Biol Fert Soils (1985) 1:201–207

Biology and Fertility of Soils

Effect of habitat on decomposition of standard leaf-litter species

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Summary. Decomposition of a standard leaf-litter species, *Quercus leucotrichophora*, was studied over a 1-year period by enclosing it in 10 × 10-cm litter bags (mesh 1 mm) and placing these at five forest sites located in the northwestern part of the central Himalaya along an altitudinal gradient of 329–2150 m. The annual weight loss ranged from 75% to 99%. Rainfall, litter moisture and mean annual temperature were important factors affecting decomposition. There was a significant inverse relationship between the percentage original mass remaining and the nitrogen concentration of the residual matter. However, in two out of the five sites the data tended to follow an exponential decay curve better than a linear curve.

Key words: Central Himalaya – Standard leaf-litter decomposition – Nitrogen immobilization – Annual weight loss

Litter decomposition is the key process controlling the rate at which nutrients of the plant biomass are returned and incorporated into forest soils. Since it is an important and controlling component of nutrient cycling, its rate and mechanism have attracted considerable attention in recent years (Singh and Gupta 1977; Swift et al. 1980). Climatic variables, mainly rainfall and temperature, and substrate quality, principally nitrogen and lignin, have been used to explain and predict the decomposition rate (Meentemeyer 1977, 1978; Fogel and Cromack 1977; Gupta and Singh 1981). According to Minderman (1968), the slowly decomposing litter components, such as lignin, tend to dominate the shape of the long-term decay curve. Pandey and Singh (1982) have reported that the effect of nitrogen on decay rate declined with time while that of lignin increased. Melillo et al. (1982) found that 89% variability in the decay rate constants of hardwood leaf litter could be accounted for by the variability in initial lignin/nitrogen ratio.

The objective of the present study was to examine the weight loss and the relationship between the percentage mass remaining and nitrogen concentration of the residual material in a standard leaf-litter species (to provide for a constant substrate quality) placed in different habitats. The habitat varied in altitude and supported different forest types. The standard leaf-litter material was of *Quercus leucotrichophora* A. Camus, which is an evergreen species and is widely distributed in the region (Champion and Seth 1968).

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Materials and methods

The experimental sites are located in the north-western part of the central Himalaya (lat. 29°7′ to 29°26′ N and long. 79°15′ to 79°38′ E) along an altitudinal gradient of 329–2150 m and support five distinct forest types ranging from subtropical moist deciduous to temperate moist evergreen broadleaf: (1) sal (*Shorea robusta* Gaertn.) forest, dominated by *Shorea robusta*; (2) mixed broadleaf forest of *Quercus* *leucotrichophora* A. Camus, *Quercus glauca* Thumb. and *Lyonia ovalifolia* (Wall.) Drude; (3) pine forest dominated by *Pinus roxburghii* Sarg.; (4) mixed oak-pine forest of *Q. leucotrichophora* and *P. roxburghii*; and (5) mixed oak forest of *Q. lanuginosa* Don., *Q. floribunda* Lindl. and *Q. leucotrichophora*. These sites form a network of experimental sites for an integrated study in which various aspects of ecosystem structure and function were examined (Singh and Singh 1984). Important site characteristics are given in Table 1.

Climatic conditions varied from site to site (Fig. 1). The year on all sites is divisible into rainy (mid-June to September), winter (November to February) and summer seasons (April to mid-June). The sal forest site located at 329 m represents the warmest habitat, with mean daily temperature ranging from 12° to 32°C. The annual rainfall is 2076 mm, 88% of which occurs in the rainy season. The mixed broadleaf and pine forest sites are located in the elevational range of 1350–1750 m, with a range in mean daily temperature from 8° to 24°C. The annual rainfall ranges from 2005 to 2185 mm, with 80% occurring in the rainy season. On the mixed oak-pine forest site situated at 1850 m, the mean daily temperature ranges between 7.0° and 19.3°C and the annual rainfall is 1313 mm. Seventy-six percent of the annual rainfall occurs during the rainy season. The mixed oak forest site is situated at the highest elevation (2150 m), with mean daily temperature ranging between 4.5° and 22°C. Annual rainfall is 2488 mm, with 88% occuring in the rainy season. Snow falls between late December and late February; however, no quantitative data exist for its magnitude.

