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Red oak litter promotes a microarthropod functional group that accelerates its decomposition

Randi A. Hansen
*Department of Biological Sciences, University of South Carolina, Columbia, South Carolina 29208, USA**

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Abstract

The contribution of microarthropod activity to litter decomposition varies widely but can be substantial. Oribatid mites are the most diverse and abundant of the microarthropod groups in forest litter. This experiment was designed to examine the effect of litter type and complexity on the diversity and species composition of oribatid mites, and to test whether alterations in species composition due to litter type affected litter decomposition. In an array of plots on a mixed-hardwood site in the mountains of North Carolina, I exposed microarthropod assemblages to a range of litter types: yellow birch, sugar maple, red oak and two mixed litters. Over several years, the litter types selected oribatid mite assemblages of different species composition. By comparing the decomposition of consecutive cohorts of litter, it was possible to detect differences in decomposition accompanying the shifts in the assemblage. A comparison of the mass loss rates between the two litter cohorts over eighteen months reveals similar trajectories for four litter types. In the oak litter, however, the second cohort disappeared significantly faster than the first. In both years, the litters came from the same trees and were nearly identical in initial carbon and nitrogen contents. Since the response was specific to oak litter, it is unlikely that differences in environmental factors are responsible for the faster mass loss of oak. A significant increase of endophagous oribatid mites, those that burrow into plant material, in the second cohort of oak may account for its accelerated decomposition. The woody petioles and thick leaf-planes of oak leaves provide microhabitats for burrowing mites. Endophage activity can accelerate the litter decomposition both through direct comminution of leaf material and by facilitating microbial growth. Because of their low population growth rates, oribatid populations that are reduced by disturbance are slow to recover and by disrupting these non-resilient populations, disturbance may have long-term repercussions for decomposition.

Introduction

Rates of decomposition and nutrient cycling are determined largely by the activity of assemblages of decomposer fauna that mediate them. While this is well established, inquiry at the next level – the sensitivity of process rates to variability in the structure of those assemblages, their species membership and representation of functional feeding groups for example – has barely begun. Typically, the assemblages most intimately involved in decomposition are a diverse array of invertebrate species. Assessing the capacity of anthropogenic and natural disturbances that perturb these assemblages to alter ecosystem process rates will require an understanding of both the sensitivity of the process to assemblage structure and of assemblage structure to disturbances.

Demonstrations of species dependent effects on decomposition and nutrient cycling are available from a variety of aquatic systems. Zooplankton species of different feeding modes produce dissolved nutrient concentrations in lakes (Brett et al. 1994). The species composition of shredder assemblages in streams is a determinant of litter decomposition rates (Whiles and Wallace, 1997). Bioturbator species of the soft marine benthos set nitrification and denitrification rates based

* FAX No: (803) 777 4002. E-mail: hansen@sc.edu

on their burrow irrigation behavior (Mayer et al., 1995; Pelegri and Blackburn, 1995).

For the decomposer microarthropods of the litter and soil, such examples are accumulating. Faber and Verhoef (1991) demonstrated differences in collembolan species' effects on nitrogen mobilization. Schulz and Scheu (1994) have shown species specific effects on cellulose breakdown among oribatid mites involved in the decomposition of wood. Microarthropod assemblages of different species composition have been shown to yield different rates of leaching of mineral nutrients (Heneghan and Bolger 1996). Siepel and Maaskamp (1994) have shown that oribatid species belonging to different feeding guilds, defined by carbohydrase activity, vary in their effects on microbial respiration.

In most of these examples, differences in location of feeding or manner of processing substrates were identified by which species may be organized into more refined functional groups than those defined simply by diet. Using a compilation of such examples for soil microarthopods, Faber (1991) has proposed a functional classification that incorporates microhabitat.

