

Chapter 12

Individual and Interacting Effects of Elevated CO₂, Warming, and Hydrologic Intensification on Leaf Litter Decomposition in Streams



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Abstract Elevated atmospheric carbon dioxide (CO₂) concentration, rising water temperatures, and intensification of hydrologic regimes are characteristics of global climate change that affect rates of leaf litter decomposition in lotic ecosystems. Predicted effects of elevated atmospheric CO₂ concentration and elevated temperature negate each other. However, a recent meta-analysis found no effect of elevated atmospheric CO₂ on decomposition, while temperature consistently stimulates rates of decomposition. The sensitivity of litter decomposition to shifts in temperature is less clear due to methodological differences between studies calculating the apparent activation energy of decomposition and the multitude of biotic and abiotic variables that enhance or mitigate the effect of temperature. Both floods and droughts are becoming more frequent features of hydrologic regimes, but spatial and temporal variation in hydrologic intensification adds further challenge for predicting how climate change will alter decomposition rates. Despite these complexities, it is clear that altered rates of litter decomposition have cascading influence on the global C budget and food web dynamics. Thus, improved understanding of the individual and interactive effects of elevated atmospheric CO₂ concentration, warming, and shifting hydrology on decomposition rates remains a vital research need.

12.1 Predicted Individual Effects of Elevated Atmospheric CO₂ Concentration, Warming, and Hydrologic Intensification on Leaf Litter Decomposition

The decomposition of leaf litter is an integrative ecosystem process that fuels aquatic food webs and links biogeochemical cycles (Gessner et al., 1999; Minshall et al., 1983; Wallace et al., 1997). The decomposition process involves leaching of dissolved

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constituents, degradation by bacteria and fungi, feeding by invertebrate detritivores, and physical fragmentation, all of which are mediated by the chemistry and physical structure of leaves and environmental factors (Gessner et al., 1999; Graça, 2001; Webster & Benfield, 1986). Elevated atmospheric carbon dioxide (CO_2) concentration, rising water temperatures, and intensification of hydrologic regimes are central features of the climate crisis that affect rates of decomposition in lotic ecosystems through changes to decomposer metabolic rates and community composition, plant productivity and leaf chemistry, and the supply of water and organic matter.

Human activities have caused global atmospheric CO_2 concentration to increase from 280 ppm at the start of the Industrial Revolution to over 400 ppm (IPCC, 2014). Elevated CO_2 induces terrestrial plants to be more productive through higher rates of photosynthesis (Finzi et al., 2001; Stiling & Cornelissen, 2007), when nutrients or moisture are not limiting (Norby et al., 2010; Perry et al., 2012). In turn, increased terrestrial primary productivity can lead to greater detrital inputs to aquatic ecosystems that support the process of decomposition. However, greater availability of CO_2 also results in leaf litter with higher C:nutrient ratios and higher concentrations of polyphenolic compounds, condensed tannins, and lignin (Ferreira & Chauvet, 2011; Martins, Rezende et al., 2017; Monroy et al., 2016; Rier et al., 2002, 2005; Tuchman et al., 2002), factors that often suppress rates of decomposition (Ardón & Pringle, 2008; Lecerf & Chauvet, 2008; LeRoy et al., 2007; Martínez et al., 2014; Ostrofsky, 1997). Moreover, elevated atmospheric CO_2 concentration promotes more acidic conditions in streams and rivers with poor buffering capacity. Litter decomposition proceeds more slowly with declining pH because acidic conditions suppress microbial and detritivore activity (Boyero et al., 2016; Young et al., 2008). Overall, elevated atmospheric CO_2 concentration is predicted to inhibit rates of litter decomposition (Amani et al., 2019; Kominoski & Rosemond, 2012; Fig. 12.1a).

Mean global air temperature has risen by approximately 1.0 °C above pre-industrial levels as a result of elevated CO_2 concentration (IPCC, 2018) and increases in water temperature have been observed in many streams and rivers (Kaushal et al.,

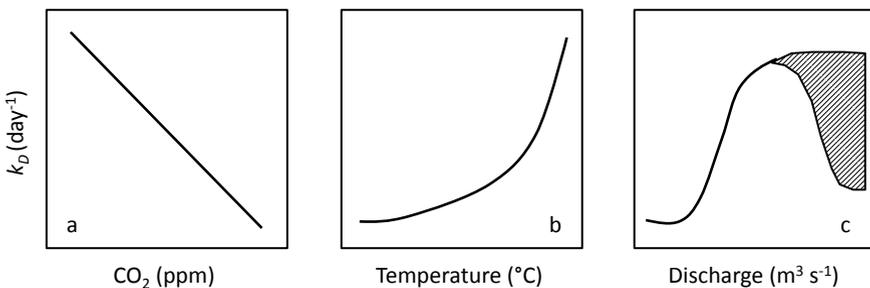


Fig. 12.1 Theoretical effects of CO_2 concentration (a), temperature (b), and water discharge (c) on leaf litter decomposition in streams and rivers. Shading in (c) denotes flushing of organic matter standing stock during high flow conditions

2010). Temperature is a key environmental factor that influences the rate at which organic matter is processed (Tank et al., 2010; Webster & Benfield, 1986; Young et al., 2008). Elevated temperature, within species tolerance limits, increases litter decomposition by stimulating metabolic rates of extant bacteria, fungi, and invertebrate decomposers (Ferreira & Chauvet, 2011; Ferreira, Chauvet et al., 2014; Ferreira et al., 2010; Flury & Gessner, 2011; Moghadam & Zimmer, 2016; Rajashekhar & Kaveriappa, 2000). In addition, higher temperatures typically favor smaller bodied organisms (Atkinson, 1994; James, 1970), which have faster metabolic rates than larger bodied organisms (Gillooly et al., 2001). Higher temperature also promotes leaching of organic matter, which can result in faster litter decomposition by removing recalcitrant compounds (Rier et al., 2005). Litter decomposition is predicted to increase exponentially with temperature (Boyero, Pearson, Gessner et al., 2011; Follstad Shah et al., 2017; Fig. 12.1b), based on first principles of thermodynamics (see *Theory* below). However, temperature and other extrinsic (e.g., resource availability, stream flow) or intrinsic (e.g., leaf litter quality) factors may co-vary, potentially dampening or enhancing the effect of temperature on litter decomposition rates (Fig. 12.2).

Global precipitation patterns are shifting in response to elevated atmospheric and marine temperature (IPCC, 2014), leading to altered flow regimes in streams and rivers (Hattermann et al., 2017; IPCC, 2008). Average annual runoff is expected to increase in high latitudes and the wet tropics, and to decrease at mid-latitudes and in dry tropical regions (IPCC, 2014; Rodell et al., 2018). Snowmelt-fed regions will likely exhibit consistently earlier peak flows, except in limited areas where increases in precipitation are expected to augment snow accumulation (IPCC, 2014). Changes to flow regimes are more varied in other areas (Gosling et al., 2017; IPCC, 2014). Yet, intensification of hydrologic events, in terms of both floods and droughts, is expected in many regions as climate patterns shift (Grimm et al., 2013; IPCC, 2008). Greater frequency of punctuated high flow events will increase the delivery of sediments, organic matter, and contaminants (Grimm et al., 2013). Heavy flow events can lead to faster decomposition of organic matter through physical fragmentation (Paul et al., 2006), unless flows bury litter standing stock with fine sediment, transport toxins and pharmaceuticals that suppress the metabolism of aquatic decomposers, or deplete individual stream reaches of organic substrates by flushing aquatic primary producers and detritus downstream (Roberts et al., 2007; Rosi-Marshall et al., 2013; Young et al., 2008). In consequence, increased stream flashiness can affect rates of litter decomposition in a non-linear fashion.

