

## Latitudinal patterns in leaf litter breakdown: is temperature really important?

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### SUMMARY

1. Forest stream food webs depend largely on input of dead riparian zone leaves for their energy, which is converted into living biomass by microbes, macroinvertebrates and fish.
2. Temperature has been invoked as important in controlling breakdown rates, and aquatic biologists have suggested that by normalizing processing rates to degree days rather than days, one can 'factor out' the effect of temperature and compare processing rates in streams with different thermal regimes (e.g. different seasons or study sites in different biomes).
3. We examined processing rates ( $k$ ) along a latitudinal (i.e. thermal) gradient by using reciprocal transplants of leafpacks. We placed leafpacks of ten tree species (representing a large range of leaf litter quality) in streams in Costa Rica, Michigan and Alaska using coarse-mesh (20 mm) litter bags. We then examined both the 'per day' ( $k_{\text{day}}$ ) and 'per degree day' ( $k_{\text{degree day}}$ ) models of leaf litter processing. While processing rates (per day) were fastest at the Costa Rica site (as expected), rates at the Alaska and Michigan sites were similar to each other, which we would not predict if temperature were the principal factor controlling breakdown rate. If using degree days eliminates any effect of differing thermal regimes, rates should be similar across latitudes; however, rates at the Alaska site were much faster (per degree day) than rates at the sites in Costa Rica and Michigan.
4. We compared our data with studies in the North American literature. Regression analysis of  $k_{\text{day}}$  and  $k_{\text{degree day}}$  against latitude of the study site revealed that processing rates ( $k_{\text{day}}$ ) of leaves (from a wide range of tree species in a wide range of stream types) showed no significant change with increasing latitude. However, when normalized for temperature ( $k_{\text{degree day}}$ ), a positive correlation was found between processing rates and latitude, causing us to reject the hypothesis that normalizing processing rates to cumulative degree days removes the effect of temperature.
5. We suggest three hypotheses: (i) shredding insect populations have adapted to the local thermal regime, and invertebrate-mediated processing rates are either similar between regions (showing no latitudinal pattern), or increase with latitude; (ii) microbial populations are less active at colder temperatures, and the rate of microbially mediated processing of leaf litter will show a decrease with latitude, and consequently (iii) the relative importance of invertebrate *v* microbial processing changes on a latitudinal gradient, with invertebrates being more important at high latitudes.

## Introduction

Leaf litter breakdown in mid-latitude Northern Hemisphere streams has been studied for several decades (e.g. Kaushik & Hynes, 1968, 1971; Anderson & Sedell, 1979; Webster & Benfield, 1986). Following a period of mass loss due to leaching (24–48 h), leaves in streams are colonized by decomposer microbes, primarily aquatic hyphomycetes. These microbes both degrade the leaf litter themselves, and condition the litter for macroinvertebrates by softening leaf tissue and increasing palatability and nitrogen concentration. Shredding macroinvertebrates then consume the leaf–microbe complex, further hastening the breakdown process. Factors invoked as important in controlling rates of litter breakdown include temperature, tree species, microbial abundance, shredder abundance, exposure technique, dissolved nutrients, dissolved oxygen and acidity (Webster & Benfield, 1986).

Water temperature has often been invoked as one of the most important variables controlling rates of litter breakdown (e.g. Kaushik & Hynes, 1971; Reice, 1974; Iversen, 1975; Suberkropp, Klug & Cummins 1975; Cummins, 1979; Paul, Benfield & Cairns, 1983; Barnes, McArthur & Cushing, 1986). However, litter can break down rapidly at temperatures close to or at 0°C (Short, Canton & Ward, 1980; Cowan *et al.*, 1983). Other studies have found that temperature does not explain the difference in breakdown rates between sites or seasons with differing thermal regimes (e.g. Hart & Howmiller, 1975; Griffith & Perry, 1991; Campbell *et al.*, 1992; Stewart, 1992). A number of aquatic biologists have suggested that, by normalizing breakdown (or processing) rates on a per-degree day basis rather than on a per-day basis, one can 'factor out' the effect of temperature and compare processing rates in streams with differing thermal regimes (e.g. Cummins, 1979; Hanson *et al.*, 1984; Webster & Benfield, 1986; McArthur *et al.*, 1988; Cummins *et al.*, 1989). Anomalies in this model have been noted, however, and are generally explained by differences in shredder abundance (e.g. Paul *et al.*, 1983; Short *et al.*, 1984; Griffith & Perry, 1991).

