Ecology, 82(4), 2001, pp. 955–964

SOIL FAUNA AND PLANT LITTER DECOMPOSITION IN TROPICAL AND SUBALPINE FORESTS

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Abstract. The decomposition of plant residues is influenced by their chemical composition, the physical–chemical environment, and the decomposer organisms. Most studies interested in latitudinal gradients of decomposition have focused on substrate quality and climate effects on decomposition, and have excluded explicit recognition of the soil organisms involved in the process. To test whether soil fauna exhibit different effects under diverse climates or substrates, we quantified decomposition rates and N fluxes in control and fauna-excluded treatments with litterbags containing relatively high-quality (*Quercus gambelii*) and low-quality (*Cecropia scheberiana*) litter in sites representing large differences in climate as measured by AET (actual evapotranspiration). Two subtropical sites included a wet and a dry forest, and two temperate sites included north- and south-facing subalpine forests. We found that: (1) all three factors (climate, substrate quality, and soil fauna) independently influenced the decomposition rate of plant litter in the tropical and subalpine forests; (2) faunal effects on decomposition rates and N mineralization of *Q. gambelii* and *C. scheberiana* were consistently higher in the tropical wet forest than in the tropical dry and subalpine forests; (3) there was no significant interaction of fauna and litter species on the annual decay rates; and (4) the density (numbers per gram of dry litter) of total fauna was highest in the tropical wet forest, intermediate in the subalpine forests, and lowest in the tropical dry forest. Our results indicate that soil fauna have a disproportionately larger effect on litter decomposition in a tropical wet forest than in a tropical dry or a subalpine forest. The annual decay rates of *Q. gambelii* and *C. scheberiana* are not influenced differentially by the soil fauna in the tropical and subalpine forests.

Key words: Cecropia scheberiana; *dry tropics; invertebrates; litter decomposition; naphthalene;* Quercus gambelii; *soil fauna; subalpine; wet tropics.*

INTRODUCTION

Most of the aboveground net primary production of terrestrial ecosystems is returned to the soil as plant litter (Coleman and Crossley 1996). The decomposition of these plant residues is influenced by the substrate quality, the physical–chemical environment, and the decomposer organisms (Swift et al. 1979). Substrate quality affects the decomposability of plant litter based on its chemical composition (e.g., Melillo et al. 1982, Palm and Sánchez 1991, Tian et al. 1997, Cotrufo et al. 1998). Physical–chemical conditions include both climate and soil parent material and help to determine abiotic soil characteristics, which, in turn, influence litter quality and ultimately the activity and composition of microbial and invertebrate communities (Wardle and Lavelle 1997). Although decomposition is mainly the result of microbial activities, soil fauna are important in conditioning the litter and in stimulating microbial actions (Coleman and Crossley 1996).

Working at regional scales, Meentemeyer (1978) found a dual control by climate and substrate quality on litter decomposition rates, using actual evapotranspiration (AET) as a measure of the concurrent availability of energy and moisture to an ecosystem, and lignin concentration as a litter quality index. Since then, most studies interested in latitudinal gradients of decomposition have focused on substrate quality and climate effects on decomposition, and have excluded explicit recognition of soil organisms in the process. For example, ecosystem models such as CENTURY (Parton et al. 1987) or GEM (Rastetter et al. 1991) use substrate quality and various indices of climate to predict decomposition. Coûteaux et al. (1995) considered climate as the dominant factor influencing decomposition in areas subjected to unfavorable (dry and cold) weather conditions, whereas litter quality was the prevailing regulator under favorable (wet and warm) conditions. The Coûteaux et al. (1995) interpretation of the controls of decomposition is concordant with the Meentemeyer (1978) model, as both identify the same causal mechanisms for decay.

All of these approaches have known limitations because they implicitly assume that the biota, the organisms responsible for decomposition, are totally constrained by climate and substrate quality characteristics. The pattern observed in the composition and abun-

Manuscript received 21 June 1999; revised 13 March 2000; accepted 16 March 2000.

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dance of the decomposer fauna would suggest that this is not the case, as the abundance and diversity of various soil fauna also change with latitude (Swift et al. 1979). In fact, the hierarchy of the determinants of decomposition might be different in temperate and tropical ecosystems (Lavelle et al. 1993). In tropical ecosystems, climatic determinants are likely to be less important than biological regulation by soil macrofauna. We know that decay in cold regions is limited by the respiration constraints of temperature on decomposers, but the reduction in functional diversity of decomposer organisms may also be an important factor to consider when evaluating decomposition rates along latitudinal gradients. Similarly, the strong controls by substrate quality on decomposition in mild climates may also be consistent with enhanced selective feeding of a more diverse decomposer community in these areas.

A large volume of literature has accumulated on the independent effects of substrate quality, climate, and fauna on litter decomposition, but field studies taking into account interactions among the three factors have not been reported. This study examines the influence of soil fauna on litter decomposition in tropical and temperate ecosystems, and tests whether the decomposer fauna exhibit different effects under diverse climates or substrates. We hypothesized that: (1) fauna will have a disproportionately larger effect on the litter decomposition rates in tropical forests where macroinvertebrates are common than in subalpine forests where these components of the fauna are rare; and (2) fauna are relatively more important in the decomposition of low-quality substrates (high in lignin) than in the decomposition of high-quality substrates (low in lignin).