Increased prevalence of streams and rivers with intermittent or ephemeral flow, particularly in regions with reduced rainfall and greater reliance on water storage in reservoirs, represents the other extreme of hydrologic intensification (Acuña et al., 2014; Detry et al., 2018). In short, the hydrological regimes of intermittent rivers and ephemeral streams are characterized by alternating flowing, non-flowing and dry phases (del Campo et al., 2020). Litter accumulation, processing, and downstream transport vary in importance amongst phases, resulting in high temporal and spatial variability of litter decomposition. Gradual re-wetting events can stimulate high rates of litter processing *in situ*, whereas pulsed high flow re-wetting events can result in export of accumulated leaf litter. Greater variability of hydrologic flow in

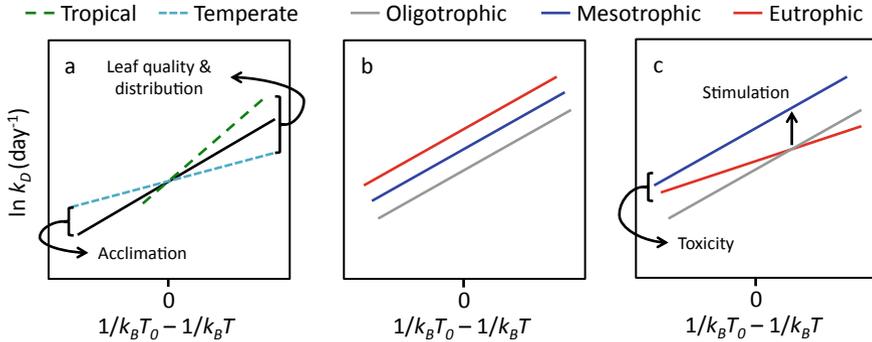


Fig. 12.2 Example mechanisms that influence the temperature dependence of leaf litter decomposition, depicted in the form of Arrhenius plots that visualize the relationship described in Eq. 12.2. The x-axis in (a–c) is normalized inverse temperature, where k_B is Boltzmann’s constant (8.62×10^{-5} eV K⁻¹), T is temperature in Kelvin (K), and T_0 is a standard temperature. This normalization centers the data at 0 on the x-axis and allows for interpretation of the intercept at the standard temperature. Temperatures cooler than the standard temperature are plotted to the left of 0, warmer temperatures to the right of 0. The y-axis is the natural logarithm of the decomposition coefficient (k_D , day⁻¹). The slope of the relationship quantifies the apparent activation energy (E_a , eV). The solid black line in (a) represents the predicted value of E_a , based on Metabolic Scaling Theory (0.65 eV; Brown et al., 2004). This value is very similar to the E_a of cellulose strip decay in streams (0.68 eV; Tiegs et al., 2019). The colored dashed lines in (a) depict values of E_a observed in temperate (turquoise; 0.27 eV) and tropical (green; 0.75 eV) biomes (Follstad Shah et al., 2017). In temperate biomes, rates may be higher than predicted in cooler water due to acclimation of microbes and detritivores to seasonal pulses of allochthonous c inputs, but lower than predicted in warmer water due to the supply of labile plant litter that decomposes rapidly. The colored lines in (b, c) represent streams and rivers categorized by trophic status: oligotrophic (gray), mesotrophic (blue), and eutrophic (red). Increasing nutrient availability can stimulate rates of decomposition (Ferreira, Chauvet et al., 2014; Rosemond et al., 2015), as illustrated by shifts in intercepts amongst systems with different trophic status (b, c). If rates increase similarly across the thermal spectrum, the E_a may remain constant amongst trophic groups (b; Jabiol et al., 2020). However, nutrient toxicity in eutrophic systems can suppress rates of decomposition, especially when aquatic organisms are near thermal maxima (Woodward et al., 2012). This phenomenon could induce shifts in both the value of E_a (i.e., slope) and the rate of decomposition at the standard temperature (i.e., intercept) in eutrophic systems (c). More details are described in the text (see *Modulation of temperature sensitivity by biotic & abiotic factors*)

river networks increases the relative importance of reservoirs for processing organic matter, as a greater fraction of detritus is transported in pulse events to these receiving water bodies (Acuña & Tockner, 2010). The effects of hydrologic intensification on litter decomposition are not unidirectional, unlike the effects of elevated CO₂ and temperature, but may be characterized as a unimodal pattern, where absence of flow severely restricts decomposition, rates increase towards a metabolic maximum as moisture becomes non-limiting, and high flow events flush organic matter from the system (Fig. 12.1c).

Here, I summarize studies that have tested predictions illustrated in Fig. 12.1 by quantifying 1) the effect size of elevated atmospheric CO₂ concentration and temperature on litter decomposition relative to controls, and 2) the temperature dependence of litter decomposition. I also assess how elevated atmospheric CO₂ concentration, elevated temperature, altered hydrologic regimes, and other major global changes (e.g., eutrophication) may interact to affect litter decomposition in streams and rivers. Finally, I describe how changes to organic matter processing in lotic ecosystems may influence the global C cycle and aquatic food webs.

12.2 Effect Size of Elevated Atmospheric CO₂ Concentration and Warming on Litter Decomposition

12.2.1 Elevated Atmospheric CO₂ Concentration

Amani et al. (2019) conducted a meta-analysis to assess the effects of elevated temperature, elevated CO₂ concentration, and their interaction on litter decomposition rates in streams and rivers. Elevated CO₂ concentration had no effect on decomposition rates relative to controls, contrary to the authors' prediction (Fig. 12.1a), perhaps because differences in leaf quality induced by elevated CO₂ are more subtle relative to the wide variation observed amongst different plant genera. In addition, leaching of leaf litter can mitigate differences in leaf quality induced by elevated CO₂ (Ferreira et al., 2010; Rier et al., 2005), conditioning by colonizing microbial communities (Ferreira et al., 2010), or the diversity of decomposers present (Rier et al., 2005). Amani et al. (2019) also found that the combined effects of elevated atmospheric CO₂ concentration and elevated temperature had no effect on decomposition rates relative to controls, perhaps due to the opposing influence of these factors on decomposition (Fig. 12.1a,b). However, the sample sizes used for comparisons were small (<20 paired control-treatment observations), suggesting their results are not broadly generalizable. Other studies have indicated that temperature has a greater influence on leaf litter decomposition relative to elevated atmospheric CO₂ concentration (Ferreira & Chauvet, 2011; Martins, Melo et al., 2017). Amani et al. (2019) concluded that additional studies are required to assess the role of elevated atmospheric CO₂ concentration and its interaction with elevated temperature on litter decomposition. Specifically, they urged that individual studies manipulate both CO₂ and temperature, utilize fast and slow decomposing litter types, and assess the role of both microbes and detritivores. They also recommended that more of these studies be carried out in the tropics.

12.2.2 *Elevated Temperature*

The meta-analysis conducted by Amani et al. (2019) showed that elevated temperature (+1 °C or more) increased rates of litter decomposition with an effect size (Hedge's g ; Hedges et al., 1999) of 1.20 (95% CI: 0.96–1.43). Stimulation of decomposition rates with elevated temperature was observed across natural streams (both correlative [$n = 71$] and manipulative studies [$n = 20$]) and laboratory experiments ($n = 57$), as well as along latitudinal gradients ($n = 22$), with an effect size > 1 in these four study types. Elevated temperature stimulated decomposition rates to a lesser extent (effect size < 1) along altitudinal gradients ($n = 32$). The effect of elevated temperature was large (> 0.80) for total litter decomposition (mediated by both microbes and detritivores) in all scenarios, whereas microbial-driven litter decomposition was strongly stimulated only in manipulative field studies conducted in an oligotrophic, low temperature stream (mean temperature of 2.8 °C) using *Quercus* leaves (a slow decomposing litter type). Elevated temperature augmented decomposition rates of leaf litter from some genera, but not others, and depended on study type. For example, decomposition of both *Alnus* (a fast decomposing litter) and *Quercus* significantly increased in laboratory studies (effect size > 1), but not along altitudinal gradients (non-significant effect size). However, in all but one study type, the sample size used to calculate genus-specific effect sizes was small (≤ 13), prohibiting broad generalization. The meta-analysis by Amani et al. (2019) demonstrates that elevated temperature generally promotes faster rates of leaf litter decomposition in freshwater ecosystems, but the type of leaf litter present and the degree to which microbes and detritivores contribute to leaf litter processing may modulate its effect.