In this study, we examined the contention that rates of leaf litter breakdown in streams are temperature dependent, that is, that they vary along a latitudinal gradient. We carried out the experiment using a reciprocal transplant of leaf litter at study streams

along the latitudinal gradient from Costa Rica (tropical) to Michigan (temperate) to Alaska (subarctic). In this paper, we begin by reporting the breakdown dynamics for the three sites. We then utilize published data to explore the relationship between breakdown rate and latitude using regression analysis. Finally, we propose a conceptual model to explain the role of water temperature in determining leaf litter breakdown rates in streams.

## Materials and methods

We chose study sites in Costa Rica (CR), Michigan (MI) and Alaska (AK) that were similar to each other in stream size, depth and velocity. El Salto Creek in Costa Rica is located at 10°N latitude and 83°W longitude near the La Selva Biological Station, operated by the Organization for Tropical Studies. It is a second-order stream about 45 m above sea level, and the study site was about 2 km from the stream origin. Ford River, a third-order stream on the upper peninsula of Michigan, is located at 46°N latitude and 87°W longitude. The study site was about 25 km from the source. Monument Creek (65°N latitude, 146°W longitude) is a second-order tributary of the Chena River, near Fairbanks, Alaska; the study site was 1 km upstream from the Chena Hot Springs Resort at an elevation of about 380 m, 14 km from the stream origin. All streams had 10–30% riparian canopy, and the experimental sites were located in riffles of moderate depth and velocity (approximately 30–50 cm deep and 0.5 ms<sup>-1</sup>). Detailed study site descriptions, methods and results of the foliar chemistry aspect of the study can be found in Irons (1993).

We placed leaves of ten different tree species in each study stream. Pairs of species, one chosen to be high in condensed tannin concentration (i.e. low litter quality: Stout, 1989; Irons, Bryant & Oswood, 1991) and one low in tannin concentration (i.e. high litter quality), were collected from five locations in North and Central America (Table 1), and shipped to each study site. Twenty-five litter bags of each species (3 g of leaves, 2 cm mesh) were placed in each stream in late summer (CR, MI) or early autumn (AK), and five replicates were collected on each of five dates. Lengths of the processing studies were 84 days (CR), 112 days (MI) and 75 days (AK). Water temperature was recorded (hourly in MI and AK, daily maximum

**Table 1** Species, location of origin and collecting-investigator of leaves used in the analysis of latitudinal patterns of leaf litter processing rates. Leaf litter quality (Qual) is tabulated as species high in condensed tannin concentration (H) or species low in tannin concentration (L)

Species	Common name	Family	Collection		
			Qual	Location	Investigator
<i>Pithecellobium longifolium</i> (H. & B.) Standley	Sotacaballo	Leguminosae	H	Costa Rica	C.M. Pringle
<i>Trema micrantha</i> (L.) Blume	Capulfa	Ulmaceae	L	Costa Rica	C.M. Pringle
<i>Cornus florida</i> L.	Flowering Dogwood	Cornaceae	L	North Carolina	S.R. Reice
<i>Quercus falcata</i> Michx.	Southern Red Oak	Fagaceae	H	North Carolina	S.R. Reice
<i>Acer saccharum</i> Marshall	Sugar Maple	Aceraceae	L	New York	W.H. McDowell
<i>Fagus grandifolia</i> Ehrh.	American Beech	Fagaceae	H	New York	W.H. McDowell
<i>Alnus rugosa</i> (Du Roi) Spreng.	Tag Alder	Betulaceae	L	Michigan	R.J. Stout
<i>Quercus rubra</i> L.	Northern Red Oak	Fagaceae	H	Michigan	R.J. Stout
<i>Alnus crispa</i> (Ait.) Pursh	Green Alder	Betulaceae	L	Alaska	J.G. Irons, M.W. Oswood
<i>Salix alaxensis</i> (Anderss.) Cov.	Feltleaf Willow	Salicaceae	H	Alaska	J.G. Irons, M.W. Oswood

and minimum in CR) for determination of accumulated degree days above 0°C.