Methods

Study sites

Four sites representing large differences in climate as measured by AET were chosen in the summer of 1997: two subtropical sites that included a wet and a dry forest, and two temperate sites that included north- and south-facing subalpine forests. The subtropical wet forest is located in the Luquillo Experimental Forest, LEF (18°20′ N, 65°49′ W), and the subtropical dry forest is located in the Guánica Biosphere Reserve (17°57′ N, 65°52′ W) of Puerto Rico. Annual air temperature in Luquillo is 22.3°C (Brown et al. 1983) and mean annual precipitation is 3524 mm (García-Martinó et al. 1996), with rainfall distributed more or less evenly throughout the year. Vegetation at this elevation (420 m) is called tabonuco forest, after the dominant plant species *Dacryodes excelsa* Vahl. (Zimmerman et al. 1995). The dominant soils are moderately well drained Oxisols of volcanic and sedimentary origin (Soil Survey Staff 1995). Detailed descriptions of the geomorphology, vegetation, and soils in the LEF can be found in Scatena and Lugo (1995). Annual air temperature in Guánica is 25.1°C and average precipitation is 860 mm. Elevation is 160 m and the plant communities are typical of a semideciduous forest (Murphy and Lugo 1986). Soils have developed from limestone bedrock and are categorized as stony, shallow, and dry (Carter 1965). AET values for the study period (July 1997–January 1999) in the LEF and Guánica forests were 1342 and 891 mm, respectively. Detailed descriptions of the forest structure and nutrient dynamics in Guánica can be found in Lugo and Murphy (1986) and Farnsworth (1993). The temperate north- and south-facing subalpine forests are located in Niwot Ridge, NWT (40°03′ N, 105°36′ W), 50 km west of Boulder, Colorado, USA, on the eastern slope of the Rocky Mountains. Both LEF and NWT are part of the Long Term Ecological Research (LTER) network. The subalpine sites are at an elevation of ~ 3400 m. Annual air temperature is 1.3°C and average precipitation is 692 mm (Greenland 1989). Vegetation is dominated by lodgepole pine *Pinus contorta* var. *latifolia* Engel. (Marr 1961), and soils are shallow and coarse textured (Johnson and Cline 1965). Peet (1981) has provided extensive descriptions of the vegetation and soils of the subalpine forests. The AET value for the study period was 320 mm for the subalpine forests.

Experimental design

Within each of the four sites (tropical wet and dry, and north- and south-facing subalpine forests), we established a randomized block design of four blocks with two plots within each block. Plots were 0.8 × 1.5 m in the tropics and 0.8 × 0.8 m in the subalpine forests. Two treatments (fauna excluded vs. control) were randomly assigned to the plots of each of the four blocks. In total, eight plots were established within each site (four fauna excluded and four controls). Fauna-excluded plots were created by (1) removing the litter; (2) sieving and removing the macroinvertebrates from the soil to a depth of ~ 20 cm; (3) placing a weed/gardening liner, before replacing the litter and soil, to prevent immigration of soil fauna into the plot from the bottom and sides; (4) placing an aluminum fence (15 cm tall) around the plot; and (5) using naphthalene, an arthropod repellent, to prevent recolonization of the litter in the plot. The gardening liner permitted oxygen and water exchange between the soils on either side of the liner, so no difference in moisture condition was visible in the plots as compared to the surrounding soil. Naphthalene flakes were applied at a rate of 100 g/m^2 every 2 wk in the tropics. Naphthalene application in the subalpine sites was stopped during the winter months because evaporation of naphthalene under the snow is negligible (G. González, *personal observation*). Control plots had (1) the litter removed, (2) the soil sieved, (3) the liner, and (4) the fence, but all macroinvertebrates were left within the plots and naphthalene was not applied. Vertical migrations of fauna in the control treatment could have been inhibited by

TABLE 1. Initial percentage composition of cellulose, lignin, carbon, and nitrogen, and carbon : nitrogen and lignin : nitrogen ratios of *Quercus gambelii* and *Cecropia scheberiana* leaves contained in litterbags.

Litter species	Cellulose	Lignin†	C	N†	C : N	Lignin : N
Q. gambelii	41.16 (1.16)	19.95 (0.37)	48.84 (0.01)	0.77 (0.002)	63.58 (1.58)	25.96 (0.71)
C. scheberiana	46.12 (1.20)	34.59 (0.96)	46.13 (0.29)	1.31 (0.005)	35.56 (1.21)	26.65 (1.14)
F‡	8.78**	272.18***	80.21***	135.09***	197.39***	0.26

Note: Values are means (± 1 SE); $n = 8$.
** $P \leq 0.01$; *** $P \leq 0.001$.
† Statistics were performed on the log-transformed data.
‡ F values (all df = 1, 14) were calculated for mean differences between litter species (one-way ANOVA).

the liner. If that occurred here, then faunal contributions to decomposition rates would be underestimated by this study. This procedure is a modification of previous plot experiments by Seastedt and Crossley (1981) and Heneghan et al. (1999). Two species of foliar litter, of varying substrate quality, were compared across the four sites. *Cecropia scheberiana* Miq. (yagrumo) leaves have a higher concentration of extractable-free residues (e.g., cellulose and lignin) than *Quercus gambelii* Nuttall (scrub oak) leaves (Table 1). Therefore, *Quercus gambelii* was used as a relatively high-quality litter and *Cecropia scheberiana* as a relatively low-quality litter. Neither species was native to the research sites used here.