12.3 Quantifying the Temperature Dependence of Litter Decomposition

12.3.1 *Theory*

Increased capacity to predict changes to ecosystem process rates with shifts in temperature is needed to better assess the effect of global warming on organic matter decomposition. Metabolic Scaling Theory purports that ecosystem flux rates reflect the combined metabolic rates of individuals within the ecosystem, and can thus be predicted from allometric and thermal scaling relationships (Brown et al., 2004; Enquist et al., 2003). The theory assumes that resources are in steady state supply (Brown et al., 2004). Under such conditions, allometric scaling relationships for individual metabolic rate and the density of organisms in a population using a common resource are predicted to be the inverse of one another, leading to mass invariant community energy flux rates (Damuth, 1981; Enquist & Niklas, 2001). This phenomenon, called the 'energy equivalence rule', suggests ecosystem flux rates should be invariant with biomass standing stock, yet still dependent on shifts

in temperature (Enquist et al., 2003). If so, then the magnitude of change in litter decomposition rates with a given change in temperature (i.e., the temperature dependence) can be quantified as an activation energy, using the linearized form of the Arrhenius equation (Arrhenius, 1915):

$$\ln k_D = \ln r_0 - E \times \frac{1}{k_B T} \quad (12.1)$$

where k_D is the litter decomposition rate coefficient (day⁻¹), r_0 is a normalization constant, E is the activation energy (eV; 1 eV = 1.6 × 10⁻¹⁹ J, or 96 kJ mol⁻¹), k_B is Boltzmann's constant (8.62 × 10⁻⁵ eV K⁻¹), and T is temperature in Kelvin (K).

Typically, temperature data are centered using a normalization, such that values of 0 on the x-axis represent rates at a standard temperature (Allen et al., 2005; Demars et al., 2016; Follstad Shah et al., 2017; Yvon-Durocher et al., 2012):

$$\ln k_D = \ln r_0 - E \times \left(\frac{1}{k_B T_0} - \frac{1}{k_B T} \right) \quad (12.2)$$

where T_0 is the standard water temperature (e.g., the average observed temperature in K). Empirical estimates of the activation energy are considered *apparent* (denoted as E_a) rather than *intrinsic* (E) values, because it is difficult to isolate the effect of temperature from the multitude of abiotic (e.g., stream discharge) and biotic (e.g., leaf litter quality) factors that influence rates of decomposition and the interaction of these factors with temperature (Fig. 12.2). The values reported herein represent *apparent* estimates of temperature dependence. Ecosystem C flux rates should reflect the average temperature dependence of organismal metabolism (Enquist et al., 2003), found to be ~ 0.65 eV (Gillooly et al., 2001; Table 12.1). Empirical data show that the average E_a of a multitude of thermal biological response rates associated with freshwater organisms is 0.77 eV (95% CI: 0.64–0.91 eV; Dell et al., 2011; Table 12.1).

12.3.2 Results from Past Studies

Several studies have quantified the temperature sensitivity of organic matter decomposition in aquatic habitats, providing estimates that range from 0.34 to 0.68 eV for microbe-mediated decomposition and 0 to 0.34 eV for total decomposition (Boyero, Pearson, Gessner et al., 2011; Follstad Shah et al., 2017; Tiegs et al., 2019; Fig. 12.2; Table 12.2). Boyero, Pearson, Gessner et al. (2011) conducted a litter decomposition experiment, using *Alnus glutinosa* leaves decaying in fine (0.5 mm) and coarse (10 mm) mesh bags, at 24 sites spanning absolute latitudes ranging from 0.37° to 47.80°. Their experiment lasted 56 days and coincided with the dry season in the tropics and autumn in temperate biomes. The E_a of litter decomposition (0.41 ± 0.21 eV) mediated by microbes differed from the E_a of total decomposition, which

Table 12.1 Comparison of the apparent activation energy (E_a , eV) of metabolic rates by taxonomic group. ‘NA’ denotes where data were not available

Category	Metabolic process	Taxonomic group	Sample size (#)	E_a		Citation
				(eV)	95% CI (eV)	
<i>Plants</i>						
	Respiration ^a	Plants	67	0.66	NA	Gillooly et al. (2001)
	Varied	Plants	20	0.57	0.50–0.62	Dell et al. (2011)
<i>Microbes</i>						
	Respiration ^a	Unicells	30	0.76	NA	Gillooly et al. (2001)
	Varied	Unicells	12	0.51	0.32–0.68	Dell et al. (2011)
	Varied	Fungi	4	0.95	0.75–1.15	Dell et al. (2011)
	Respiration	Bacteria	205	0.59	NA	Lopez Urritia and Moran (2007)
	Respiration	Microbes	48	1.00	NA	Jabiol et al. (2020)
	Respiration ^a	Fungi	48	0.55	NA	Jabiol et al. (2020)
	Production	Bacteria	851	0.58	NA	Lopez Urritia and Moran (2007)
	Production	Bacteria	353	0.50	NA	Lopez Urritia and Moran (2007)
	Production	Bacteria	190	0.42	NA	Lopez Urritia and Moran (2007)
	Production	Bacteria	50	0.86	0.56–1.17	Sinsabaugh and Follstad Shah (2010)
<i>Invertebrates</i>						
	Respiration ^a	Invertebrates	20	0.79	NA	Gillooly et al. (2001)

(continued)

Table 12.1 (continued)

Category	Metabolic process	Taxonomic group	Sample size (#)	E_a		Citation
				(eV)	95% CI (eV)	
	Varied	Invertebrates	81	0.87	0.76–0.95	Dell et al. (2011)
	Varied	Insects	128	0.63	0.47–0.78	Dell et al. (2011)
	Respiration	<i>Ephemeroptera</i>	NA	0.75–1.38 ^b	NA	Shah et al. (2019)
	Respiration	<i>Ephemeroptera</i>	NA	0.56–0.84 ^b	NA	Shah et al. (2019)
	Respiration	<i>Plecoptera</i>	NA	0.59–1.14 ^b	NA	Shah et al. (2019)
	Respiration	<i>Plecoptera</i>	NA	1.23–1.24 ^b	NA	Shah et al. (2019)
	Respiration	<i>Gammarus</i>	48	1.15	NA	Jabiol et al. (2020)
	Respiration	<i>Potamophylax</i>	48	0.99	NA	Jabiol et al. (2020)
	Respiration	<i>Sericostoma</i>	48	0.55	NA	Jabiol et al. (2020)
<i>Vertebrates</i>						
	Respiration ^a	Fish	113	0.43	NA	Gillooly et al. (2001)
	Respiration ^a	Amphibians	64	0.50	NA	Gillooly et al. (2001)
	Respiration ^a	Reptiles	105	0.76	NA	Gillooly et al. (2001)
	Respiration ^a	Bird & mammals	142	0.78	NA	Gillooly et al. (2001)
	Varied	Vertebrate	127	0.51	0.36–0.67	Dell et al. (2011)
<i>Ecosystem</i>						
	Varied	Freshwater organisms	89	0.77	0.64–0.91	Dell et al. (2011)
	Varied	Marine organisms	78	0.62	0.52–0.68	Dell et al. (2011)
	Varied	Terrestrial organisms	205	0.64	0.57–0.68	Dell et al. (2011)

(continued)

Table 12.1 (continued)

Category	Metabolic process	Taxonomic group	Sample size (#)	E_a		Citation
				(eV)	95% CI (eV)	
<i>Trophic Group</i>						
	Varied	Producer	24	0.54	0.44–0.64	Dell et al. (2011)
	Varied	Detritivore	4	0.46	0.00–0.97	Dell et al. (2011)
	Varied	Herbivore	50	0.83	0.66–0.99	Dell et al. (2011)
	Varied	Omnivore	100	0.63	0.53–0.73	Dell et al. (2011)
	Varied	Carnivore	181	0.61	0.56–0.67	Dell et al. (2011)

^aMass-specific respiration rate

^bConverted from reported range of Q_{10} values at temperatures considered not stressful to the organisms studied. No average value was reported

was invariant with respect to temperature (Table 12.2). Follstad Shah et al. (2017) synthesized a dataset of 169 studies conducted between absolute latitudes 0° to 60° , comprised of 1,025 observations (169 from fine mesh [≤ 1 mm], 856 from coarse mesh [> 1 mm]) of litter decomposition for 85 plant genera. These authors found a common value of E_a for litter decomposition mediated by microbes and total decomposition (0.34 ± 0.04 eV; Table 12.1). However, they also found that the E_a varied across temperate (0.27 ± 0.05 eV, 95% CI: 0.18–0.37 eV) and tropical (0.75 ± 0.13 eV, 95% CI: 0.50–1.01 eV) biomes and amongst twelve plant genera (Fig. 12.2). Tiegs et al. (2019) coordinated a global-scale standardized assay in which cotton strips were deployed for 30 days in 514 streams spanning 140° latitude, with representation from all of Earth's biomes. The temperature dependence of cotton strip decay, measured as the loss of tensile strength, was 0.68 eV. All of these studies relied on mean temperatures reported during decomposition experiments, which is an important caveat. A recent modeling effort shows that the use of central tendencies of temperature can underestimate the value of E_a as compared to calculations including variation in temperature over the course of leaf incubation (Tomczyk et al., 2020).