The soil at the sal forest site is alluvial, while on other sites it is residual. Soil texture was determined by soil hydrometer (Buoyoucos 1951), organic carbon by Walkley and Black's (1934) rapid titration method and total nitrogen by macrokjeldahl method

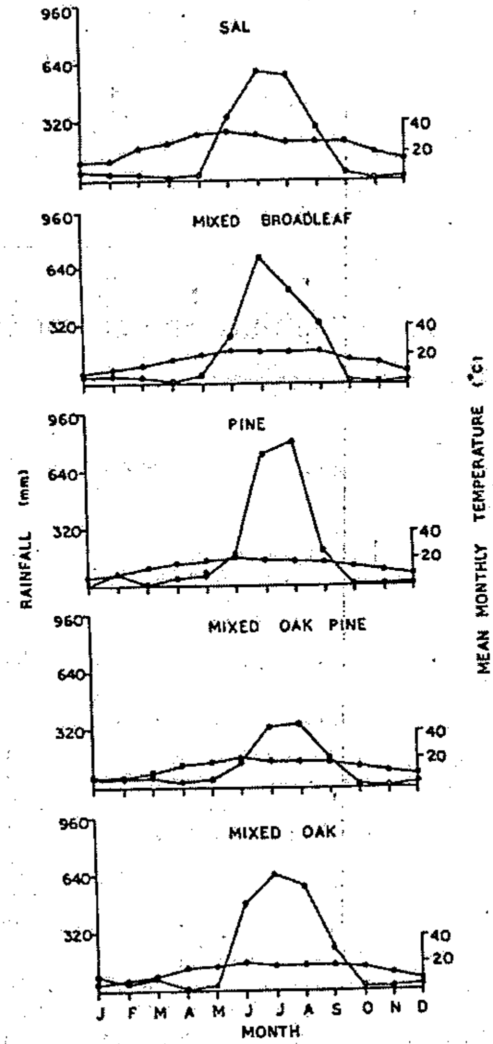

Fig. 1. Rainfall per month (o–o) and mean monthly temperature (•–•) for the experimental sites

Table 1. Characteristics of the experimental sites (values are from Singh and Singh 1984)

Site/ forest type	Dominant species	Elevation (m)	Soil characteristics						
			Organic C(%)	Total N(%)	C : N ratio	Sand (%)	Silt (%)	Clay (%)	pH
Sal	*Shorea robusta* Gartn	329	1.1	0.15	7.1	80	14	6	6.8
Mixed broadleaf	*Quercus leucotrichophora* A. Camus *Quercus glauca* Thumb. *Lyonia ovalifolia* (Wall.) Drude	1350	3.5	0.30	11.6	82	10	8	6.6
Pine	*Pinus roxburghii* Sargent	1750	3.7	0.26	14.2	66	24	10	5.7
Mixed oak-pine	*Quercus leucotrichophora* *Pinus roxburghii*	1850	3.5	0.33	10.6	61	26	13	6.1
Mixed oak	*Quercus lanuginosa* Don. *Quercus floribunda* Lindl. *Quercus leucotrichophora*	2150	4.2	0.46	9.1	62	22	16	6.0

as described by Piper (1944). Sand predominates in the soil (61%–82%), while the silt and clay contents are 12%–26% and 6%–16%, respectively. Organic carbon ranged between 1.10% and 4.20% and total N between 0.15% and 0.46%. The soil pH ranged between 6.1 and 6.8 across all sites.

