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Applied Soil Ecology 9 (1998) 33–38

Applied
Soil Ecology

Soil microarthropod community structure and litter decomposition dynamics: A study of tropical and temperate sites

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Received 26 July 1996; accepted 4 July 1997

Abstract

The influence of climate, substrate quality and microarthropods on decomposition was studied by comparing the mass loss of litter at three forested sites: two tropical and one temperate. At each site, litterbags containing a dominant local litter were placed in the field in replicated plots. Half the bags were treated with naphthalene to reduce microarthropod abundance. The pattern of mass loss was markedly seasonal at the temperate site. The amount of mass remaining after 250 days was strongly related to the initial %N of the three litter types ($r^2=0.997$). The faunated litterbags lost more mass at all sites and for all litters studied than the litterbags with reduced microarthropod populations. The effect was minimal at the temperate site where the fauna tended to increase the decomposition rate only towards the end of the year. In contrast, the effect of the fauna at the tropical sites was marked within months of the start of the experiment. Species richness of microarthropods in samples of 300 cm² of leaf litter was similar at the three sites. However, diversity (measured using Fisher's α index) was greatest at the tropical sites. © 1998 Elsevier Science B.V.

Keywords: Tropical-temperate comparison; Decomposition; Litter quality; Microarthropods; Litterbags; Biological systems of regulation (BSR's)

1. Introduction

The general determinants of decomposition dynamics are well known and apply ubiquitously (Swift et al., 1979). Principally these are climate, edaphic properties, resource quality, and organismic activity. Their influence is hierarchically arranged with higher level factors, such as climate, constraining lower level ones, such as organismic interactions (Lavelle et al., 1993). The rate of mass loss from

decomposing leaf litter will result from the unique interplay of factors found at a site of interest. General models of litter decay based upon climatic and resource quality indices have been successfully applied at a regional scale (Dyer et al., 1990). The use of correlation-regression approaches to determining mass loss rates often obscures the importance of fauna in the process of decomposition. For example, Andrén et al. (1995) applied a four-compartment decomposition model to the mass loss of barley straw. They concluded that abiotic controls on decomposition were paramount and that organismic biomass

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dynamics and interactions were not relevant factors in predicting rates. Because of the cosmopolitan distribution of microarthropods they may represent a constant in most field studies on litter decomposition. Adopting an experimental approach to reduce arthropod populations has shown arthropods to be influential in determining mass loss from litterbags (Seastedt, 1984).

In this paper, we attempt to confirm the influence of climate, substrate quality and fauna on decomposition dynamics. We performed an experimental manipulation of microarthropods to evaluate their contribution to mass loss of litter confined in litterbags. Examining decomposition of three litter types, from three sites (two in the tropics and one temperate), we investigated the generality of microarthropod influences on decomposition.

2. Materials and methods

2.1. Site descriptions

Three sites were chosen for this experiment, one temperate site at Coweeta Hydrologic Laboratory (CWT), and two tropical sites: Luquillo Experimental Forest in Puerto Rico (LUQ) and La Selva Biological Station (LAS) in Costa Rica.

2.1.1. Coweeta, North Carolina, USA (CWT)

Coweeta Hydrologic Laboratory, located in the Southern Appalachians of western North Carolina (35°00'N; 83°30'W), is a 2185 ha forested basin containing numerous small watersheds. The native hardwood forest is dominated by *Quercus*, *Carya* and *Acer* spp. Mean annual rainfall is approximately 1700 mm at lower elevations and this rainfall is somewhat variably distributed throughout the year (Fig. 1). Mean annual temperature is 13°C. Watershed 18, where this experiment was carried out, is a lower elevation (720 m) mixed hardwood and has been undisturbed since 1927 (Swank and Crossley, 1988). The soil at this site is an ultisol, in the Cowee-Evard gravelly loam series.