Within the oribatid mites, the functional classification that has been most widely used is based on adult diet and designates microphytophages, which feed exclusively on microflora, macrophytophages which feed directly on decaying substrates and panphytophages whose diet is broad and includes both these categories (Shuster, 1956; Luxton 1972). Endophages are another category comprised of species that are obligate burrowers in woody microhabitats during juvenile stages. The endophages include the macrophytophages but also include species that are panphytophagous as adults. This group is functionally cohesive and significant in its specialization on the most recalcitrant substrates. Because juvenile abundance and activity are substantial relative to that of adults, endophagy delineates a more accurate functional classification than does macrophytophagy defined by adult diets.

Arthropod exclusion studies, reviewed by Seastedt (1984), reveal a wide variation in the arthropod contribution to decomposition among leaf types and across sites. For deciduous litter, the presence of microarthropods has been found to increase first year mass-loss from deciduous litter by anywhere from 4% (Anderson, 1973) to 43% (Cromack, 1973) and 49% (Elkins and Whitford, 1982). The wide range of faunal influence is not surprising when one considers the ways in which microarthropods accelerate decay. As with the invertebrates in many aquatic examples, their primary role is that of a catalyst for microbial growth, facilitating fungi and bacteria by exposing, inoculating and conditioning substrates. The variety of arthropod species is typically prodigious, encompassing a wide range of feeding habits and microhabitat preferences. The variation in species composition across sites can be quite high as well (Lamoncha, 1994). The contribution of the microarthropod assemblage to decomposition can be expected to vary with its species membership and on the interactions of those species with the array of food resources and microhabitats the local litter type supplies.

In this field study, I exposed microarthropod assemblages to a range of litter types over several years to assess whether habitats of different litter types supported assemblages of different species composition and diversity. Over the course of three years, different litter types were found to select oribatid assemblages that differed in their diversity and species composition (Hansen, in press; Hansen and Coleman, 1998). I compared the decomposition rates of treatment litters from two successive years, while these shifts in the assemblage were taking place. The second litter cohort of each litter type decomposed in the presence of an assemblage that had shifted due to exposure to that litter type. By comparing the decomposition rate of successive litter cohorts, it was possible to detect changes in decomposition accompanying the shifts in the assemblage.

Materials and methods

The experiment was carried out on a 0.3 ha mixed hardwood site at the Coweeta U.S. Forest Service Hydrological Laboratory in the Nantahala mountains of western North Carolina, within the Blue ridge Physiographic Province, USA, latitude 35° 03′ N, longitude 83° 25′ W. In October 1993, forty-two one m^2 plots were established in a grid across the site. Plots were sheltered from natural litterfall with a covering of 1 cm mesh hardware cloth. In November 1993 and 1994, each plot received 400 g of leaf litter in one of five treatment litter types. Litter of the three dominant tree species on the site, yellow birch (*Betula alleganiensis*), sugar maple (*Acer saccharinum*), red oak (*Quercus rubra*), were each represented in six plots. Two mixed litters were each represented in 12 plots. One was a mixture of equal portions oak, birch and maple (3-Mix) and the other a mixture that included

equal portions of seven litters, oak, birch, maple and an additional four litter types: green ash (*Fraxinus pennsylvanica*), striped maple (*Acer pensylvanicum*), and American chestnut (*Castanea dentata*) and mixed herb litter (7-Mix). The five treatment types were distributed in a randomized design. All litter types were collected on the site with the exception of birch and maple litter, collected nearby. Treatment litter was collected from the ground at leaf fall and air dried in the lab. Samples of each leaf type were ground and carbon and nitrogen contents determined using a Carlo-Erba NA1500 model C/N analyzer.

In each year, plots received litterbags of 15 cm × 15 cm nylon mesh holding eight grams of dried litter. Six collections of 1993 litter and five of 1994 litter yielded an eighteen-month decomposition trajectory for each of the two litter cohorts. Following extraction of microarthropods, the dried litter was weighed to determine mass loss. In the final litterbag collections of the two cohorts, in April of 1995 and April of 1996, the density of petioles and thickness of leaf planes for the oak litter were quantified. Petiole density was calculated from the weight and volume of all petioles in each bag, volume being measured by displacement of water. Squares of one cm^2 of leaf plane, 20 per litterbag, were weighed to obtain a measure of leaf plane thickness. Differences between years in litter mass loss measures and final nitrogen concentrations were tested using unpaired *t*-tests (SAS Institute 1989).