Mature, nearly senesced but attached leaves of *Q. leucotrichophora* were collected from the middle canopy of a single tree in July 1981 and air dried in shade. In this species, leaf fall occurs year-round, but the maximum fall occurs in April and in the 1st week of July (Pandey and Singh 1981). The air-dried leaves were thoroughly mixed and 5-g samples were enclosed in 10 × 10-cm nylon bags (Crossley and Hoglund 1962). Mesh size was 1 mm, which excluded macroarthropods but was large enough to permit aerobic microbial activity and free entry of soil microfauna. On the sal forest site, steel-wire netting bags with the same mesh size, painted with synthetic enamel to avoid rusting, were used because of the preponderance of termites. One hundred and twenty litter bags were placed on the forest floor at each site in the beginning of the rainy season of 1981. No spatial displacement of bags due to wind action, etc. was noticed during the study. At this time five replicates (5 g each) from stock litter sample were dried at 60°C to calculate the dry weight of the enclosed litter. Five litter bags were randomly recovered from each site at 1-month intervals over a 1-year period. The remaining bags were used for the periodic determination of microbial population in a related study. The samples were weighed as moist then dried at 60°C to constant weight to calculate their weight loss. The samples were ground in Wiley mill and stored for chemical analysis. Ash content was determined by igniting three subsamples in a muffle furnace at 550°C, nitrogen by the microkjeldahl technique (Piper 1944), carbon according to McBrayer and Cromack (1980) and lignin according to Edwards (1973). The estimate by Edwards' method also includes malanines and darkbrown colours of leaves. The percentage weight loss of leaves was calculated on an ash-free dry weight basis.

The microbial population was determined using the dilution plate count technique of Waksman (1927). Three replicates of litter samples, 1 g each, from the bags were homogenized with sterilized distilled water, and differrent dilutions were plated on different media. For fungi the dilution was 10^4 and the medium potato dextrose agar (Riker and Riker 1936) and Czapek agar (Raper and Thom 1949); for bacteria the dilution was 10^6 and the medium nutrient agar (Difco Manual 1953); and for actinomycetes the dilution was 10^6 and the medium soil extract agar (Bunt and Rovira 1955). Colonies of fungi (by species) and of bacteria and actinomycetes were counted. Litter samples, collected from the forest floor each month from 1-m² sampling plots, were placed on Tulgren funnels. Reflected light of a 60-W incandescent bulb, placed 30 cm above each funnel, was used to heat the samples to drive out the microarthropods which were collected in 75% alcohol (Murphy 1962).

Results and discussion

After 1 month of litter incubation the percentage weights remaining were 71%, 83%, 84%, 91% and 72% and at the end of the annual cycle the percentage biomasses remaining were 1%, 12%, 25%, 23% and 12%, respectively, at sal, mixed broadleaf, pine, mixed oak-pine and mixed oak forest sites.

The relationship between the natural log of the percentage weight remaining and time elapsed since placing the bags on the forest floor was significant at all sites (r = -0.79 to -0.98, P < 0.01) (Table 2), indicating a continued weight loss throughout the year. Nevertheless, the weight loss was maximum during the rainy season at all sites. To test for the overall differences in the time pattern of decomposition on different sites, the results of the regression

Table 2. Coefficients of correlation, slopes and intercepts of regressions relating $\log_n$ of percentage biomass remaining (y) to time (x, days elapsed) for *Quercus leucotrichophora* leaf litter

Forest site	Slope	Intercept	r
Sal	−0.0110	4.70	−0.960
Mixed broadleaf	−0.0050	4.66	−0.954
Pine	−0.0030	4.59	−0.960
Mixed oak-pine	−0.0036	4.57	−0.980
Mixed oak	−0.0030	3.92	−0.790[a]

All r values are significant at P < 0.01 expect for [a], which is significant at P < 0.05. df = 5

Table 3. F values for differences between regression slopes, relating percentage biomass remaining to time interval for different sites

Forest site	Mixed broadleaf	Pine	Mixed oak-pine	Mixed oak
Sal	14.43**	26.90**	25.96**	15.40**
Mixed broadleaf		14.40**	3.61	0.98
Pine			0.26	0.06
Mixed oak-pine				0.02
Mixed oak				

** Significant at P < 0.01

analyses were used to calculate the F values as described by Sokal and Rohlf (1969) (Table 3). The pattern on the sal forest site was different from those of all other sites and in addition that on the mixed broadleaf site was different from that on the pine forest site. Since the standard litter provided the same initial relative proportion of labile to resistant fraction, the differences in the pattern and magnitude of weight loss among sites are a result of site differences which control the differential rates at which labile and resistant fractions decompose (Wieder 1978; Wieder et al. 1983).