Processing coefficients were calculated using a negative exponential model:

$$M_t/M_i = (M_0/M_i)e^{-kt}$$

where  $M_i$  is the initial mass (approximately 3 g in this study),  $M_t$  is the mass remaining at time  $t$  (thus,  $M_t/M_i$  is the proportion of the initial mass remaining at time  $t$ ),  $k$  is the rate constant, and the intercept,  $M_0/M_i$ , represents the proportion of the original mass that would remain at time  $t=0$  if the mass lost to leaching were removed instantaneously. Processing coefficients were calculated by non-linear regression using SYSTAT (Wilkinson, 1990). For degree day calculations, we substituted for time ( $t$ ) the thermal sum in degree days above 0°C on the collection day (i.e. the sum of each daily mean water temperature over the period that the leafpacks were in the water). Some species were completely gone before the study period ended (especially in Costa Rica): for these species we used the first collection date with zero mass remaining as a data point, but not subsequent zero dates. Rate coefficients based on days were abbreviated  $k_{\text{day}}$  and coefficients based on thermal sums were abbreviated  $k_{\text{degree day}}$ . Breakdown rates were compared among the Alaska, Michigan and Costa Rica sites using one-way ANOVA, with *post-hoc* comparison of means provided by Scheffé's F procedure.

We tabulated breakdown rates from twenty-eight published studies (see Appendix 1), resulting in 222 estimates of  $k_{\text{day}}$  and 217 estimates of  $k_{\text{degree day}}$ . Workers investigating the breakdown of leaf litter in streams have used a variety of mathematical models to describe breakdown curves. Most have used the negative exponential model (e.g. Petersen & Cummins, 1974); however, there were several ways to fit this model. The most common differences arise when investigators either calculate an intercept ( $M_0$ ) or force the curve through 1.0. We did not attempt to correct for the use of a calculated intercept or an equation forced through  $M_0 = M_i$ . A rough estimate of  $k_{\text{degree day}}$  was often possible in those studies that did not report it: if mean daily temperature was reported, we divided  $k_{\text{day}}$  by mean temperature; if the length of the study and the total thermal sum were reported, we divided  $k_{\text{day}}$  by the ratio of degree days to days (which equals the daily mean temperature). We then compared the resulting breakdown coefficients (including our own), on both a per day and a per degree day basis, with latitude (as a correlate of temperature). All comparisons were made with regression analysis using SYSTAT (Wilkinson, 1990). We also plotted estimates of the relative proportion of mass loss attributable to microbial processing and biomass of shredders per gram of leaf material against latitude, using data obtained from several studies (Petersen & Cummins, 1974; Short & Ward, 1980; Wallace, Webster & Cuffney, 1982; Mutch

et al., 1983; Mulholland et al., 1987). This subsample of the literature was used to build a conceptual, testable model.

## Results

Leafpacks at the Alaska site accumulated only about 22 degree days above zero in 75 days, whereas those in Michigan accumulated about 950 in 112 days (Fig. 1). The Costa Rican study lasted for 84 days (2200 degree days); however, all leafpacks in the high litter quality group were completely gone by Day 28 (750 degree days) and most leafpacks in the low quality group were gone by Day 40 (1100 degree days). Although the Alaskan, and to a lesser extent, the Michigan data, fit a linear model better than an exponential one, only the negative exponential coefficients are reported here to facilitate comparisons with other studies.

The five bars on the left side of each site in Fig. 2 are species with low quality litter (from left to right: *Pithecellobium longifolium*, *Quercus falcata*, *Fagus grandifolia*, *Quercus rubra* and *Salix alaxensis*) and the five bars on the right side are species with high quality litter (from left to right: *Trema micrantha*, *Cornus florida*, *Acer saccharum*, *Alnus rugosa* and *Alnus crispa*). Processing rates, based on days (rather than degree day sums), were fastest in Costa Rica, while rates in Michigan and Alaska were similar and much lower (Fig. 2). Differences among sites were very highly significant ( $F = 9.69$ ,  $P = 0.0007$ ) with rates in Costa Rica significantly ( $P < 0.05$ ) different from those in both Michigan and Alaska which did not differ significantly from each other. Processing rates based upon degree days sums above freezing were an order of magnitude faster in Alaska than in Michigan or Costa Rica (Fig. 2). Differences among sites were very highly significant ( $F = 13.56$ ,  $P = 0.001$ )