The range of E_a estimates for litter decomposition in aquatic habitats is generally lower than E_a values predicted by Metabolic Scaling Theory, as well as empirically derived estimates of E_a for decomposition of plant roots, shoots, and large woody debris in terrestrial habitats, and short-term rates of soil respiration, biofilm respiration, and aquatic ecosystem respiration (Table 12.2). However, a study of benthic respiration with small samples size found its temperature sensitivity to be similar to the observed range of E_a estimates for litter decomposition (Table 12.2).

Table 12.2 Comparison of the apparent activation energy (E_a , eV) of ecosystem processes. 'NA' denotes where data were not available

Process & habitat	Type	Method	Sample Size (#)	E_a			Citation
				(eV)	95% CI (eV)	SE	
<i>Decomposition</i>							
Streams	Leaf litter ^a	Field experiment	22	0.41	NA	0.21	Boyero, Pearson, Gessner et al. (2011)
Streams	Leaf litter ^b	Field experiment	22	0.00	NA	NA	Boyero, Pearson, Gessner et al. (2011)
Streams & rivers	Leaf litter ^a	Data synthesis	169	0.37	0.19–0.56	0.09	Follstad Shah et al. (2017)
Streams & rivers	Leaf litter ^b	Data synthesis	856	0.33	0.25–0.40	0.04	Follstad Shah et al. (2017)
Streams & rivers	Leaf litter ^c	Data synthesis	1025	0.34	0.27–0.40	0.04	Follstad Shah et al. (2017)
Aquatic mesocosms	Leaf litter ^b	Lab experiment	48	0.56	NA	0.53	Jabiol et al. (2020)
Aquatic mesocosms	Leaf litter ^c	Lab experiment	192	0.12	NA	0.31	Jabiol et al. (2020)
Streams	Cotton strip	Field experiment	360	0.68	NA	NA	Tiegs et al. (2019)
Terrestrial	Cotton strip	Field experiment	346	0.40	NA	NA	Tiegs et al. (2019)
Terrestrial	Root	Data synthesis	48	0.75	0.44–1.06	NA	Allen et al. (2005)
Terrestrial	Plant litter	Lab experiment	75	0.53–0.92 ^g	NA	NA	Craine et al. (2010)
Terrestrial	Wood	Field experiment	2016	0.50	0.48–0.52	NA	Hu et al. (2018, 2020)
<i>Primary production</i>							
Aquatic mesocosms	Net	Field experiment	131	0.41	0.32–0.50	NA	Yvon-Durocher et al. (2010)
Aquatic mesocosms	Gross	Field experiment	131	0.45	0.38–0.53	NA	Yvon-Durocher et al. (2010)
Geothermal streams	Gross	Field experiment	13	0.54	NA	0.24	Demars et al. (2011)

(continued)

Table 12.2 (continued)

Process & habitat	Type	Method	Sample Size	E_a			Citation
				(#)	(eV)	95% CI (eV)	
Geothermal streams	Gross	Field experiment	39	0.50	0.35–0.65	0.07	Demars et al. (2016)
Streams	Gross	Field experiment ^e	222	1.15	NA	0.16	Demars et al. (2016)
Streams	Gross ^d	Data synthesis ^e	222	0.92	NA	0.16	Demars et al. (2016)
Streams	Gross	Field experiment	292	0.71 ^h	NA	NA	Song et al. (2018)
Terrestrial & wetland	Net	Data synthesis ^e	1599	0.00	NA	NA	Kerkhoff et al. (2005)
<i>Respiration</i>							
Biofilms	Biofilm	Lab experiment	94	0.54	NA	0.12	Acuña et al. (2008)
Geothermal streams	Benthic	Field experiment	13	0.66	0.21–1.11	NA	Perkins et al. (2012)
Sediment	Benthic	Lab experiment	13	0.47	0.31–0.63	NA	Perkins et al. (2012)
Soils	Soil	Data synthesis	174	0.65	0.60–0.70	NA	Allen et al. (2005)
Soils	Soil	Data synthesis ^f	133	0.41	0.28–0.54	NA	Allen et al. (2005)
Soils	Soil	Lab experiment	420	0.85	NA	NA	Craine et al. (2010)
Soils	Soil	Lab experiment ^f	420	0.93	NA	NA	Craine et al. (2010)
Soils	Soil	Data synthesis	206	0.54–1.53 ^g	NA	NA	Craine et al. (2010)
Streams	Ecosystem	Field experiment ^e	18	0.63	NA	0.17	Valett et al. (2008)
Streams & rivers	Ecosystem	Data synthesis ^e	222	0.59	NA	0.10	Demars et al. (2016)
Streams & rivers	Ecosystem ^d	Data synthesis ^e	222	0.44	NA	0.10	Demars et al. (2016)
Streams	Ecosystem	Field experiment	292	0.70	NA	NA	Song et al. (2018)
Aquatic mesocosms	Ecosystem	Field experiment	131	0.62	0.55–0.69	NA	Yvon-Durocher et al. (2010)

(continued)

Table 12.2 (continued)

Process & habitat	Type	Method	Sample Size	E_a			Citation
				(#)	(eV)	95% CI (eV)	
Geothermal streams	Ecosystem	Field experiment	13	0.67	0.17–1.17	0.23	Demars et al. (2011)
Forest canopy	Ecosystem	Data synthesis	8999	0.62	NA	NA	Yvon-Durocher et al. (2012)
Non-forest canopy	Ecosystem	Data synthesis	3271	0.70 ^h	NA	NA	Yvon-Durocher et al. (2012)
Soils	Ecosystem	Data synthesis	4160	0.65	NA	NA	Yvon-Durocher et al. (2012)
Estuarine pelagic	Ecosystem	Data synthesis	1018	0.59	NA	NA	Yvon-Durocher et al. (2012)
Estuarine benthic	Ecosystem	Data synthesis	443	0.63	NA	NA	Yvon-Durocher et al. (2012)
Lake pelagic	Ecosystem	Data synthesis	3666	0.63	NA	NA	Yvon-Durocher et al. (2012)
Lake benthic	Ecosystem	Data synthesis	428	0.55	NA	NA	Yvon-Durocher et al. (2012)
Rivers	Ecosystem	Data synthesis	154	0.58	NA	NA	Yvon-Durocher et al. (2012)
Ocean microbial	Ecosystem	Data synthesis	438	0.57	NA	NA	Yvon-Durocher et al. (2012)

^aMediated by microbes alone^bMediated by both microbes and detritivores^cPooled value across microbial and total decomposition^dDischarge-corrected rates^eRates measured over one season. Other rates were measured on a short-term basis, unless noted otherwise^fRates measured over one year. Other rates were measured on a short-term basis, unless noted otherwise^gRange of reported values. No average value was reported^hMedian value

12.3.3 Modulation of Temperature Sensitivity by Biotic and Abiotic Factors

The results of studies quantifying the temperature dependence of litter decomposition vary, potentially, due to differences in methodology (i.e., standardized experiment vs. data synthesis, sample size, timing and duration of assays, and organic substrates assessed). However, factors that can affect the E_a of decomposition or co-vary with temperature must also be considered. Interactions of these factors with temperature may also help to explain the observed differences in the E_a of litter decomposition relative to the temperature sensitivities of other types of organic matter utilization. Some of these factors include the biogeography of detritivores and plant genera, thermal acclimation capacity of biota, variation in litter quality, and variation in key

environmental controls (Fig. 12.2). Each of these factors is explored in more detail below.