The weight loss rate on each site was markedly affected by rainfall; the weight loss per month and the rainfall per month were positively related (Table 4). The moisture content of decomposing leaf litter varied markedly on all sites as did the periodic weight loss (Fig. 2). The above two parameters were positively related, when the data were pooled for all sites, according to the following regression:

$$Y = 8.10 + 0.041\ X\ (r = 0.463,\ \text{d.f.} = 33,\ P < 0.01),$$

where Y = % weight loss per 60 days and X = % moisture content, on each 60th day in residual litter. The annual variation in litter moisture is given in Table 5. With the exception of the sal forest site, there existed an inverse relationship between percentage weight remaining at the end of the annual cycle and the minimum (as well as the maximum) litter moisture content. At the sal forest site warmer temperature may have compensated for the low value of litter moisture. Williams and Gray (1974) and Sain and Broadbent (1975) have stressed the positive effect of the moisture content on decomposition rate. The annual percentage weight remaining varied inversely with mean annual temperature except for the mixed oak forest site, where the greater rainfall may have compensated for the low temperature. A linear

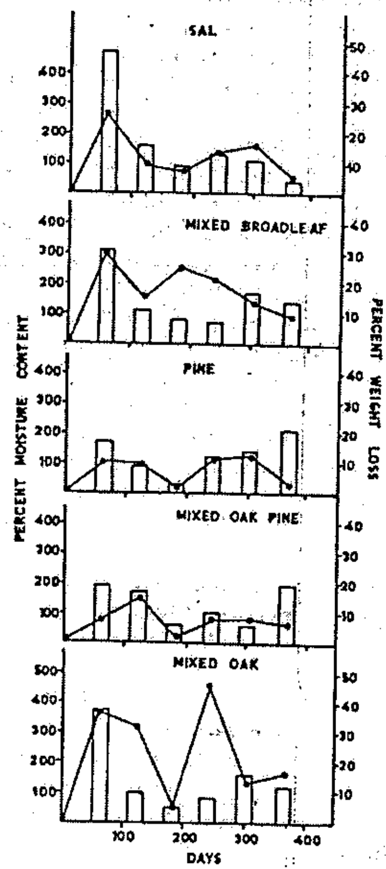

Fig. 2. Relationship between moisture content (*curve*) and percentage weight loss (*bar*) of the leaf litter of *Quercus leucotrichophora*

combination of rainfall and temperature explained about 45% of the variability in weight loss, across all sites, according to the following regression:

$$Y = 3.31 + 0.0151\ X_1 + 0.070\ X_2\ (r^2 = 0.446,\ P < 0.01),$$

where Y = % weight loss per month, X_1 = rainfall per month (mm) and X_2 = mean monthly temperature (°C).

The litter placed on the sal forest site supported the greatest microbial population (in conformity with the greatest weight loss) while the mixed broadleaf and mixed oak forest sites, which had equal weight loss reflected the second and the third greatest population size, respectively (Table 6). The litter on the pine forest site reflected the lowest weight loss and had the minimum microbial population. Though the population densities are not significantly different, the percentage similarity in the fungal communities (determined through Jaccards' 1912 community coefficients) was ≤ 30%, indicating that on each forest site

Table 4. Coefficients of correlation, slope and intercepts of linear regressions relating percentage weight loss per month (%, Y) to rainfall per month (mm, X) for *Quercus leucotrichophora* leaf litter

Forest sites	Slope	Intercept	r
Sal	0.023	4.29	0.700**
Mixed bradleaf	0.019	3.18	0.882**
Pine	0.001	6.08	0.587*
Mixed oak-pine	0.032	3.30	0.806**
Mixed oak	0.015	2.86	0.816**

* Significant at $P < 0.05$;
** Significant at $P < 0.01$

Table 5. Annual percentage weight remaining, rainfall, mean annual temperature and moisture content of *Quercus leucotrichophora* leaves

Forest site	Percentage weight remaining (% ± 1 SE)	Rainfall (mm)	Mean annual temperature (°C)	Minimum litter moisture (% ± 1 SE)	Maximum litter moisture (% ± 1 SE)
Sal	1 ± 0.4	2076	23	30 ± 6	271 ± 12
Mixed broadleaf	12 ± 0.7	2005	18	46 ± 6	322 ± 18
Pine	25 ± 1.6	2185	16	13 ± 1	120 ± 8
Mixed oak-pine	23 ± 1.1	1313	16	25 ± 2	154 ± 18
Mixed oak	12 ± 0.6	2488	13	53 ± 7	463 ± 12