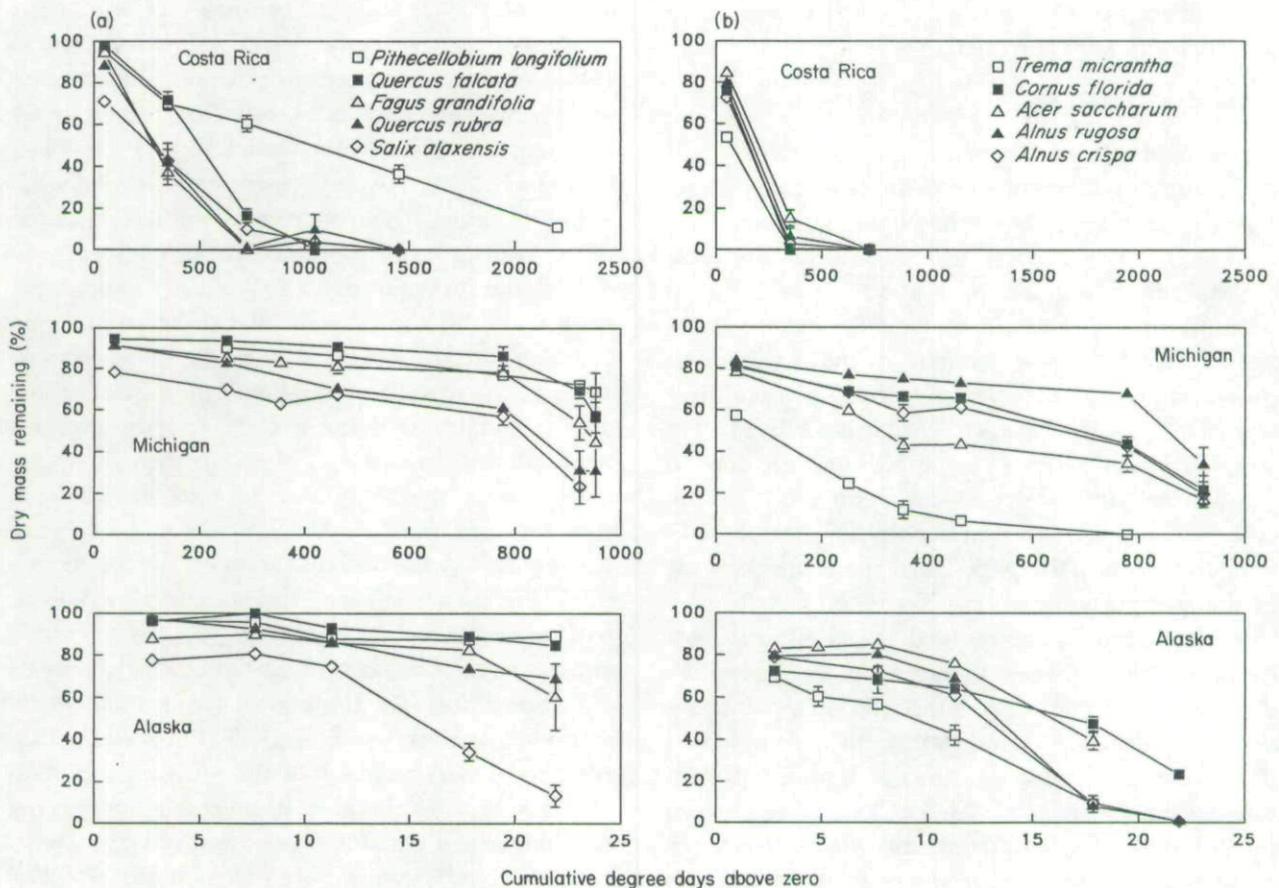


Fig. 1 Processing curves for 3 g leafpacks from (a) five tree species with low quality litter, and (b) five tree species with high quality leaf litter, in three streams of differing latitude: Costa Rica, 10°N; Michigan, 43°N; and Alaska, 65°N.

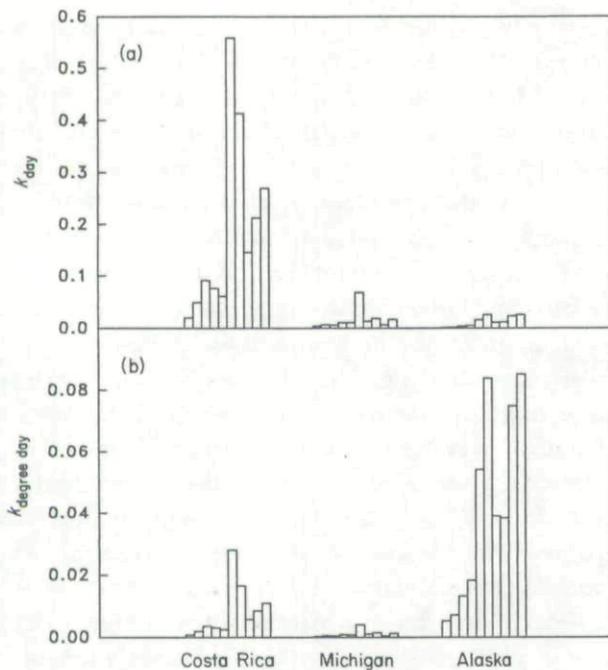


Fig. 2 Processing coefficients ( $k$ ) for the ten species and three study sites shown in Fig. 1, on (a) a per day basis, and (b) a per degree day basis.

with rates in Alaska differing from those in both Michigan and Costa Rica ( $P < 0.05$ ). Rates in Costa Rica and Michigan did not differ significantly from one another.