Microarthropods were extracted from each set of bags using modified Tullgren funnels and the adult oribatid mites were identified to species. In most collections, the number of mites was very low and the animals from only four collection dates are reported on here, two in the late summer and early fall of 1994 and two from the same period in 1995. For analysis of the changes in mite abundance and richness between years, the litterbags from the two collection dates in each year were pooled.

Endophages were classified as species belonging to several higher taxa for which all known species are endophagous: the Ptyctima, or box mites (Michael, 1888), Liacaroidae, (R.A. Norton, pers. comm.; Lions and Gourbière, 1988), Xenillidae, Hermaniellidae (Michael, 1882), Carabodoidea (Michael, 1882; Reeves, 1991, 1992) and Cepheidae (Wallwork, 1958; Nannelli, 1979). While there are no reports of members of Xenillidae, Hermaniellidae or Carabodoidea burrowing in leaf material, Xenillidae and Hermaniellidae have been reported in wood, and Carabodoidea, in wood, lichens and fungal fruiting bodies. Since such data are very limited, these taxa are included in the analyses because of their potential to burrow in the litter material. To inspect litter for traces of animal activity, I dissected dry leaves and petioles from the oak and maple litterbags from the final collection of each cohort. To observe the locations and habits of live endophages, I also dissected leaves of the treatment litter types and pieces of woody debris from the site, using fresh material in the fall of 1996.

Results

For all litter types, initial litter quality, as measured by initial carbon and nitrogen concentrations, did not differ between the two years for any litter type (Table 1). Likewise, for four of the five litter types, the mass lost in eighteen months was not different for 1993 and 1994 litter (Figure 1 a–d). The second cohort of red oak litter, however, decomposed markedly faster than the previous year's litter. (Figure 1e). After 18 months in the field, 1994 oak litter had lost 10% more of its mass than 1993 litter (Table 1). The density of oak petioles declined significantly from 0.72 g/cm^3 ± 0.028 in 1993 litter to 0.65 g/cm^3 ± 0.047 in 1994 litter (t=3.07, df=10, p=0.012) and oak leaf planes were 13% lighter per unit area, though the difference was marginally insignificant (t=1.78, df=10, p=0.11). The nitrogen content of oak litter at 18 months was significantly higher in the second cohort while other litters did not differ between years (Table 1).

The total abundance of oribatid mites in the bags did not differ among the litter types or between years (Hansen and Coleman, 1998). Among the endophages, however, there was a marked response to the oak and oak containing litters. The adults of twenty-seven species of endophagous oribatid mites were collected from the bags (Table 2). In the pure oak litter, endophage abundance doubled in the second year's litterbags and increased to a lesser extent in the mixtures containing oak (Table 3). This response was not confined to one or two endophagous species. Endophage richness, the number of species per bag, increased similarly in accord with the representation of oak in the litter (Table 3). A regression of the changes in endophage abundance and richness from the first to second litter cohort against the proportion of oak in each litter type shows the development of the correlation between endophages and oak litter (Figure 2).

Table 1. Initial carbon and nitrogen concentrations for the treatment litter types in the first and second year, and N concentrations and % mass remaining after 18 months in the field. Data are means and standard errors. N=6 bags per year for birch, maple and oak. N=12 bags per year for the two mixed litters. Unpaired *t*-tests were used to test for differences between years: $^{*}p<0.01$, $^{**}p<0.001$

Litter type	Initial %C		Initial %N		Final %N			% Mass remaining		
	1993	1994	1993	1994	1993	1994	*t*	1993	1994	*t*
Oak	51.22	50.92	0.88	0.82	1.40 ± 0.04	1.67 ± 0.06	3.66*	56 ± 1.3	46 ± 1.6	4.68**
Birch	52.60	50.99	1.01	1.04	1.64 ± 0.08	1.68 ± 0.05	0.57	62 ± 3.5	61 ± 1.2	0.18
Maple	50.47	49.36	0.76	0.71	1.43 ± 0.08	1.56 ± 0.06	0.90	53 ± 3.3	58 ± 4.7	0.88
3-Mix	51.43	50.46	0.88	0.86	1.56 ± 0.03	1.56 ± 0.05	0.03	56 ± 2.4	54 ± 1.5	0.74
7-Mix	49.18	48.17	0.99	1.01	1.96 ± 0.10	1.82 ± 0.03	1.42	52 ± 1.1	52 ± 1.6	0.21