Litterbags

Recently senesced leaves of *Q. gambelii* and *C. scheberiana* were collected in the fall of 1996 at Roxborough Park in Colorado and at LEF in Puerto Rico from the forest floor, respectively. Measured amounts of ~ 3 g of *Q. gambelii* and 5 g of *C. scheberiana* air-dried leaves were placed separately in 16 × 16 cm fiberglass litterbags (1.8 × 1.6 mm mesh). This mesh size prevents the loss of litter fragments and does not inhibit indirect effects of earthworms casts. In the summer of 1997, we placed a total of 832 litterbags in the field: 544 litterbags in the tropical and 288 litterbags in the subalpine sites. A subsample of 64 litterbags (16 litterbags per site, eight each of *Quercus* and *Cecropia*) was collected and returned to the laboratory immediately after placement in the field. These bags were oven-dried at 60°C to establish handling loss, dry mass relations, initial organic-chemical composition, and C and N concentrations (e.g., Seastedt et al. 1992). From July 1997 to January 1999, litterbags were collected randomly from each of the tropical and subalpine plots every 2–3 mo and every 5–6 mo, respectively ($n = 2$ bags per species per plot per date). Litter retrieved from litterbags at 272 d and 528 d was analyzed for total C and N. Litterbags placed on the Tullgren extractor were oven-dried (60°C) and reweighed to determine the remaining mass after faunal removal.

The carbon fractions of the plant litter were determined by the forest products determination technique (Ryan et al. 1990). During this technique, litter samples are analyzed with a series of digestions in which fats, sugars, cellulose, and lignin are determined gravimetrically. These fractions were not corrected for ash content because ash seems to be removed in proportion with mass loss during the extraction steps (Newman et al. 1994). Total carbon and nitrogen concentrations of the plant litter were determined by using a Fisons 1108 CHN Elemental Analyzer (Fisons, Milan, Italy).

Faunal extractions

A subset of four litterbags per site per collecting date was placed in modified Tullgren extractors. This extraction technique removes mites and collembolans from the litterbags and also allows for a conservative estimate of other microarthropods (e.g., Protura, Psocoptera, Zoraptera, pseudoscorpions, diplopods, chilopods, etc.). Fauna were classified as Cryptostigmata, Mesostigmata, Prostigmata (suborders, Acarina), Collembola (springtails) and other microarthropods. Faunal densities were calculated per gram of dry litter at the time of sampling. Earthworms were hand-sorted from the soil within each plot at the end of the experiment. Dry mass values for earthworms were obtained after worms were rinsed with water, freeze-killed, and oven-dried at 70°C for 72 h.

Data analysis

Data were tested for homogeneity of variance by using the Levene's test of equality of error variances, and skewness (SPSS 1998). Log transformations were employed when the data did not meet the assumptions of normality. Mass loss and N concentration data were used to calculate changes in the absolute amount of N (net immobilization or mineralization). Annual decomposition rates (k) were calculated using a single negative exponential decay model (Olson 1963) by regressing the natural logarithm of the mean percentage of mass remaining per plot vs. time. Although this model does not always provide a "best fit" description of the data, it allowed us to use all of the data from a single plot to calculate an average decay rate. This produced four replicate estimates of decay for each treatment of each litter species at each site.

Mean differences in initial nutrient concentrations and lignin and cellulose percentage between *Q. gambelii* and *C. scheberiana* leaves were analyzed by a one-way ANOVA using the general linear model

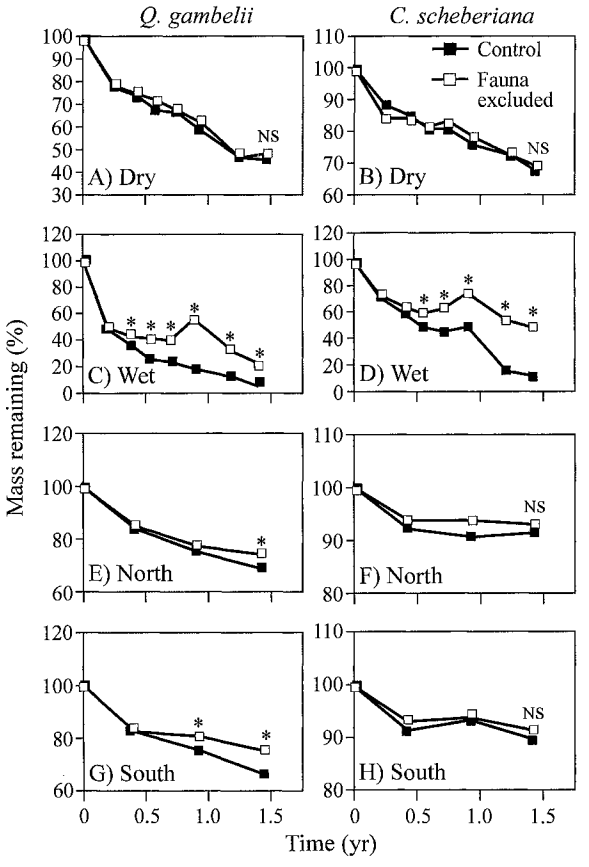

FIG. 1. Changes in the mass of *Quercus gambelii* and *Cecropia scheberiana* litter in tropical dry (A–B) and wet (C–D) forests, and in north-facing (E–F) and south-facing (G–H) subalpine forests. Asterisks indicate a significant treatment effect within a site and day; NS indicates no significant effect (one-way ANOVA; $\alpha = 0.05$).

(GLM) procedure. ANOVA was used to determine the significance of the three main factors (fauna exclusion treatment, site, and litter species) and their interactions on the annual decay rates (dependent variable). The effects of fauna and forest site (independent variables) on the C and N (percentage) concentrations, the C:N ratio, and the decay rates (k) of *Q. gambelii* and *C. scheberiana* (dependent variables) were tested with two-way ANOVAs. The SNK (Student-Neuman-Keuls) test was used to compare forest site means ($\alpha = 0.05$) within each litter type (SAS 1987).