In Table 2, processing rates are categorized as slow,

intermediate or fast, based on days (Petersen & Cummins, 1974) and on degree days (Cummins *et al.*, 1989). When based on days, species chosen to have poor litter quality were classified as fast species in Costa Rica, but the same species were classified as slow species in Alaska (except *S. alaxensis*, which was classified as fast in Alaska). In Michigan, the low quality species ranged from slow (*P. longifolium*) to medium (*Q. falcata*, *F. grandifolia*) to fast (*Q. rubra*, *S. alaxensis*). Leaves of higher quality broke down extremely fast in Costa Rica (for some species faster than any rate that we could locate in the literature), and were also classified as fast in Alaska and Michigan. An exception was *A. rugosa*, which was classified as medium in Michigan. When compared on a degree day basis, however, patterns were different: all species were classified as fast in Alaska, most species as slow in Michigan, and all but one as fast in Costa Rica.

Using 252 processing coefficients obtained from twenty-eight studies in the literature (see Appendix 1) and this study, we found that there was a low but statistically significant ( $P = 0.033$ ) negative correlation between latitude and  $k_{\text{day}}$  that explained only 1.8% of the variance (Fig. 3a). These literature values came from more than forty tree species (with associated differences in litter quality), from permanent and intermittent streams, from a wide variety of habitats, elevations, and precipitation regimes,

**Table 2** Coefficients of leaf litter mass loss calculated on a per day and on a per degree day basis for ten species of leaves placed in streams in Alaska (Monument Creek), Michigan (Ford River) and Costa Rica (El Salto Creek) in autumn, 1988. The coefficient is the decay constant ( $k$ ) from  $M_t = M_0 e^{-kt}$ , where  $t$  is days or cumulative degree days above  $0^\circ\text{C}$ , calculated via non-linear regression. H = high quality (low tannin concentration) litter group, L = low quality litter group. Coefficients are classified as slow (S), medium (M) or fast (F); see text for explanation

Species		Processing coefficients					
		Alaska		Michigan		Costa Rica	
		$k_{\text{day}}$	$k_{\text{degree day}}$	$k_{\text{day}}$	$k_{\text{degree day}}$	$k_{\text{day}}$	$k_{\text{degree day}}$
<i>Pithecellobium</i>	L	-0.00130 S	-0.00524 F	-0.00359 S	-0.00037 S	-0.02000 F	-0.00077 S
<i>Quercus falcata</i>	L	-0.00197 S	-0.00717 F	-0.00660 M	-0.00057 S	-0.04924 F	-0.00191 F
<i>Fagus grandifolia</i>	L	-0.00372 S	-0.01321 F	-0.00569 M	-0.00049 S	-0.09144 F	-0.00361 F
<i>Quercus rubra</i>	L	-0.00499 S	-0.01830 F	-0.01058 F	-0.00093 S	-0.07721 F	-0.00303 F
<i>Salix alaxensis</i>	L	-0.01596 F	-0.05411 F	-0.01049 F	-0.00081 S	-0.06172 F	-0.00240 F
<i>Trema micrantha</i>	H	-0.02631 F	-0.08389 F	-0.06841 F	-0.00403 F	-0.55864 F	-0.02800 F
<i>Cornus florida</i>	H	-0.01100 F	-0.03906 F	-0.01342 F	-0.00102 M	-0.41317 F	-0.01653 F
<i>Acer saccharum</i>	H	-0.01172 F	-0.03838 F	-0.01877 F	-0.00143 M	-0.14513 F	-0.00578 F
<i>Alnus rugosa</i>	H	-0.02310 F	-0.07488 F	-0.00620 M	-0.00050 S	-0.21220 F	-0.00848 F
<i>Alnus crispa</i>	H	-0.02592 F	-0.08517 F	-0.01633 F	-0.00123 M	-0.26951 F	-0.01078 F