2.1.2. Luquillo, Puerto Rico (LUQ)

The site is at the El Verde field station at Luquillo Experimental Forest (18°20'N 65°49'W). The site is

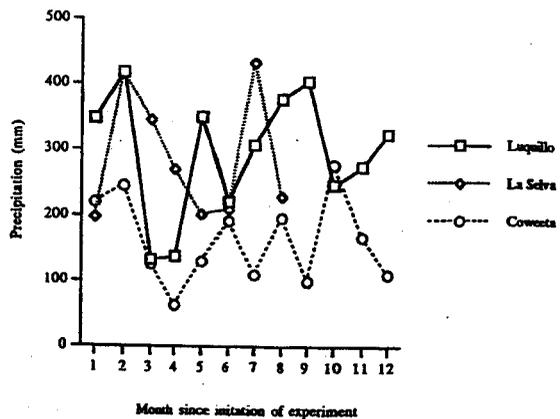


Fig. 1. Precipitation at Coweeta (CWT), Luquillo (LUQ) and La Selva (LAS) for the period of the experiment.

classified as lower montane rain forest (Odum and Pigeon, 1970). Elevation ranges between 300–600 m. Mean monthly temperature varies from 20.8–24.4°C with a mean annual precipitation of 3456 mm (Brown et al., 1983). Precipitation during this experiment amounted to 3531.7 mm (Fig. 1). Soils are dominated by Zarzal series that are deep Oxisols of volcanic origin (Huffaker, 1995).

2.1.3. La selva, Costa Rica (LAS)

The study site was at the La Selva Biological Station (10°26'N, 83°59'W) which is operated by the Organization for Tropical Studies (OTS) and is located in the Atlantic lowland rainforest (McDade and Hartshorn, 1994). The plot was in a small patch of secondary forest dominated by *Ochroma lagopus*. The mean monthly temperatures is 25.8°C and the average annual rainfall is 4000 mm (OTS, *pers. comm.* (Fig. 1)). The soils are alluvial and the plots are adjacent to the Rio Puerto Viejo.

2.2. Experimental design

Recently, senesced leaves were collected at each site: *Rhododendron maximum* at CWT, *Drypetes glauca* at LUQ and *Cedrela odorata* at LAS. Three grams of air-dried litter were placed in individually marked fiberglass litterbags measuring 10×10 cm. Three sets of bags were oven dried at 50°C to establish the relationship between air dry and oven-dry mass. At each site, 144 litterbags were established in each of the

three adjacent plots giving a total of 432 bags at each site. Half of the litter bags were treated each month (CWT) or bi-weekly (LAS and LUQ) with naphthalene, a biocide which repels microarthropods. The rate of application was 100 g per m² per month (all sites) and the naphthalene was distributed around the litterbags so that fauna would be repelled from the portion of the plots containing these bags. This is because there is evidence from microcosm studies that naphthalene can affect microbial activity (Seastedt and Crossley, 1983; Blair et al., 1989). Although there is no evidence that application at the rates used in this study affect microbial activity, this caveat must be borne in mind when the results are being assessed.

Each month six litterbags (3 from naphthalene treated subplots and 3 from subplots where the animals had unrestricted access) from each of the three replicated plots were collected at random at all sites (54 bags total per month)

Litterbags were oven-dried at 50°C and weighed. The litter was subsequently ground and subsamples ignited at 500°C to determine the ash-free dry weight (AFDW). Differences in mass loss from litterbags with and without microarthropods and across sites were analyzed by analysis of variance (ANOVA). Differences in treatment effects discussed below are significant at the $p < .05$ level or below unless otherwise stated. The three litterbags from each subplot were averaged since they did not represent independent estimates of the mean (Hurlbert, 1984).

2.3. Litter quality

%C and %N of litter, recently senesced litter, was analyzed by compustion using a Carlo Erba C/N analyzer (instrument NA1500). %N and C:N ratios were fitted to the mean litter mass remaining for all litter types after approximately 250 days using simple linear regression.