Table 6. Mean annual microbial counts on *Quercus leucotrichophora* leaf litter placed at different forest sites. Values are × 10^4 g^{-1} for fungi and × 10^6 g^{-1} for bacteria and Actinomycetes (means ± 1 SE)

Microbes	Sal	Mixed broadleaf	Pine	Mixed oak-pine	Mixed oak
Fungi	39.08 ± 4.40 (*Aspergillus niger*)	36.04 ± 4.30 (*Aspergillus niger*)	27.09 ± 1.79 (*Penicillium spinulosum*)	29.19 ± 3.43 (*Trichoderma viride*)	32.49 ± 2.82 (*Trichoderma viride*)
Bacteria	57.67 ± 10.73	53.67 ± 10.57	39.04 ± 7.83	43.12 ± 8.45	50.73 ± 9.13
Actinomycetes	7.04 ± 1.50	5.73 ± 1.08	3.03 ± 0.38	3.56 ± 0.92	4.99 ± 0.72

Names of the most abundant fungi are given in parentheses

conspicuously different fungal communities developed on the standard litter material (Singh and Singh 1984). The year-round most abundant fungus was *Aspergillus niger* Van Tieghem on the sal forest site, *Trichoderma viride* Pers. ex Gray on the mixed oak forest site and *Penicillium spinulosum* Thom on the pine forest site.

The nitrogen concentration in the residual litter increased throughout the study but the carbon/nitrogen ratio decreased with time (Table 7). Berg and Ekbohm (1983) found no fixed C/N ratios for immobilization and release of nitrogen for Scots pine needle litter. Several authors (e.g. Aber and Melillo 1980; Melillo et al. 1982) have explored the relationship between weight loss and N concentration by plotting the percentage of biomass remaining as a function of N concentration in the residual material. Figure 3 expresses this inverse relationship in the present study. Aber and Melillo (1980) and Melillo et al. (1982) have emphasized the significance of this relationship in the framework of immobilization and mineralization of nitrogen during decomposition. The weight loss in enclosed litter and increased N concentration in the residual material reflect carbon metabolization and N immobilization, respectively, by the microorganisms. Aber and Melillo (1980) have generalized that this relationship is inverse linear where (1) physical removal of material from bags is minimized, (2) nitrogen is sufficiently low in concentration in the litter material to be limiting to microbes and (3) a continuous external source of nitrogen is

Table 7. C/N ratios in decomposing *Quercus leucotrichophora* leaf litter placed on the floor of different forests

Days	Sal	Mixed broadleaf	Pine	Mixed oak-pine	Mixed oak
0	44	44	44	44	44
62	41	41	44	43	42
184	34	33	40	42	50
304	29	28	35	27	32
365	23	26	30	27	21

available. In the present study the linear relationship was statistically significant for all sites (Table 8). However, while the linear relationship was readily apparent on three forest sites, viz. mixed broadleaf, pine and mixed oak-pine, the data for sal and mixed oak forest sites tended to follow an exponential decay curve (broken curves in Fig. 3). Thus the weight loss per unit N immobilized was initially faster and greater on the two latter sites compared with the other sites. Aber and Melillo (1980) have argued that in cases where a continuous external source of N is not available, results are better described by an exponential rather than a linear curve. However, in the present study there is no reason to believe that there would be little or no addition of exogenous N on sal and mixed oak forest sites as compared with the other sites.

At the sal forest site the mean micro-arthropod population on the forest floor was highest followed by the mixed oak forest and least at the pine forest