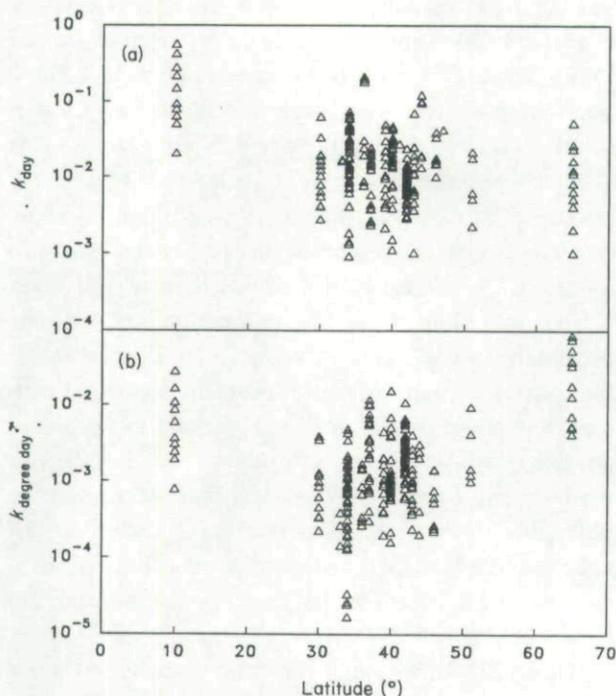


Fig. 3 Processing coefficients plotted against latitude on (a) a per day basis, and (b) a per degree day basis. Data points are from this study and twenty-eight other North American studies (see Appendix 1). Note logarithmic y-axes.

and from biomes across North and Central America. Conversely, a positive correlation ( $P < 0.00001$ , explaining 16.4% of the variance) was found between latitude and  $k_{\text{degree day}}$  (Fig. 3b). Because of the leverage exerted by the ten points from Costa Rica and the ten points from Alaska, we also ran the regression analyses excluding the data points from our study (resulting in  $n = 222$ ). The resulting regression based on  $k_{\text{day}}$  was not significant ( $P = 0.228$ ); however, the regression based on  $k_{\text{degree day}}$  was significant ( $P < 0.00001$ ). Thus, rather than the expected relationship of a negative correlation between  $k_{\text{day}}$  and latitude (i.e. slower breakdown with increasing latitude and decreasing temperature), which one would expect if temperature is a determining variable in leaf litter breakdown, little or no correlation was found. Conversely, when the regressions were based on thermal sums rather than elapsed time, a positive correlation was apparent between latitude and breakdown rate.

Several studies done at different latitudes have estimated the relative contributions of microbes and shredding macroinvertebrates to leaf litter pro-

cessing in streams (e.g. Petersen & Cummins, 1974; Short & Ward, 1980; Wallace *et al.*, 1982; Mutch *et al.*, 1983; Mulholland *et al.*, 1987). As one goes farther north and probably to higher elevations, the relative contribution of microbes to leaf litter breakdown decreases, and the biomass of shredders found on leafpacks increases (Fig. 4). We feel that a testable model regarding the relative contributions of microbial and invertebrate processing to leaf litter breakdown can be built from these trends. We propose the following: the absolute amount of leaf litter that is processed by macroinvertebrate shredders in a given time period increases with increasing latitude and elevation (and hence decreasing thermal resources). Conversely, the absolute amount of microbial processing of leaf litter decreases with latitude and elevation and decreasing thermal resources. When these two trends are combined, the rate of processing per day ( $k_{\text{day}}$ ) becomes a function of latitude that declines steeply at first, and then plateaus or increases at higher latitudes (Fig. 5). Such a model would result in the patterns of breakdown rates seen in Fig. 2(a).