Three studies have shown that temperature-corrected rates (i.e., reported per degree-day) of total decomposition increase with absolute latitude (Boyero, Pearson, Gessner et al., 2011; Follstad Shah et al., 2017; Irons et al., 1994), but the mechanisms driving this trend are not yet clear. Temperate streams generally have greater density, relative abundance, and diversity of detritivores relative to streams in the tropics (Boyero, Pearson, Dudgeon et al., 2011). Boyero, Pearson, Gessner et al. (2011) hypothesized that greater densities of detritivores in temperate biomes relative to the tropics contributed to elevated temperature-corrected rates of litter decomposition at higher latitudes, thereby dampening the E_a . In other words, greater densities of metabolically active detritivores can lead to faster rates of decomposition, despite lower temperature. Detritivore density data within *Alnus* leaf packs at half of the sites studied by Boyero, Pearson, Gessner et al. (2011), where such data were available, supported this hypothesis (\log_e detritivore density = $1.36 + 0.10 \cdot \text{latitude}$, $r^2 = 0.50$, $P = 0.015$, $n = 11$). In contrast, Follstad Shah et al. (2017) did not find a correlation between detritivore density and absolute latitude for the subset of observations within their global database that had the appropriate data to analyze ($P > 0.05$, $n = 61$). Irons et al. (1994) provided two alternative hypotheses for the observed positive correlation between temperature-corrected decomposition and absolute latitude. First, they proposed that microbes may be less metabolically active in colder water relative to detritivores. If so, the rate of temperature-corrected microbe-mediated decomposition should decrease with absolute latitude. Second, they proposed that detritivores may be more important than microbes to decomposition in temperate zones. If so, temperature-corrected decomposition rate at higher latitudes should be greater for detritivores than microbes. Results from Boyero, Pearson, Gessner et al. (2011) and Follstad Shah et al. (2017) provided mixed support for these hypotheses. The former study found that temperature-corrected, microbe-mediated decomposition was invariant with respect to absolute latitude. In contrast, the latter study found a positive correlation between temperature-corrected, microbe-mediated decomposition and absolute latitude, suggesting that microbes also compensate for lower temperatures in temperate biomes. In both studies, rates of total decomposition at higher latitudes were greater than rates of microbe-mediated decomposition. However, new approaches have been developed to isolate the effect of detritivores from total decomposition rates (Lecerf, 2017; Woodward et al., 2012). Application of these approaches would allow for more robust testing of these hypotheses, and help determine whether these mechanisms influence the E_a of litter decomposition.

Many streams and rivers receive seasonal pulses of organic matter inputs from adjacent terrestrial habitats, particularly in temperate biomes. Yet, organic substrates derived from both autochthonous and allochthonous sources can be scarce in heavily shaded streams at the peak of the growing season, coincident with higher water temperature in temperate biomes (Roberts et al., 2007). Based on these observations, Follstad Shah et al. (2017) suggested that selection pressures on aquatic organisms that utilize pulsed litter inputs at low temperatures could have led to physiological adaptations (e.g., properties of enzymes and maximum growth rates associated with

microbial communities; Bradford, 2013; Wallenstein et al., 2010); aquatic community compositions (Dang et al., 2009; Findlay et al., 2008; Friberg et al., 2009; Handa et al., 2014; Martínez et al., 2014; Strickland et al., 2015); functional redundancies (Nelson et al., 2020); and trophic interactions (Rall et al., 2010) that facilitate high activity at low temperature and rapid litter exploitation (Benstead & Huryn, 2011). Evolutionary adaptations within both microbial and detritivore communities that allow for utilization of pulsed resources at colder temperatures would promote the observed relationship between temperature-corrected decomposition rates and absolute latitude. Thermal acclimation via evolutionary adaptation also helps to explain the weaker temperature sensitivity of total decomposition observed in temperate biomes relative to the tropics (Follstad Shah et al., 2017). This ‘thermal acclimation hypothesis’ is somewhat supported by a recent study using controlled metabolic chambers set at non-stressful temperatures (7.5 °C and 15 °C; Shah et al., 2019), which showed that the respiration rate of Ephemeroptera species collected from temperate streams have a weaker temperature sensitivity than congeners from tropical streams (Table 12.2). However, this pattern did not hold for Plecoptera species. Many studies have been conducted to quantify the temperature sensitivity of metabolic rates for microbes, invertebrates, and fish (Table 12.1). However, few have assessed the temperature sensitivity of metabolic rates for aquatic organisms collected from different biomes. Further experimentation or synthesis of existing data is required to better test the thermal acclimation hypothesis.

Variation in light availability and seasonal pulses of organic matter inputs from terrestrial vegetation to streams and rivers in temperate biomes violate the Metabolic Scaling Theory assumption of steady state resource supply. More constant litter inputs to tropical streams and rivers relative to temperate biomes may explain why the temperature sensitivity of total decomposition in the tropics observed by Follstad Shah et al. (2017) was similar to the canonical value predicted by Metabolic Scaling Theory, while the value of E_a was much lower for leaf litter processed within streams and rivers from temperate biomes. However, some studies suggest resource pulses may augment the temperature sensitivity of organic matter utilization. Estimates of E_a range from 0.58 to 0.70 eV for ecosystem respiration in streams and rivers calculated over short timescales (Demars et al., 2011, 2016; Song et al., 2018; Valett et al., 2008; Yvon-Durocher et al., 2012; Table 12.2). Most of estimates were made under steady state conditions (i.e., when rates of gross primary production [GPP] and ecosystem respiration [ER] were correlated within systems; Demars et al., 2016; Song et al., 2018). Over annual timescales, Yvon-Durocher et al. (2012) found that ecosystem respiration had greater values of E_a (0.57–1.08 eV) relative to terrestrial ecosystems (0–0.42 eV), possibly due to a stronger influence of allochthonous C subsidies relative to autochthonous primary production in aquatic ecosystems. In Walker Branch, a heavily studied temperate spring-fed stream in North America, GPP and ER are correlated over annual timescales (Roberts et al., 2007), yet neither is related to temperature in a way predicted by thermodynamics due to shifting resource availability (Fig. 12.3). Hence, calculating the E_a for individual systems or particular seasons in temperate systems can be confounded by shifting light and C supply. The same concept applies to estimates of E_a for litter decomposition derived

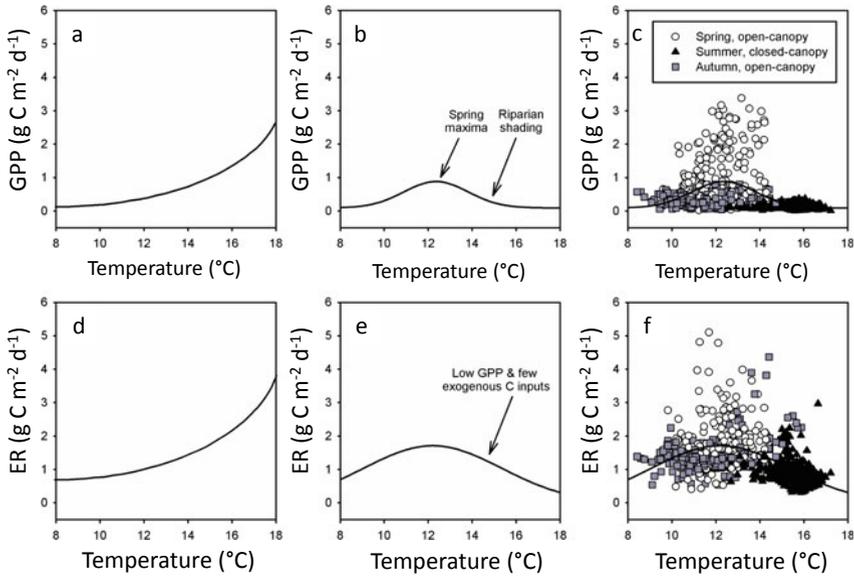


Fig. 12.3 Theoretical (a, d) and empirical (b, c, e, f) relationships between temperature and rates of gross primary production (a–c) and ecosystem respiration (d–f) in Walker Branch, Tennessee, USA. Data from Roberts et al. (2007). Symbols denote different rates in different seasons and forest canopy conditions

from individual systems. For example, Griffiths and Tiegs (2016) found the E_a of litter decomposition to range from 3.3 to 6.3 eV for *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus alba* decomposing within Walker Branch. However, this study was conducted over a narrow temperature range (mean daily difference of ≤ 1.1 °C between sites) in autumn. In addition, summer conditions at this site are marked by low rates of GPP (Fig. 12.3) and organic matter standing stocks (Roberts et al., 2007). Release from substrate limitation may have thus induced the extremely strong E_a observed.