Faunal effects on decomposition were quantified by using the formula adapted from Seastedt (1984): Faunal effect = $L_{\text{fauna}}/L_{\text{total}}$, where L_{fauna} is the percentage of litter mass loss resulting from all direct and indirect faunal activities, and obtained from the difference of the litter mass loss in the control and fauna-excluded plots. L_{total} is the percentage of litter mass loss obtained from the control plots, and recognizes abiotic, microbial, and faunal effects. A MANOVA (GLM) was used to evaluate the effects of treatment, site, and litter species on the density of major groups of fauna (SPPS 1998).

RESULTS

After 1.5 yr, *Quercus gambelii* showed significant differences ($P < 0.05$) in the percentage of mass remaining between the control and fauna exclusion treatments in the tropical wet and the subalpine forests (Fig. 1). *Cecropia scheberiana* showed consistent significant differences ($P < 0.05$) in the percentage of mass remaining between the control and fauna exclusion treatments after 0.5 yr in the tropical wet forest (Fig. 1D). Litter mass losses were more rapid in the control than in the fauna-excluded treatment.

There was a significant effect of site on the final N concentration and C:N ratio of *Q. gambelii* and *C. scheberiana* (Table 2). On average, the final N concentration of both litter species was higher in the tropical than in the subalpine forests, whereas the C:N ratio was sig-

TABLE 2. Carbon and nitrogen concentration (%), and carbon : nitrogen ratios of *Quercus gambelii* and *Cecropia scheberiana* litter in control and fauna-excluded treatments after 1.5 yr in the field.

Site type	Control			Fauna excluded		
	C	N†	C:N	C	N	C:N
Q. gambelii						
Tropical, dry	$46.9^{a} \pm 1.0$	$1.6^{ab} \pm 0.1$	$28.7^{bc} \pm 1.3$	$48.3^{a} \pm 0.6$	$1.8^{a} \pm 0.1$	$26.7^{c} \pm 1.9$
Tropical, wet	$44.5^{a} \pm 2.2$	$1.9^{a} \pm 0.5$	$23.8^{c*} \pm 0.7$	$49.5^{a} \pm 0.4$	$1.8^{a} \pm 0.1$	$27.8^{bc} \pm 1.1$
Subalpine, north	$49.4^{a} \pm 0.3$	$1.4^{bc} \pm 0.0$	$34.4^{ab} \pm 1.2$	$49.6^{a} \pm 0.2$	$1.2^{b} \pm 0.1$	$40.0^{ab} \pm 2.3$
Subalpine, south	$49.6^{a} \pm 0.3$	$1.3^{c} \pm 0.1$	$39.0^{a} \pm 3.5$	$49.9^{a} \pm 0.2$	$1.2^{b} \pm 0.1$	$40.4^{a} \pm 3.1$
C. scheberiana						
Tropical, dry	$45.7^{a} \pm 1.2$	$2.3^{a} \pm 0.3$	$20.7^{b} \pm 2.5$	$46.0^{a} \pm 0.3$	$2.4^{a} \pm 0.3$	$19.9^{b} \pm 2.4$
Tropical, wet	$41.0^{a} \pm 2.9$	$2.1^{a} \pm 0.1$	$19.7^{b*} \pm 0.3$	$47.1^{a} \pm 2.6$	$2.2^{ab} \pm 0.1$	$21.3^{b} \pm 0.4$
Subalpine, north	$47.0^{a} \pm 0.7$	$1.4^{b} \pm 0.1$	$33.5^{a} \pm 1.6$	$47.0^{a} \pm 0.4$	$1.6^{b} \pm 0.1$	$29.4^{a} \pm 2.5$
Subalpine, south	$45.8^{a*} \pm 0.7$	$1.5^{b} \pm 0.1$	$30.9^{a} \pm 1.5$	$48.0^{a} \pm 0.4$	$1.6^{b} \pm 0.1$	$29.6^{a} \pm 2.0$

Note: Values are means ± 1 SE ($n = 4$). Common superscript letters within a column and litter species indicate no significant difference among sites using SNK (Student-Neuman-Keuls) tests; $\alpha = 0.05$.

* Significant within-site treatment effect (one-way ANOVA; $\alpha = 0.05$).

† Statistical tests were performed on log-transformed data.

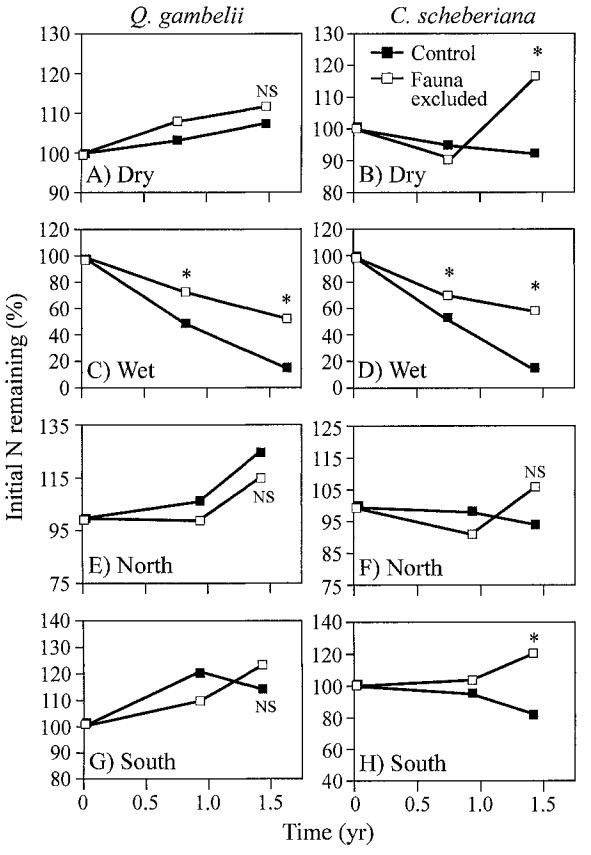

FIG. 2. Changes in absolute amounts of nitrogen in *Quercus gambelii* and *Cecropia scheberiana* litter in tropical dry (A–B) and wet (C–D) forests, and in north-facing (E–F) and south-facing (G–H) subalpine forests. Asterisks indicate a significant treatment effect within a site and day; NS indicates no significant effect (one-way ANOVA; $\alpha = 0.05$).