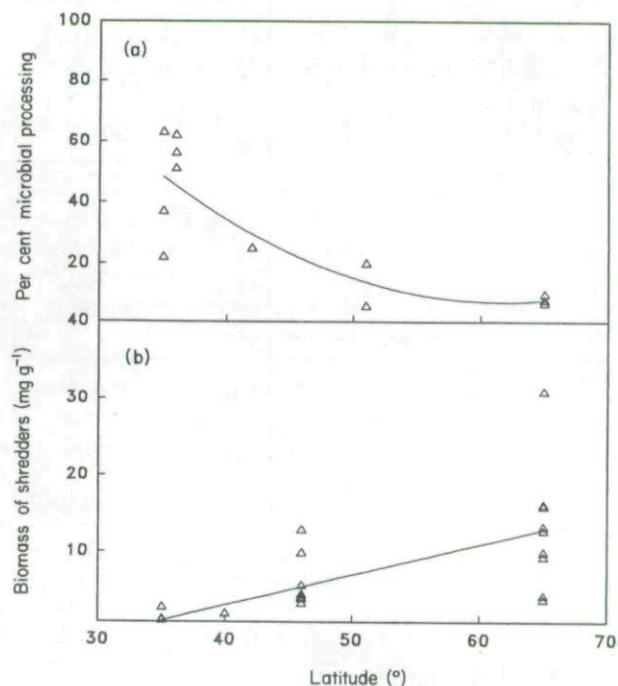


Fig. 4 (a) The percentage of total leaf litter breakdown attributable to microbial processing along a latitudinal gradient. (b) Biomass of shredders on leafpacks on a per gram of leaf material remaining basis. Data were taken from several studies in the literature (see Results for references).

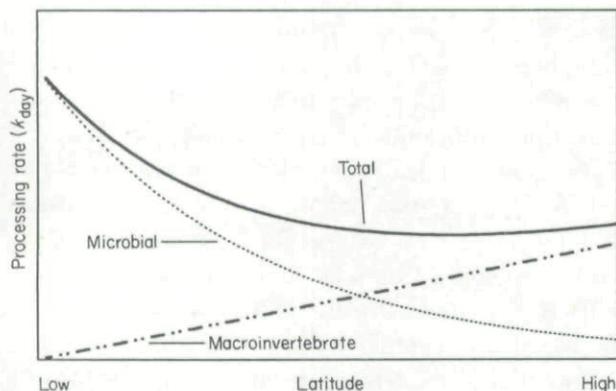


Fig. 5 Conceptual model of the relative contributions of microbial and invertebrate processing to total leaf litter breakdown rates on a per day basis.

## Discussion

Latitudinal gradients have long been noted by ecologists, both on a continental (e.g. Pianka, 1966, 1978; MacArthur, 1972; Schall & Pianka, 1978) and a regional scale (e.g. MacLean, 1975; MacLean & Hodkinson, 1980). Gradients have been shown to exist in such traits as species richness and abundance, primary productivity, and body size of conspecific and congeneric taxa. Hypotheses advanced to explain these phenomena include time since glaciation, climate and intensity of competition (Pianka, 1966). While the mechanisms generating these gradients remain hotly debated (temperature remains a leading contender), all agree that temperature is well correlated with latitude. This enables latitude to be used as a correlate of the long-term (e.g. evolutionary time scale) thermal regime of a region.

Water temperature has been cited widely as an important controlling variable for stream ecosystem processes, including the evolution and ecology of aquatic insects (e.g. Vannote & Sweeney, 1980; Ward & Stanford, 1982), microbial dynamics (Suberkropp & Klug, 1976), and leaf litter breakdown rates (Kaushik & Hynes, 1971; Anderson & Sedell, 1979; Webster & Benfield, 1986). The effect of differing thermal regimes in space and time on leaf litter breakdown in streams has been well documented. For instance, there is often a very strong correlation between water temperature and rates of leaf litter breakdown in field (Reice, 1974; Hart & Howmiller, 1975; Iversen, 1975, 1980; Hildrew *et al.*, 1984) and laboratory studies

(Hynes & Kaushik, 1969; Kaushik & Hynes 1971; Suberkropp *et al.*, 1975).

Conversely, many studies have shown that temperature is not necessarily the overriding controlling factor. Mass loss rates of leaves in cold streams at high altitude (Short *et al.*, 1980) and high latitude (Cowan *et al.*, 1983) are as high as or higher than breakdown rates of similar species in warmer streams. Decomposer microbes have been shown to grow actively and respire at temperatures very close to freezing (Bärlocher & Kendrick, 1974; Buttimore *et al.*, 1984). Processing rates calculated on a degree day basis are often faster at colder water temperatures than at warmer ones (Cummins, 1979; Short & Ward, 1980; Paul *et al.*, 1983; Short *et al.*, 1984). Some authors have attempted to explain this 'anomaly' by suggesting that the shredder community is more depauperate in warmer waters, e.g. below an impoundment (Cummins, 1979; Short & Ward, 1980), in streams of early successional forests (Griffith & Perry, 1991), and in prairie streams of Texas (Short *et al.*, 1984). Suberkropp, Godshalk & Klug (1976) expected to find an increase in processing rates as stream temperatures warmed in spring, and attributed the lack of such an increase to the accumulation of refractory compounds in leaves, overriding the temperature effect.