Evolutionary history and adaption to climate shape plant traits, in addition to traits associated with microbes and aquatic invertebrates. Plant traits are strong determinants of litter decomposition rates in aquatic ecosystems (Ardón & Pringle, 2008; Gessner & Chauvet, 1994; Martínez et al., 2014; Ostrofsky, 1997). An experimental study conducted along latitudinal gradients using litter mixtures (Boyer et al., 2016) and a large data synthesis of single species decay rates (LeRoy et al., 2020) found that phylogeny, which influences plant traits (Cornwell et al., 2014), is a better predictor of decomposition rate than climate in streams and rivers. Similarly, plant traits are a stronger driver of leaf and wood decomposition than climate in terrestrial systems (Cornwell et al., 2008; Hu et al., 2018). Follstad Shah et al. (2017) found that variance in the E_a of genus-specific litter decomposition rates could be explained by plant traits, including leaf %N and ratios of C:N, lignin:N, and lignin:P. Lower values of E_a were associated with higher quality litter, similar to studies of litter and soil

organic matter processing conducted in terrestrial systems (Conant, Drijber et al., 2008; Conant, Steinweg et al., 2008; Fierer et al., 2005; Hobbie, 1996; Ramirez et al., 2012; Wang et al., 2019). Higher values of E_a are expected for the decomposition of recalcitrant litter because microbial conditioning facilitates detritivore consumption of structurally complex litter (Gessner & Chauvet, 1994; Suberkropp, 1992; Wright & Covich, 2005). Enzymatic reactions required by microbes to metabolize complex, low-quality macromolecules have higher apparent activation energies than enzymatic reactions that metabolize chemically simpler leaf constituents (Bosatta & Ågren, 1999; Conant et al., 2011; Wagai et al., 2013). For example, enzymes expressed to degrade lignocellulose and polyphenols have temperature sensitivities ranging from 0.45 to 0.56 eV, while the E_a of polysaccharide hydrolysis and nutrient mineralization ranges from 0.31 to 0.41 eV (Sinsabaugh & Follstad Shah, 2012; Wang et al., 2012).

Plant biogeography may influence the temperature sensitivity of litter decomposition due to co-variation with plant traits. Faster decomposing genera are typically found at higher, colder latitudes, while slower decomposing genera are typically found at lower, warmer altitudes (Boyero et al., 2017). However, Zhang et al. (2019) found no difference in litter decomposition when rates were categorized amongst three biomes, likely due to a wide variation of plant traits within each biome. Correlations between plant traits and values of E_a observed by Follstad Shah et al. (2017) were strongly influenced by the inclusion of *Alnus*, the sole plant capable of N-fixation within the analyses. Furthermore, no difference was found in the E_a of litter decomposition when all 85 plant genera were categorized as 'fast', 'medium', or 'slow' decomposing leaves (common slope of 0.23 ± 0.03 eV, 95% CI: 0.18–0.29 eV), based on the distinctions established by Peterson and Cummins (1974). The database compiled by Follstad Shah et al. (2017) was biased towards experiments using *Alnus* and *Quercus* leaves, together representing 38.4% of total decomposition rate observations. The mean E_a across the twelve plant genera for which temperature sensitivity could be quantified was 0.64 eV. The weighted mean, accounting for the number of observations per genus, was 0.40 eV (Fig. 12.4). This weighted mean value was close to the E_a of total decomposition calculated across all plant genera (0.33 eV; Table 12.2). *Alnus* and *Quercus* are two plant genera broadly distributed throughout temperate biomes. Genus-specific values of E_a for *Alnus* and *Quercus* calculated by Follstad Shah et al. (2017) were weaker than the other ten plant genera (0.16 eV and 0.32 eV, respectively; Fig. 12.4). The distribution of *Alnus* and *Quercus*, combined with their relatively weak sensitivity to temperature, likely influenced the difference in biome-specific estimates of E_a .

Abiotic factors can influence the apparent temperature sensitivity of litter decomposition, in addition to biotic factors. Tiegs et al. (2019) removed the influence of leaf quality on decomposition by using a standard substrate to show that environmental variation, such as nutrient availability and differences in pH, leads to distinct signatures of cotton strip decay amongst biomes. They also found that the E_a of cotton strip decay was stronger in streams (0.60 eV) relative to the surfaces of riparian soils (0.40 eV), and attributed the difference to variation in moisture between habitats. Biotic factors still played a role in this study. Microbial activity contributes to

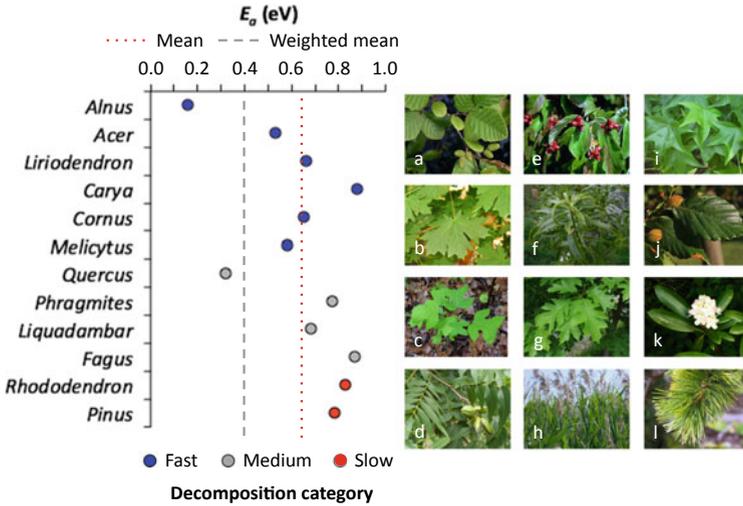


Fig. 12.4 Comparison of the genus-specific apparent activation energy (E_a , eV) amongst twelve plant genera (sample size; panel photo): *Alnus* (224; a), *Acer* (68; b), *Liriodendron* (23; c), *Carya* (14; d), *Cornus* (12; e), *Melicytus* (10; f), *Quercus* (105; g), *Phragmites* (23; h), *Liquidambar* (22; i), *Fagus* (14; j), *Rhododendron* (21; k), *Pinus* (13; l). The mean (0.64 eV) and weighted mean (0.40 eV) genus-specific E_a values are denoted by the red dotted line and gray dashed line, respectively. Colored symbols represent categories of leaf litter decomposition coefficients (k_D) associated with each genus, based on Peterson and Cummins (1974): fast ($k_D > 0.0100 \text{ day}^{-1}$), medium ($k_D = 0.0050\text{--}0.0100 \text{ day}^{-1}$), slow ($k_D < 0.0050 \text{ day}^{-1}$). Photos were obtained from various websites, including but not limited to the USDA Plants Database (<https://plants.sc.egov.usda.gov/java/>), iNaturalist (<https://www.inaturalist.org/>), Wikipedia (<https://en.wikipedia.org/>), and Wikimedia (<https://commons.wikimedia.org/>). Photo credits with copyrights: J.S. Peterson (b); J. McMillan (c); T. Rodd (d); W.S. Justice (e); Rudolph89 (f); A. Huster (g); W. Mark and J. Reimer (i); P. Rothrock (j); S. McDougal (l)

cotton strip decay, in addition to environmental factors (Colas et al., 2019). The E_a for cotton strip decay in streams was similar to the canonical value predicted by Metabolic Scaling Theory (0.65 eV; Brown et al., 2004) and within the range of E_a values observed for bacterial and fungal metabolic rates (0.42–0.95 eV; Table 12.1). In addition, it was closer to the E_a of lignocellulose degradation (0.45–0.54 eV) than the E_a of polysaccharide hydrolysis and nutrient mineralization (0.31–0.41 eV; Sinsabaugh & Follstad Shah, 2012; Wang et al., 2012), reflecting that cotton strips are largely comprised of cellulose. The E_a for cotton strip decay in streams was stronger than the E_a for microbe-mediated litter decomposition (Boyero, Pearson, Gessner et al., 2011; Follstad Shah et al., 2017; Table 12.2), supporting the idea that variation in leaf quality has a strong influence on the temperature dependence of litter decomposition.