nificantly higher in the latter. There was a significant treatment effect on the C:N ratio of *Q. gambelii* and *C. scheberiana* in the tropical wet forest. The C:N ratio was significantly higher in the fauna-excluded treatment than in the control. Both litter species exhibited a net immobilization of N above 100% of the initial amount during decomposition in all sites except the tropical wet forest (Fig. 2). *Q. gambelii* showed a significant difference in the percentage of initial N remaining between treatment means in the tropical wet forest. After 1.5 yr, *C. scheberiana* showed significant differences in the percentage of initial N remaining between treatment means in the tropics and the south-facing subalpine forest. Net N loss was enhanced in the control as compared to the fauna-excluded treatment (Fig. 2).

Annual decay rates showed significant differences between litter species, treatments, and among-site means (Table 3). There was a significant treatment and site interaction, but no interaction between fauna and litter species on the annual decay rates. On average, *Q. gambelii* decayed faster than *C. scheberiana*. In the presence of fauna, mean annual decay rates (k) of *Q. gambelii* and *C. scheberiana* were significantly higher in the tropical wet forest than in the tropical dry and the subalpine forests. However, in the fauna-excluded treatment, both litter species decayed faster in the tropical than in the subalpine forests, and the differences in decayed rates (k) between the two tropical or the two subalpine forests were notably reduced (Table 4). Annual decay rates of *Q. gambelii* and *C. scheberiana* were, on average, reduced by a factor of 2.5 and 5, respectively, in the absence of fauna as compared to the control treatment. Both litter species decayed significantly faster in the control than in the fauna-excluded treatment in the tropical wet forest. *Q. gambelii* also decayed significantly faster in the control than in the fauna-excluded treatment in the north-facing subalpine forest (Table 4). The faunal effect on the decomposition of both litter species was highest in the tropical wet forest and lowest in the tropical dry forest (Table 4).

A comparison of the density of the major groups of mites, collembolans, and other microarthropods among sites in the litterbags from control plots demonstrated that: (1) the density of oribatid (Cryptostigmata) and mesostigmatid mites was highest in the tropical wet forest (see Plate 1); (2) prostigmatid mites and collembolans were significantly more abundant in the subalpine than in the tropical sites; (3) the density of other microarthropods was highest in the tropical wet forest; and (4) the density of total litter fauna was highest in the tropical wet forest, intermediate in the subalpine forests, and lowest in the tropical dry forest (Table 5). The abundance of other microarthropods (a category that excludes mites and collembolans) and total litter fauna was significantly reduced in the fauna-excluded treatments of all forests. Litter species did not have an influence on the density of mites, collembolans, or total litter fauna (Table 6). The density of these groups of litter fauna showed significant differences among sites and between treatments, and there was a significant interaction of treatment and site. By the end of the experiment, earthworms were found only in the tropical wet forest. For *Pontoscolex corethrurus*, the only worm

TABLE 3. Results of a three-way ANOVA for the effects of fauna, forest site, and litter species on the annual decomposition rate, k.

Source	df	F	P
Fauna (F)	1	102.54	< 0.001
Site (S)	3	184.84	< 0.001
Litter (L)	1	30.57	< 0.001
F × S	3	81.98	< 0.001
F × L	1	0.02	0.88
S × L	3	1.26	0.30
F × S × L	3	0.60	0.62
Error	48		

Note: $n = 64$; $R^2 = 0.95$.

TABLE 4. Mean decay rates (k) for *Quercus gambelii* and *Cecropia scheberiana* litter from a single negative exponential model in control and fauna-excluded treatments over a period of 1.5 yr in the field.

Site type	Control		Fauna excluded		Faunal effect (%)
	k	r^2†	k	r^2†	
Q. gambelii					
Tropical, dry	$-0.493^{b} \pm 0.03$	0.92	$-0.483^{a} \pm 0.03$	0.90	1.6
Tropical, wet	$-1.986^{a*} \pm 0.22$	0.84	$-0.642^{a} \pm 0.15$	0.63	45.2
Subalpine, north	$-0.207^{b*} \pm 0.02$	0.93	$-0.130^{b} \pm 0.02$	0.77	35.6
Subalpine, south	$-0.170^{b} \pm 0.04$	0.93	$-0.097^{b} \pm 0.01$	0.82	39.1
C. scheberiana					
Tropical, dry	$-0.226^{b} \pm 0.05$	0.63	$-0.171^{b} \pm 0.04$	0.66	23.9
Tropical, wet	$-1.465^{a*} \pm 0.32$	0.87	$-0.305^{a} \pm 0.05$	0.61	66.2
Subalpine, north	$-0.022^{b} \pm 0.01$	0.38	$-0.011^{c} \pm 0.00$	0.54	49.8
Subalpine, south	$-0.024^{b} \pm 0.01$	0.59	$-0.021^{c} \pm 0.00$	0.71	12.4

Notes: Values are means ± 1 SE (n = 4). Common superscript letters within a column and litter species indicate no significant difference among sites (SNK, α = 0.05).

