). Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science, 336*, 1438–1440.