2.4. Characterization of fauna

Initial results from the analysis of assemblage structure from the three sites are presented here. A litter sample from 300 cm² was taken at each site (dates in Table 2). The animals were extracted using Berlese type funnels. Oribatid mites were slide mounted and separated into morphospecies. Species

richness (number of species in the sample) and Fisher's α index was calculated. This latter index is recommended (Magurran, 1988) because of its high discriminant ability and its relative insensitivity to sample size. The score is given by the equation: $\alpha = N(1-x)/x$; where x is the iterative solution of $S/N = (1-x)/x[-\ln(1-x)]$. S is the species richness and N is the abundance of animals in the sample.

3. Results

3.1. Decomposition rates

Decomposition was influenced by fauna at each site and for all litter species. Fauna was found to have little effect on mass loss of *Rhododendron*. During the initial months the mass loss rates seem marginally retarded by the presence of fauna but this was not statistically significant. On one occasion, during the last 100 days of first year, the fauna had a positive influence of mass loss of *Rhododendron* (Fig. 2). At the end of the sampling period (347 days) *Rhododendron* had lost 15% of its original mass.

The presence of faunal strongly influenced the decomposition rates of *Drypetes* at LUQ (Fig. 3). Within 50 days the trend was apparent and the mass loss was significantly accelerated after 150 day in the field. At the end of the period, reported on here (251 days), less than 20% of the initial mass remained in

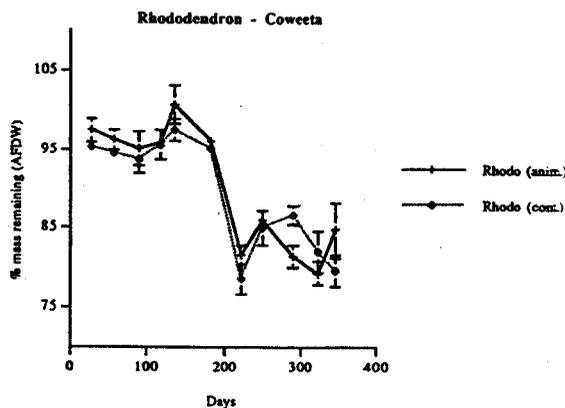


Fig. 2. Mass remaining (% ash-free dry weight - AFDW) in *Rhododendron maximum* litterbags over time at Coweeta (CWT). Anim.=litterbag to which fauna has unrestricted access; com.= litterbags from plots which received naphthalene.

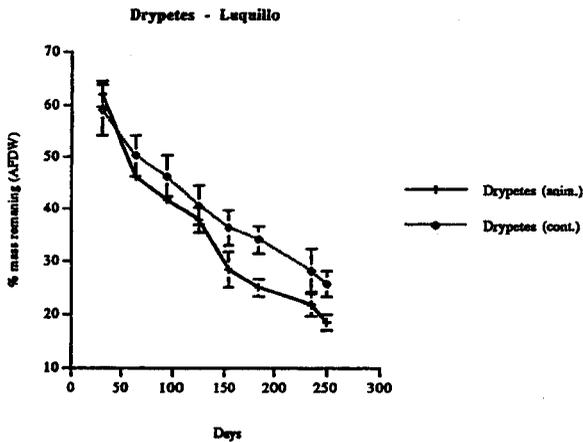


Fig. 3. Mass remaining (%AFDW) in *Drypetes* sp. litterbags over time at Luquillo (LUQ). Anim.=litterbag to which fauna has unrestricted access; cont.=litterbags from plots which received naphthalene.

litterbags with a faunal presence. There was a 28% mass loss difference between the bags which afforded to fauna access and those which had received naphthalene.

Decomposition at LAS was consistently affected by the presence of fauna (Fig. 4). The pattern for more slowly decomposing *Cedrela* was the same although the faunal effects was slight for the first 150 days. At the end of 281 days an average of 36% of *Cedrela* had been lost from the litterbags. There was an increase of 17% mass loss in faunated litterbags containing *Cedrela*.