* Significant within-site treatment effect (one-way ANOVA; α = 0.05).

† Coefficients of determination indicate goodness of fit of the data to the model.

species found, the mean density was 26 worms/m^2 and the mean dry mass was 2.04 g/m^2.

Annual decay rates of *Q. gambelii* and *C. scheberiana* were significantly correlated with the AET in the fauna-excluded treatment (Table 7). However, AET did not correlate with the annual decay rates in the control treatment. Instead, AET correlated with the abundance of total litter fauna contained in the litterbags in the control treatment.

DISCUSSION

The goal of this experiment was to examine whether soil fauna differentially contribute to plant litter decomposition across gradients of climate and substrate quality. We found that all three factors independently affected the decomposition rate of plant litter in tropical and subalpine forests. Soil fauna influenced the percentage of litter mass loss and nitrogen mineralization rates at a given point in time (Figs. 1 and 2). However, in hypothesis 1, we expected to find faster decomposition and mineralization rates of *Quercus gambelii* and *Cecropia scheberiana* in the presence of fauna in the tropical forests than in the subalpine forests, based on a higher abundance of macroinvertebrates in the tropical sites. In fact, there was a significant interaction of fauna and site on the annual decay rates of both litter species, indicating a differential effect of soil fauna on litter decomposition among the study sites. Annual decomposition rates of both litter species were significantly higher in the control than in the fauna-excluded treatment in the tropical wet forest. However, there was no significant treatment effect on the decomposition of *Q. gambelii* and *C. scheberiana* in the tropical dry forest. Absolute nitrogen amounts in decaying litter increased throughout the study in all sites except the tropical wet forest, and the percentage of initial N remaining was significantly lower in the control than in the fauna-excluded treatment in the tropical wet forest. Quantification of the faunal effects on decomposition rates of *Q. gambelii* and *C. scheberiana* yielded values that were consistently higher in the tropical wet forest than in the tropical dry and the subalpine forests. Earthworms were found solely in the tropical wet forest. These findings indicate that soil fauna play a relatively

TABLE 5. Densities (number per gram of dry litter) of major groups of mites, collembolans, and other microarthropods in control and fauna-excluded treatments within each site in *Quercus gambelii* and *Cecropia scheberiana* litterbags.

Treatment and site	Cryptostigmata	Mesostigmata	Prostigmata	Collembola	Other†	Total
Control						
Tropical, dry	$1.45^{c*} \pm 0.79$	$0.10^{b} \pm 0.04$	$0.19^{b} \pm 0.13$	$0.01^{b} \pm 0.01$	$0.64^{b*} \pm 0.18$	$2.39^{c*} \pm 1.10$
Tropical, wet	$43.17^{a*} \pm 7.54$	$8.90^{a*} \pm 2.35$	$0.72^{ab} \pm 0.26$	$1.48^{a} \pm 0.54$	$25.88^{a*} \pm 9.20$	$80.15^{a*} \pm 17.71$
Subalpine, north	$1.45^{bc*} \pm 0.59$	$2.27^{a*} \pm 0.67$	$1.07^{a*} \pm 0.35$	$0.92^{a*} \pm 0.39$	$0.21^{b*} \pm 0.08$	$5.92^{b*} \pm 1.67$
Subalpine, south	$4.97^{b*} \pm 2.58$	$3.07^{a*} \pm 0.78$	$0.85^{a*} \pm 0.30$	$0.82^{a*} \pm 0.19$	$1.48^{b*} \pm 0.87$	$11.19^{b*} \pm 3.74$
Fauna-excluded						
Tropical, dry	$0.01^{b} \pm 0.01$	$0.03^{b} \pm 0.02$	$0.03^{b} \pm 0.02$	0^{a}	$0.26^{b} \pm 0.09$	$0.33^{b} \pm 0.11$
Tropical, wet	$1.66^{a} \pm 0.48$	$1.92^{a} \pm 0.59$	$0.25^{a} \pm 0.08$	$1.15^{a} \pm 0.52$	$4.21^{a} \pm 1.25$	$9.20^{a} \pm 2.48$
Subalpine, north	$0.05^{b} \pm 0.03$	$0.13^{b} \pm 0.10$	0^{b}	$0.05^{a} \pm 0.04$	$0.05^{b} \pm 0.03$	$0.28^{b} \pm 0.17$
Subalpine, south	$0.01^{b} \pm 0.01$	$0.04^{b} \pm 0.02$	$0.01^{b} \pm 0.01$	$0.03^{a} \pm 0.01$	$0.02^{b} \pm 0.02$	$0.11^{b} \pm 0.03$

Notes: Values are means ± 1 SE. Common superscript letters within a column and treatment indicate no significant difference among sites (SNK, α = 0.05). Statistics were performed on log-transformed data.

* Significant within-site treatment effect (one-way ANOVA; α = 0.05).

† Other microarthropods excluding mites and collembolans.

TABLE 6. Effects of treatment, site, and litter species on the densities (numbers per gram of dry litter) of Cryptostigmata, Mesostigmata, Prostigmata, Collembola, and total litter fauna in *Quercus gambelii* and *Cecropia scheberiana* litterbags.

Source	df	F	P	Power
Fauna (F)	5, 140	15.78	< 0.001	1.00
Site (S)	15, 426	8.21	< 0.001	1.00
Litter (L)	5, 140	1.21	0.31	0.42
F × S	15, 426	6.27	< 0.001	1.00
F × L	5, 140	0.64	0.67	0.23
S × L	15, 426	0.89	0.58	0.59
F × S × L	15, 426	0.51	0.94	0.33

Note: Statistical values are based on a three-way MANOVA (n = 160) using a Pillai's Trace test.

more important role in litter decomposition and N mineralization rates in the tropical wet forest than in the tropical dry or subalpine forests. Therefore, we accept hypothesis 1.