Aquatic insects in several orders, especially those with many species of shredders, may have evolved in cool running waters (e.g. Hynes, 1970; Edmunds, 1972; Wiggins, 1977). Webster & Benfield (1986) suggested that temperature affects primarily 'microbial processes', and that invertebrates seem to be less affected, so that the relative effect of invertebrate feeding may at times overshadow the role of microbes in leaf litter breakdown. Some other studies corroborate this suggestion: breakdown rates of litter in two southern African streams were much more rapid in the stream with an abundant shredder fauna (Stewart, 1992). Likewise, elimination of shredders by insecticide in an Appalachian Mountain stream reduced breakdown rates (Wallace *et al.*, 1982). We suggest that the 'anomalous' results mentioned above be taken at face value, and that the reason that conclusions differ between studies is in part a function of the relative roles of microbes and macroinvertebrate shredders.

Cummins *et al.* (1989) proposed a model that included 'categorization of riparian plant communities

on the basis of temperature-specific, in-stream processing rates of their litter'. The categories proposed for breakdown rates (fast species:  $k_{\text{degree day}} > 0.0015$ , medium:  $0.001 < k_{\text{degree day}} < 0.0015$ , and slow:  $k_{\text{degree day}} < 0.001$ ) were considered to be 'transferable between streams in different watersheds, in different biomes, and on different continents'. We suggest that this is not the case. When leaves of the same ten tree species were tested in three different biomes (tropical, temperate and subarctic) in the present study, processing rates on a degree day basis differed. One would expect that processing rates ( $k_{\text{degree day}}$ ) of the same species would fall into the same processing category if the temperature-specific processing rate model is valid; however, most individual leaf species in our transfer experiment spanned the range from slow to fast (Table 2).

We propose a slightly different model. We suggest that, while temperature has an important influence on processing rates within an individual stream or geographical location, different biological processes operate at different efficiencies or rates in widely separated areas with differing biotas and thermal regimes. Thus, the microbial and insect components of litter breakdown may be influenced by temperature in different ways in different biomes, because of their differing evolutionary histories. It is readily apparent that, when using degree days as the independent variable, rates at the subarctic Alaska site were at least an order of magnitude faster than those at the temperate Michigan and tropical Costa Rica sites (Fig. 2). When comparing differing thermal regimes within a region, studies of biotic processes are drawing from the same pool of microbes and shredders, which are presumably adapted to the long-term thermal regime of the area. On the other hand, studies such as ours that compare differing thermal regimes across broad biogeographic regions are drawing their decomposer flora and fauna from species variously adapted to the local climate of each biogeographic region.

Macroinvertebrates are generally well adapted to the thermal regimes of their parent streams, and shredders adapted to high latitude or high altitude conditions can process leaf litter at temperatures very close to freezing (Short *et al.*, 1980; Cowan *et al.*, 1983; this study). Indeed, shredder abundance on leafpacks showed an increase with increasing latitude (and decreasing thermal regime) at the three sites in this

study, both in numbers and biomass (Stout *et al.*, unpublished data). The microbial community, on the other hand, appears to be less able to process leaf inputs efficiently at colder water temperatures. The amount of leaf litter mass loss attributable to microbial respiration in Monument Creek, Alaska is only about 10% or less (Buttimore *et al.*, 1984), and most mass loss was therefore assumed to be related to shredder activity (Cowan *et al.*, 1983). In Michigan, Petersen, Cummins & Ward (1989) found that shredders contributed only about 10% to total leaf processing, whereas in the southern Appalachian Mountains of North Carolina the equivalent fraction was 27% (Webster, 1983). At a given water temperature, respiration of the Alaskan microbial community was much lower than that in temperate regions, although respiration continued at temperatures very close to freezing (Buttimore *et al.*, 1984). Thus, it appears that latitudinal gradients in leaf litter processing rates are related to the proportion of mass loss attributable to microbial decomposition relative to the amount attributable to macroinvertebrate feeding.

These preliminary results suggest several testable hypotheses.

1 Shredder insect populations are evolutionarily adapted to the thermal regimes found in cool running waters (their habitat of origin), and insect-mediated processing rates for a given plant species either (i) increase with increasing latitude or (ii) show no latitudinal pattern.

2 Microbial populations are physiologically less able to maintain optimal metabolic rates at colder temperatures, and the rate of microbially mediated processing of leaf litter will decrease with increasing latitude.

3 Consequently (all other factors being equal), the relative importance of invertebrate *v* microbial processing changes on a latitudinal gradient, with invertebrates being more important in the colder waters of high latitudes and high altitudes.

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#### Appendix 1 Citations for the twenty-eight studies used in latitudinal gradient analyses

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