3.2. Litter quality

Litter ranked, by initial %N, went from *Drypetes*>*Cedrela*>*Rhododendron* (Table 1). The carbon concentration was similar in all the three litters. A linear negative relationship between initial %N and mass of litter remaining after 250 days is described by the equation $y = -25.99x + 97.147$, $r^2 = 0.997$. A linear

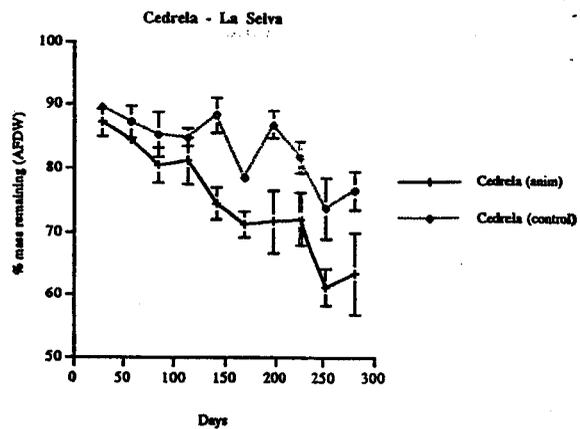


Fig. 4. Mass remaining (%AFDW) in *Cedrela odorata* litterbags over time at La Selva (LAS). Anim.=litterbag to which fauna has unrestricted access; cont.=litterbags from plots which received naphthalene.

model of litter remaining fitted to initial C:N is described by $y = 0.403x + 34.519$, $r^2 = 0.41$.

3.3. Microarthropod assemblages

Applications of naphthalene were effective in reducing abundance of microarthropods in litterbags. A reduction of abundance in excess of 58% was found.

Oribatid mites were the numerically dominant group amongst the microarthropods at all sites (Table 2). They represented an almost constant portion (68.72–69.89%) of the fauna in both the tropical and temperate sites. Collembola were the next most abundant component of the microarthropod fauna at CWT (18.54%) but represented less than 12% of the tropical fauna. Mesostigmatid mites formed a greater component of the tropical faunas than at the CWT. Astigmatid and Prostigmatid mites and Protura were minor components (<3%) of all faunas.

Species richness of oribatid mites was comparable in a 300 cm² sample at all sites (49–51 species);

Table 1
C (%), N (%) and C:N ratios of three litter types at start of experiment. Numbers are means of three samples (standard error in brackets)

| Litter | Site | N% | C% | C:N |
|-----------------------------|----------------|--------------|---------------|---------------|
| <i>Rhododendron maximum</i> | Coweeta (CWT) | 0.42 (0.02) | 48.25 (0.1) | 114.45 (4.46) |
| <i>Cedrela odorata</i> | La Selva (LAS) | 1.35 (0.02) | 43.57 (0.468) | 32.22 (0.63) |
| <i>Drypetes glauca</i> | Luquillo (LUQ) | 2.94 (0.136) | 47.44 (0.38) | 16.12 (0.55) |

Table 2

Abundance and proportion of animals in principal microarthropod groups from three study sites. Abundance is from a sample of 300 cm². The CWT figures are a mean of three samples taken on the same date (25 October 1995). Samples were taken at LUQ (1st May 1996) and LAS (23 April 1996)

| | CWT | | LUQ | | LAS | |
|--------------|-----------------------|-------|----------------------|-------|----------------------|-------|
| | Abundance (n=1451) | % | Abundance (n=857) | % | Abundance (n=209) | % |
| Acari | | | | | | |
| Oribatids | 1292.33 | 69.96 | 591 | 68.72 | 144 | 68.89 |
| Mesostigmata | 136.33 | 7.05 | 141 | 16.39 | 45 | 21.53 |
| Astigmata | 2.66 | 0.45 | 10 | 1.2 | 3 | 1.43 |
| Prostigmata | 47.33 | 2.51 | 11 | 1.27 | 2 | 0.95 |
| Collembola | 360.66 | 18.54 | 100 | 11.6 | 15 | 7.17 |
| Protura | 35 | 1.73 | 4 | 0.46 | 0 | 0 |