The greater effect of fauna on litter decomposition and N release in the tropical wet forest than in other sites in this study could be explained by: (1) the higher densities of soil fauna; and (2) a more diverse assemblage of fauna, because the density of microarthropods (other than mites and collembolans) and earthworms was also the highest on this site (Table 5). These results are somewhat consistent with those presented by Setälä et al. (1996), who showed that a system with a mix of micro-, meso-, and macrofauna was more effective in providing nutrients for plant growth. More importantly, these results suggest a difference in the abundance of fauna in litter and soil layers in tropical and subalpine systems. Seastedt (1984) summarized studies indicating that the densities of microarthropods in the soil are typically higher in boreal forests than in the tropics. Densities of arthropods are approximately ≥ 300 000/m^2 in boreal systems vs. < 50 000/m^2 in the tropical forests. However, this study showed that the density of microarthropods per gram of litter were much higher in the tropical wet forest than the tropical dry and subalpine forests. Thus, not only the functional diversity but also the actual abundance of microarthropods per gram of litter is amplified in the tropical wet forest. Given warmer annual temperatures, the relative activity of these fauna is also presumably higher in the tropics.

Increases in the absolute amounts of nitrogen, above initial conditions, in the tropical dry and the subalpine forests could be explained by incorporation from exogenous sources, including absorption of atmospheric ammonia, throughfall, leachate, or fungal translocation (Melillo et al. 1982, Blair 1988). Still, although not always statistically significant, the percentage of N remaining was consistently lower in the presence of fauna than in its absence (Fig. 2). Blair et al. (1989) showed that the final nitrogen concentrations could be reduced in naphthalene-treated litter. González (1999) measured the effects of the naphthalene application in the fauna exclusion treatment on the microbial biomass of salycilate mineralizers, a functional group of microbes likely to be stimulated by the addition of naphthalene. It was found that the microbial biomass of the salycilate mineralizers was significantly enhanced in the fauna exclusion treatment in the tropical wet forest and the south-facing subalpine forest (González 1999). Therefore, effects of fauna on N mineralization could have been diminished by the stimulation of microbial immobilization in the fauna-excluded treatments via an indirect effect of naphthalene addition on microbial populations. This finding is consistent with earlier studies indicating that naphthalene enhanced immobilization of soil inorganic N (Blair et al. 1989), and that the use of naphthalene contributes to a conservative estimate of the impacts of fauna. Thus, faunal effects on decomposition and mineralization rates in the tropical wet forests could have been underestimated by this study.

In hypothesis 2, because of an initially higher lignin content in *C. scheberiana* leaves than in *Q. gambelii,* we expected an acceleration of the decomposition rate of the former litter species through faunal effects. The data indicated no differential effect of fauna on the litter species; there was no significant interaction of fauna and litter species on the annual decay rates (Table 3). Thus, we must reject the second hypothesis and state that the effects of fauna did not vary between the litter species studied here.

Litter of *Quercus* spp. is generally thought of as a recalcitrant material because of its relatively high lignin content. Heneghan et al. (1999) used *Q. prinus* as a single substrate in a cross-site study that involved two humid tropical forests and one temperate forest. In this study, *C. scheberiana* was used in order to expand the range of low-quality litter. However, the use of lignin as a standard index of substrate quality should

TABLE 7. Pearson correlation coefficients, r (with two-tailed probability values in parentheses) for annual decay rates (k) of *Quercus gambelii* and *Cecropia scheberiana* litter and actual evapotranspiration rates (AET; in millimeters), and for k and mean abundance of total fauna (numbers per gram of dry litter) collected from the litterbags in control and fauna-excluded treatments (n = 4 forest sites).

	Control		Fauna excluded	
Litter species	AET	Total litter fauna	AET	Total litter fauna
Q. gambelii	0.918 (0.082)	0.950 (0.050)	0.990 (0.010)	0.773 (0.227)
C. scheberiana	0.908 (0.092)	0.983 (0.017)	0.999 (0.001)	0.856 (0.144)

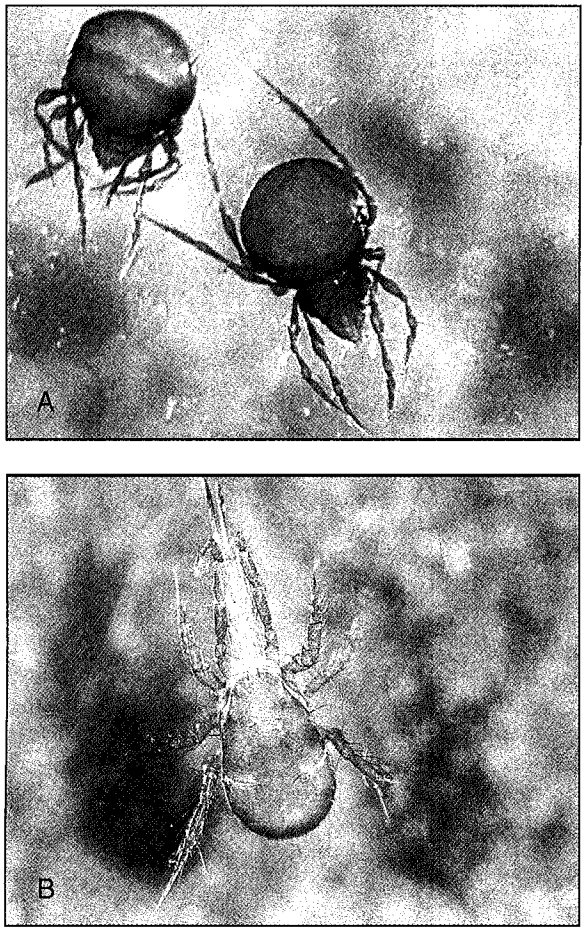

PLATE 1. Photographs of (A) oribatid and (B) mesostigmatid mites (magnifications of 25× and 32×, respectively). The abundance of these mites was highest in the tropical wet forest.