Eutrophication is an abiotic global change affecting streams and rivers (Galloway et al., 2008; Manning et al., 2020), but few studies have examined the interactive effects of temperature and nutrient supply on aquatic ecosystem processes (Cross

et al., 2014). Moderate levels of nutrient availability generally stimulate rates of leaf litter decomposition at the scale of leaf packs (Ferreira, Castagnyrol et al., 2014; Rosemond et al., 2015; Woodward et al., 2012; Young et al., 2008), particularly when neither N nor P is limiting (Duarte et al., 2009; Kominoski et al., 2015). However, decomposition rates generally decline in hypertrophic streams due to declines in microbial diversity and biomass (Duarte et al., 2009), shifts in macroinvertebrate community composition (Woodward et al., 2012), stoichiometric imbalance between detritus and consumers (Tonin et al., 2017), or effects of toxins (e.g., high ammonia concentrations or loading of pesticides and pharmaceuticals coincident with nutrient inputs) on the physiology and abundance of aquatic organisms (Duarte et al., 2009; Fernandes et al., 2014; Lecerf et al., 2006; Rosi-Marshall et al., 2013; Schäfer et al., 2007, 2012). The limited number of small-scale studies that have experimentally manipulated both temperature and nutrients within mesocosms or stream-side channels indicate that interaction effects between these two factors are inconsistent. In some cases, additive or synergistic effects of temperature and nutrients have led to faster rates of microbe-mediated and total decomposition for *Alder glutinosa*, *Melicytus ramiflorus*, and *Betula pendula* (Martínez et al., 2014; Moghadam & Zimmer, 2016; Piggott et al., 2015). However, Fernandes et al. (2014) found that elevated temperature stimulated decomposition rates of *Alder glutinosa* and *Quercus robur* mediated by microbes only at low N concentrations ($< 0.1 \text{ mg N L}^{-1}$). Other studies show that the interaction of temperature and nutrients had no effect on total decomposition rates of *Melicytus ramiflorus* (Piggott et al., 2012) or the decomposition of *Corylus* sp. mediated by microbes or detritivores (Gossiaux et al., 2020; Jabiol et al., 2020). The disparate results amongst these studies suggest that interaction effects of temperature and nutrients on litter decomposition may vary by the dominant taxonomic group processing leaves and characteristics of nutrient gradients in streams and rivers. Only one study to date has assessed whether nutrient supply modulates the apparent temperature dependence of litter decomposition. Jabiol et al. (2020) found that four N concentrations ranging from 0.71–2.81 mg N L⁻¹ had no effect on the E_a of litter decomposition mediated by microbes or detritivores. Additional study is needed to determine if this pattern holds over a broader range of nutrient availability and spatial scales.

12.4 Interactions Between Elevated CO₂, Elevated Temperature, and Altered Hydrologic Flow on Litter Decomposition Mediated by Microbes and Detritivores

The combined effects of elevated atmospheric CO₂ concentration, elevated temperature, and hydrologic intensification may vary in different regions of the world due to shifts in vegetation and variation in hydrologic response to climate change. Figure 12.5 illustrates how these factors may interact within tundra, temperate rainforest, desert, and tropical rainforest biomes under future climate scenarios. In the

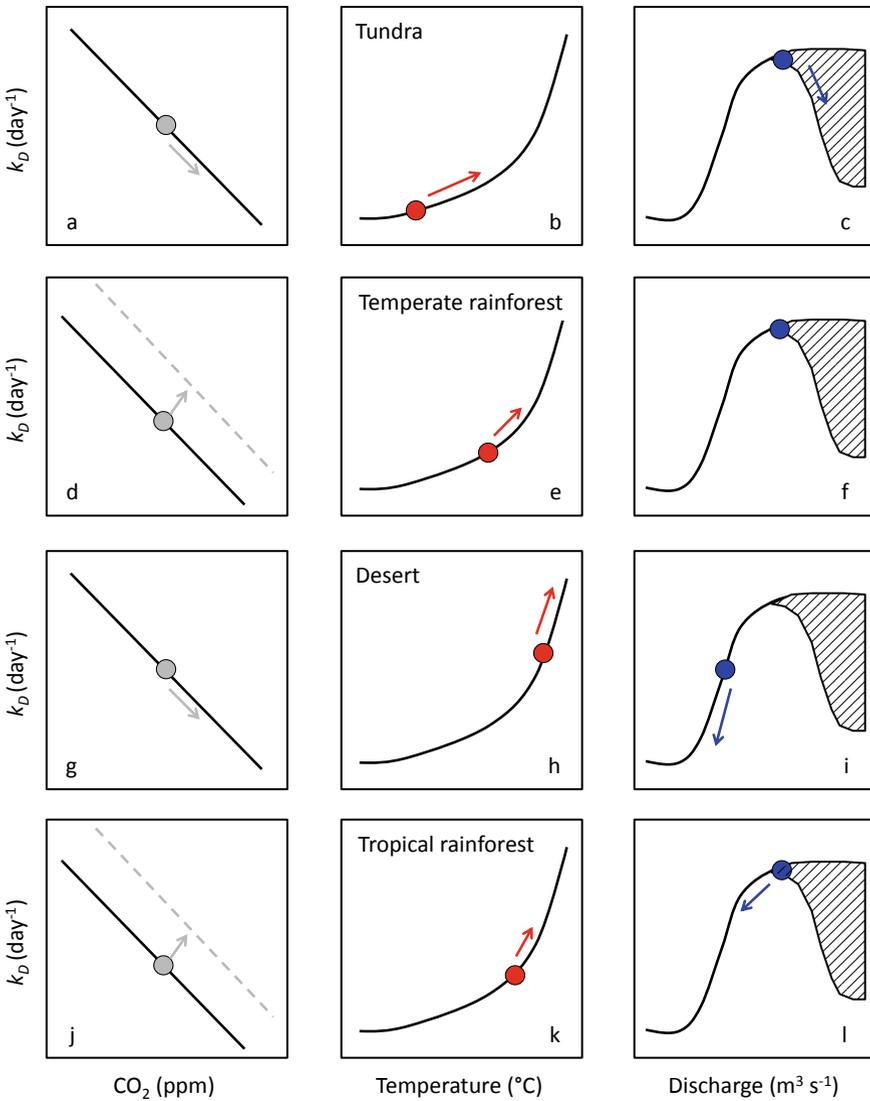


Fig. 12.5 Conceptual figure summarizing potential differences in climate change effects on leaf litter decomposition in tundra (a–c), temperate rainforest (d–f), desert (g–i), and tropical rainforest (j–l) biomes. Symbols represent current conditions, while arrows indicate direction of predicted change in each biome. Gray dashed lines in (d, j) denote more labile leaf litter with elevated CO₂ concentration due to shifts in vegetation. Shaded areas in (c, f, i, l) denote high magnitude hydrologic flow that flushes organic matter from the system

tundra, warmer temperatures and increased precipitation are predicted to stimulate productivity and promote taller vegetation, albeit within narrower riparian zones (Nilsson et al., 2013). However, elevated atmospheric CO₂ concentration may result in lower litter quality and more acidic surface water. Warmer, wetter conditions and potentially greater allochthonous inputs to aquatic ecosystems should favor faster rates of organic matter processing. However, the magnitude of these rates could be modulated or negated by lower litter quality, declining pH, and variable flow in areas of permafrost, decreasing discharge in non-permafrost areas, and glacial outburst flooding (Nilsson et al., 2015). Vegetation in the temperate rainforest of the U.S. Pacific Northwest is shifting to greater dominance of deciduous trees relative to conifers in response to warming (Ball et al., 2010; Kominoski et al., 2013), despite relatively constant water supply (Rodell et al., 2018). Deciduous plants have higher litter quality than conifers and may be more productive with higher CO₂ availability, warmer temperature, and adequate moisture. These conditions should promote faster rates of leaf litter decomposition (Kominoski et al., 2011). In semi-arid to arid western North America, combined effects of elevated temperature, greater frequency and intensity of drought, and river regulation are expected to favor herbaceous (e.g., *Bromus tectorum*) and non-native drought-tolerant (e.g., *Tamarix*) species over native, early-successional tree species (e.g., *Populus* and *Salix*; Perry et al., 2012; Reynolds & Shafroth, 2017). In addition, plant productivity is predicted to decline as higher water demand limits photosynthetic capacity (Perry et al., 2012). Decomposition rates may increase because streams and rivers in this region will be warmer, receive fewer allochthonous inputs of organic matter (Bailey et al., 2001), and be buffered from elevated CO₂ by their alkaline nature. However, rates may be suppressed by greater probability of intermittent flow (Perry et al., 2020). Large portions of the Brazilian rainforest are expected to shift to savannah as annual precipitation and rainfall variability decline (Ciemer et al., 2019). Temperature is predicted to stay relatively constant (Ciemer et al., 2019), yet small shifts can have a large influence on decomposition given strong temperature sensitivity in the tropics. For example, a roughly 10% increase in litter decomposition rate requires only a 1 °C rise in water temperature in the tropical systems but a 4 °C rise in temperate systems, given differences in the E_a observed in these biomes (Follstad Shah et al., 2017). In some cases, grasses do not have lower quality litter when grown at elevated atmospheric CO₂ concentration (Monroy et al., 2016). Hence, decomposition rates may significantly increase with lower allochthonous inputs of litter and warmer temperature, if streams remain perennial. These scenarios suggest that the response of organic matter decomposition to multiple interacting factors associated with climate change will be context specific and coupled to responses of adjacent riparian vegetation.