Table 3

Oribatid diversity at the three study sites. Species richness is the number of species in a sample of 300 cm². Fisher's α is a diversity index which is recommended for its good discriminant abilities and its relative insensitivity to sample size

| | CWT | LUQ | LAS |
|-------------------|-------|--------|--------|
| Species richness | 49 | 49 | 51 |
| Abundance | 987 | 472 | 114 |
| Fisher's α | 10.84 | 13.737 | 35.378 |

however, the diversity, measured by Fisher's α , was greater in both tropical sites than at the temperate site (Table 3). Highest diversity was found at LAS.

4. Discussion

We have shown here that decomposition at the tropical sites proceeds at more even rates than at the temperate site, where the slow rate of decomposition is punctuated by seasonally dependent spurts of rapid mass loss (contrast Fig. 2 with Figs. 3 and 4).

The overall ranking of mass remaining in litter bags after 250 days was strongly related to the initial %N of the litter types ($r^2=0.997$). Such a strong relationship between %N and decomposition amounts is unusual over a large geographical area. Berg et al. (1996) found a relationship between mass loss limits and N concentration in an analysis of 41 decomposition studies from eight forest types from latitudes 40° 05' to 60° 49'. The relationship was weaker than we

report ($r^2_{adj}=0.45$). Dyer et al. (1990) also report a weak relationship between mass loss and initial %N ($r^2=0.09$). Their survey included 92 studies from climatic regions ranging from boreal to tropical forests. The strong relationship reported here must be appraised with caution considering the limited number of litter types included. However, unlike other studies where several litters of variable quality are studied we have applied a uniform methodology across a broad geographical range.

Decomposition was affected by the presence of fauna in this experiment. This result clearly resonates with the large number of studies affirming the generality of this observation (Seastedt, 1984). What is clear from the present study is that faunal influences are strongest in the tropics. This lends support to a suggestion by Lavelle et al. (1993) that biological systems of regulation on organic matter turnover are most strongly expressed in moist tropical situations, where optimal conditions of temperature and humidity remove the higher level constraint of climate over biota.

Patterns of assemblage structure of microarthropods revealed broad similarities between the tropical and temperate sites. The lower abundance of microarthropods at the tropical sites confirms similar observations by many researchers (Anderson et al., 1983; Collins, 1980; Pfeiffer, 1996; Levings and Windsor, 1996). Oribatid mite diversity is similar in pattern to those previously reported by Stanton (1979) who compared diversity in Costa Rican habitats with paired habitats in Wyoming, USA and showed a constancy of

species richness in all forests (12–14 species per 100 g) but a larger turnover of species across the landscape yielding a higher beta diversity at the tropical location.

In summary, we have demonstrated that climate, substrate quality and fauna influence decomposition in a cross-site study. Seasonality strongly influenced the course of decomposition at the temperate site. When tropical sites were compared decomposition rate was greatest for the leaf type with the greatest initial %N. The fauna had some influence on decomposition at all sites but were most influential at tropical sites. To further elucidate the relationship between the faunal assemblages and decomposition we have initiated studies on the decomposition of a single substrate (*Quercus prinus* L.) across our three study sites (Heneghan et al. in prep.).

Acknowledgements

This study has been funded by the National Science Foundation (DEB9416819). We thank the Organization of Tropical Research (OTS) and the members of the Huertos project, particularly Dr. J.J. Ewel, Ankila Hiremath and Seth Bigelow for their hospitality at La Selva, and very specially to Silvino Villegas – for his very meticulous maintenance of the project there. Thanks to the Luquillo LTER site for extending their facilities to us. We are much indebted to Katherine Dowell whose hard-work and patience sped up progress on this project. Finally, we would like to thank Jim Fuller and Tom Maddox in the soil chemistry lab at the Institute of Ecology for providing the litter chemistry data.

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