be evaluated, because *C. scheberiana* had an initial high content of both lignin and nitrogen. Nitrogen has been described as good predictor of plant litter decomposition (e.g., Melillo et al. 1982, Coûteaux et al. 1991). The lignin:N ratio has also been shown to correlate with annual decay rates (e.g., Melillo et al. 1982). However, other studies have shown that lignin content has more control over plant litter decomposition rates than does nitrogen (e.g., Bollen 1953, Fogel and Cromack 1977). This latter statement seems to be supported in this study, in which: (1) the lignin:N ratio did not differ between the two species; and (2) *C. scheberiana* decay was slower than *Q. gambelii* decay, even though N content was higher in the former species. Nevertheless, a thorough exploration of the controls of lignin and nitrogen on litter decomposition will require a wider range of substrate quality than presented here.

The decomposition trends for *Q. gambelii* and *C. scheberiana* can also be explained by the large differences in climate among the study sites. Both litter species decay significantly faster in the tropics than in the subalpine forests in the absence of fauna (Table 4). In fact, the annual decomposition rates were significantly correlated with AET in the fauna-excluded treatment (Table 7). However, there was a significant effect of fauna on decomposition beyond that predicted by climate alone, because the annual decay rates of both litter species were lower in the absence of fauna than in the control treatment in the tropical wet forest (Table 4). In the control treatment, the annual decay of both litter species combined is better correlated with the density of total litter fauna than with AET itself (Table 7). Coûteaux et al. (1995) claim that "litter quality largely prevails as the regulator of litter decomposition under climatic favorable conditions." In this study, in the absence of fauna, litter decomposition of *C. scheberiana* was twice as fast as that of *Q. gambelii* in the tropical wet forest; such data support the contention of Coûteaux et al. (1995). Yet, the fact that the annual decay rates were consistently enhanced in the control treatments in the tropical wet forest, independent of litter species, argues for recognition of soil fauna as a major regulating factor of decomposition under favorable conditions as well.

Meentemeyer (1978) reported that the relative control by lignin over decomposition rate is not uniform over different climatic regions, and that lignin has a larger influence under favorable climatic conditions. In contrast, this study did not show any amplification effect of substrate quality on litter decomposition, as there was no significant interaction of litter species and site on the annual decay rates (Table 3). We initially thought that the reduced control by lignin in cool climates was a result of reduced fragmentation ability of the fauna, and assumed that the functional diversity of the fauna would increase from the temperate systems to the tropics as a function of AET. Certainly, this hypothesis did not hold, as the lowest density of fauna was found in the tropical dry forest, a site with an intermediate value for AET in comparison to the tropical wet and the subalpine forests (Table 5). The inconsistent relationship between the densities of litter fauna and AET shows the difficulty of predicting decomposition rate by using a single regulating factor. For example, Whitford et al. (1981) and Schaefer et al. (1985) have demonstrated that decomposition in desert ecosystems can be more rapid than predicted from models based on substrate quality and climate alone. Those studies showed that the fauna (largely termites) are capable of improving the microclimate and fragmentation of the litter, consequently affecting its decomposition.

Heneghan et al. (1999) found that the decomposition of oak litter proceeded faster in Puerto Rican and Costa Rican forests (tropical sites) than in a temperate forest in North Carolina. Microarthropods had little effect in the temperate forest, whereas their influence was pronounced at tropical sites. Moreover, rates of decomposition of litter with fauna differed between the tropical sites, but decay in the absence of fauna was not

significantly different. Similarly, we found that when fauna are excluded, differences in the annual decay rates of *Q. gambelii* and *C. scheberiana* are substantially reduced when we compare sites within the tropical and the subalpine forests. Results from the Heneghan et al. (1999) study indicate that there is a site-specific faunal contribution to decomposition, suggesting that exclusion of soil fauna in tropical forests may have important ecosystem consequences.

A major implication of our study is that ecosystem models might not accurately predict plant litter decomposition unless they explicitly recognize the composition and abundance of soil organisms as a major regulating factor. Previous decomposition models have been based on data derived from temperate ecosystems, where faunal contributions to plant litter decay could be relatively small. However, this study shows that plant litter decomposition and N mineralization rates can be influenced by biotic factors in a tropical wet forest, and that these ecosystem processes cannot be explained by climate and substrate quality alone.

Acknowledgments

We thank Robert N. Addington, Elianid Espinosa, Zhigang Liu, Gustavo Lugo, Lu Anne Lupfer, Angel Meléndez, Liz M. Sánchez, David Stahl, and Xiaoming Zou for invaluable field and laboratory assistance. Don Edmonds provided invaluable logistical support. We thank Xiaoming Zou and two anonymous reviewers for commenting on an earlier version of the manuscript. This research was supported by the Biosphere Atmosphere Research Training Program (BART) to the University of Colorado at Boulder, the Long Term Ecological Research (LTER) program, and a NASA (NAGW 4059) grant to the University of Puerto Rico.

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