The relative contribution of microbes and detritivores to litter decomposition may shift in response to elevated atmospheric CO₂ concentration, warming, and hydrologic intensification. The responses of these taxa also may vary amongst biomes. Microbial activity diminishes to a lesser degree than detritivore activity on more recalcitrant leaf litter amongst plant genera (Hieber & Gessner, 2002; Martins, Melo et al., 2017). Similar patterns may hold for increased leaf recalcitrance associated with elevated atmospheric CO₂ concentration, which has been correlated to declines

in detritivore activity (Martins, Melo et al., 2017; Tuchman et al., 2002), but not fungal biomass or activity (Ferreira et al., 2010; Ferreira & Chauvet, 2011; Martins, Melo et al., 2017). However, bacterial production on leaves grown under elevated CO₂ concentration has declined in some studies (e.g., Tuchman et al., 2002) but remained unchanged in other studies (e.g., Rier et al., 2005). Experimental results indicate that microbial activity becomes relatively more important with elevated temperature as compared to detritivore activity (Bärlocher et al., 2008; Boyero, Pearson, Gessner et al., 2011; Jabiol et al., 2020; Martins, Melo et al., 2017; O’Gorman et al., 2012). Elevated temperature generally favors smaller bodied metazoans (‘James’ Rule’; James, 1970), due to oxygen demands and different thermal sensitivities in growth and development rate (or ‘temperature-size rule’; Atkinson, 1994). However, the temperature-size rule does not apply to unicellular organisms whose body size remains invariant with temperature (Forster et al., 2012). Taxonomic differences in temperature-body size scaling relationships can alter the temperature dependence of ecosystem processes mediated by microbes and detritivores, and subsequent energy flow through food webs. Finally, stream meiofauna and detritivore population body size-abundance scaling relationships can deviate from the energy equivalence rule (Schmid et al., 2000, 2020) due to stochastic hydrophysical processes (i.e., the frequency of high flow events; Schmid et al., 2020) and adaptations to elevated temperature (O’Gorman et al., 2012, 2017). Thus, shifts in size spectra should be considered when making predictions about detritivore-mediated litter decomposition response to climate change.

12.5 Significance of Leaf Litter Decomposition Responses to Climate Change

12.5.1 Global C Budget

Clearly, more studies are needed to better understand the effects of biotic and abiotic factors on the temperature sensitivity of litter decomposition in order to make predictions about how rates will change with shifts in temperature. However, the studies to date indicate that elevated temperature ranging from 1 °C to 4 °C will increase rates between 5.0–21.4% based on an E_a of 0.34 eV and 10.3–47.4% based on an E_a of 0.68 eV, assuming a standard water temperature of 10 °C. Litter decomposition dominated by microbial activity converts a sizeable fraction of organic matter to CO₂, while detritivores generate large amounts of fine particulate organic C due to low assimilation efficiencies (Baldy et al., 2007; Ward et al., 1994). Similarity in the temperature sensitivity of litter decomposition mediated by microbes and total decomposition observed by Follstad Shah et al. (2017) suggests that the fractions of gaseous C loss and particulate C transport attributed to litter decomposition will not significantly change over broad scales as temperatures rise. Yet, if temperature sensitivity does indeed vary with respect to taxonomic groups or their response to different

genera of leaf litter (Boyero, Pearson, Gessner et al., 2011; Ferreira & Canhoto, 2015; Jabiol et al., 2020), then the balance between these two processes may shift in the future. These differences may be more pronounced at higher latitudes, where detritivore diversity and abundance is greater than in the tropics (Boyero, Pearson, Dudgeon et al., 2011).

Organic matter catabolism fuels heterotrophic metabolism in detrital food webs, and is thus a major component of aquatic ecosystem respiration. CO₂ produced by heterotrophic metabolism contributes about 28% of CO₂ evasion from streams and rivers under current climate conditions (Hotchkiss et al., 2015). The influence of streams and rivers on global C cycling depends upon ecosystem-level rates of both GPP and ER (Battin et al., 2008; Demars et al., 2011, 2016; Song et al., 2018). A recent data synthesis of stream metabolism studies conducted in summer (Demars et al., 2016) and models utilizing stream metabolism data collected amongst six biomes (Song et al., 2018) found that the E_a of GPP and ER is of similar magnitude (Table 12.2). Demars et al. (2016) showed that net ecosystem production (NEP; i.e., the balance between GPP and ER) is invariant with respect to temperature and inferred that CO₂ emissions from lotic ecosystems should not increase with warming when GPP and ER are tightly coupled. However, Song et al. (2018) found a rise of 1 °C in water temperature leads to a 23.6% decline in NEP because of differential responses in the ratio of GPP/ER to warming in high temperature streams with greater ratios of GPP/ER on a daily basis relative to low temperature streams with lower ratios of GPP/ER. Consequently, these authors estimated that warming will result in an increase of approximately 0.02 Pg year⁻¹ from streams similar in size to the systems studied. However, dominant sources of C to streams and stream size (including seasonal desiccation) are important factors controlling the magnitude of CO₂ emitted from lotic ecosystems (Hotchkiss et al., 2015; Keller et al., 2020). It is still unclear if the E_a of NEP in streams and rivers varies in relation to these factors, both of which are changing with alteration of global climate (del Campo et al., 2020; Gosling et al., 2017; Hattermann et al., 2017; Kominoski et al., 2020; Mcdonough et al., 2020).

12.5.2 Food Webs

Altered rates of decomposition in response to factors associated with climate change is consequential to detrital food webs, but also influenced by aquatic community responses to elevated atmospheric CO₂ concentration, warming, and hydrologic intensification (Marks, 2019; O’Gorman et al., 2012, 2017). Leaf litter can be rapidly exploited by the increased metabolic demand induced by warming, particularly in systems with limited allochthonous C inputs (Roberts et al., 2007; Rosemond et al., 2015). Increases in extreme hydrologic events (floods and droughts) and decreases in retentive structures (e.g., large woody debris) from shifts in vegetation may reduce the amount of terrestrial detritus retained in stream ecosystems and support less detritivore secondary production (del Campo et al., 2020; Kominoski et al., 2020; Tank

et al., 2010). Depletion of basal resources or changes to the quality of detritus can have cascading effects on higher trophic levels throughout aquatic food webs, manifesting as changes to biotic richness, production, nutrient cycling, and whole stream metabolism (Dudgeon et al., 2006; Estes et al., 2011; Poff et al., 2007). Similarly, loss of species or specific functional groups can significantly suppress rates of leaf litter decomposition (Bärlocher et al., 2008; Boyero et al., 2012; Handa et al., 2014; Stewart et al., 2013; Tonin et al., 2018) and limit energy flow through the food web (Graça et al., 2002; Wallace et al., 1999). However, evidence from litter-poor geothermal streams in the Hengill region of Iceland shows that concomitant shifts in warming and nutrient supply can support higher basal resource (i.e., diatom) production that allow for greater body size and biomass of higher trophic groups through altered community composition (O’Gorman et al., 2012, 2017; Nelson et al., 2017, 2020). These responses promoted patterns of litter decomposition and whole-stream metabolism temperature dependence consistent with more litter-rich systems (Demars et al., 2011, 2016; Friberg et al., 2009), suggesting maintenance of ecosystem stability despite shifts in body size-abundance scaling relationships and community composition. Thus, resource supply and its interaction with other factors of global change are important considerations affecting basal food web pathways and how they support food web dynamics.

12.6 Conclusions

It is evident that climate change factors are affecting rates of litter decomposition in streams and rivers, and subsequently influencing lotic ecosystem C budgets and food web dynamics. Elevated temperature has been more widely tested and has the most consistent effect on litter decomposition, as compared to elevated atmospheric CO₂ concentration and hydrologic intensification. However, there still exists a need to better understand each of these factors in isolation, as well as their interactions. Effects of interactions between these variables are difficult to predict across broad scales due to regional differences in climate and biogeography. No studies exist that test all three factors simultaneously relative to controls and examine the responses of both microbes and detritivores. Most studies have been conducted at small scale (e.g., laboratory experiments or short-term warming of single systems) or have used space for time substitutions (e.g., latitudinal gradients or comparisons amongst closely situated geothermal systems). Additional long-term studies of change *in situ* and simulation models are required to parse individual and interacting effects under realistic climate change conditions (O’Gorman et al., 2012). The open nature of river networks and the connectedness of streams and rivers to adjacent riparian zones requires that fluctuation in resource supply must be considered in tandem to changes in atmospheric CO₂ concentration, temperature, and hydrologic regimes.

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