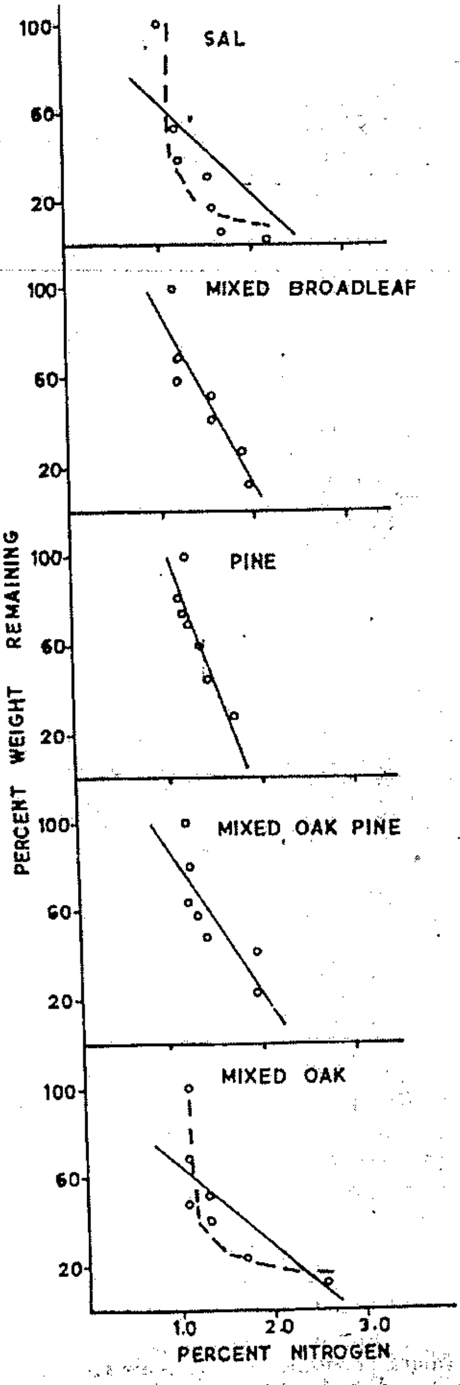

Fig. 3. Percentage of original biomass remaining as a function of nitrogen concentration in the residual leaf litter of *Quercus leucotrichophora*. The *solid curves* represent the regression equation and the *broken curves* are fitted by eye

Table 8. Coefficients of correlation, slope and intercepts of the relationships between percentage biomass remaining (*Y*) and nitrogen concentration (*X*, %) in the residual material of *Quercus leucotrichophora* leaf litter

Forest sites	Slope	Intercept	*r*
Sal	−73.81	148.19	−0.800*
Mixed broadleaf	−78.80	168.27	−0.910**
Pine	−124.53	229.00	−0.956**
Mixed oak-pine	−60.73	144.31	−0.808*
Mixed oak	−41.36	109.95	−0.760*

* Significant at $P < 0.05$
** Significant at $P < 0.01$

site (Table 9). Further, on the sal forest site there were 8 mounds ha^{-1} of the termite *Odontotermes obesus* Rambur and 44 carton nests ha^{-1} of the termite *Microcerotermes championi* Snyder. The annual mean population of these termites was 148 individuals m^{-2} for *O. obesus* and 145 individuals m^{-2} for *M. championi* (Singh and Singh 1984). Therefore, there may be a greater intensity of selective feeding in the above two sites (sal and mixed oak forest) by microarthropods of high nitrogen material being constantly produced by the microbial growth, indicating greater weight loss per unit N immobilized. The result may, however, be different if the macroarthropods and worms were not excluded due to the mesh size used in this experiment.

Selective feeding of microbes by microfauna may also explain the larger slope in the case of oak litter placed in pine forest (Table 7) where the native litter (Pine needles) (lignin/N ratio = 35) differs markedly from the oak leaf litter (lignin/N ratio = 15). The lignin and N percentages are 23.4% and 0.67%, respectively, in pine leaf litter, and 16.7% and 1.15%, respectively, in oak leaf litter. The low C/N ratio of soil in the sal and mixed oak forest sites (Table 1) may be an additional factor reducing the initial N immobilization in decomposing litter.

Table 9. Annual mean population of litter microarthropods on the forest floor of different sites (individuals $m^{-2} \pm 1$ SE)

	Sal	Mixed broadleaf	Pine	Mixed oak-pine	Mixed oak
Acarina	5431 ± 754	2073 ± 341	860 ± 86	3105 ± 622	3221 ± 716
Collembola	1256 ± 337	753 ± 158	186 ± 35	953 ± 163	1313 ± 251
Others	727 ± 149	365 ± 81	125 ± 20	614 ± 114	496 ± 116
Total	7414 ± 1142	3192 ± 560	1171 ± 131	4672 ± 859	5030 ± 1057

Acknowledgement. We gratefully acknowledge financial support from the Department of Science and Technology, New Delhi, India.

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Received March 26, 1985