Table 2. Endophagous species in litterbags: Total abundances in litterbags and microhabitat observations. Immatures of Ptyctima, and of *Liacarus*, not identifiable to species, were found in woody debris and oak petioles

Endophage taxon	Species	Abundance	Microhabitat observations
Cepheidae	*Cepheus sp. nr corae*	247	Numerous immatures on oak leaf undersides
Ptyctima	*Rhysotritia ardua*	234	Adults in oak petioles, acorns and woody debris
Ptyctima	*Synichotritia sp.*	130	
Ptyctima	*Archiphthiracarus sp. a*	105	
Liacaridae	*Liacarus latus*	92	Liacarus immatures in oak petioles and woody debris
Ptyctima	*Phthiracarus sp. a*	71	Adults in oak petioles
Ptyctima	*Mesotritia glabrata*	36	
Hermanniellidae	*Hermaniella sp.*	20	Adults and immatures in woody debris
Carabodidae	*Carabodes phylliformes*	19	
Ptyctima	*Euphthiracarus sp.*	16	Adults in woody debris
Liacaridae	*Liacarus detosus*	14	Liacarus immatures in oak petioles and woody debris
Cepheidae	*Oribatodes sp. nr mirabilisa*	13	
Carabodidae	*Carabodes spiniformes*	12	
Carabodidae	*Carabodes nantahalensis*	8	
Ptyctima	*Atropocarus striculus*	7	
Carabodidae	*Carabodes clavatus*	6	
Carabodidae	*Carabodes falcatus*	6	
Carabodidae	*Carabodes granulatus*	6	
Carabodidae	*Carabodes radiatus*	6	
Ptyctima	*Microtritia minima*	6	
Carabodidae	*Carabodes higginsi*	3	
Ptyctima	*Archiphthiracarus sp. b*	2	
Carabodidae	*Carabodes chandeleri*	2	
Carabodidae	*Carabodes interruptus*	2	
Ptyctima	*Pthiracarus sp. b*	2	
Xenillidae	*Xenillus sp.*	2	Adults and immatures in woody debris
Liacaroidea	*Tenualoides sp.*	1	

Table 3. Endophage abundance and richness in the two litter cohorts for each of the five treatments. Data are means from bags collected in two sample dates in each year and standard errors.

Litter type	Endophage abundance		Endophage richness	
(n per year)	1993	1994	1993	1994
Oak (12)	5.42 ± 1.10	11.50 ± 2.11	2.0 ± 0.4	3.8 ± 0.4
Birch (12)	2.58 ± 1.05	2.41 ± 0.63	1.7 ± 0.4	1.6 ± 0.4
Maple (12)	5.00 ± 0.78	5.83 ± 1.32	2.9 ± 0.4	2.8 ± 0.3
3-Mix (24)	5.75 ± 0.90	8.00 ± 1.05	2.8 ± 0.4	3.5 ± 0.4
7-Mix (24)	3.62 ± 0.54	5.54 ± 1.05	2.3 ± 0.3	2.8 ± 0.3

Dissections of dry and fresh treatment litter revealed the activity of several endophage types. Dry oak leaves from the litterbags contained burrows with fecal pellets within the petioles and excavations containing fecal pellets in the leaf planes where they thickened near the veins. Neither maple nor birch leaves contained such excavations. Dissection of fresh oak leaves from the plots in 1996 revealed burrowing activity in the petiole and central vein by adults of *Rhysotritia ardua* (Koch), immatures of *Liacarus*, of which two species were found as adults in the litterbags, and immatures of Ptyctima or 'box-mites', a group that includes the superfamilies Phthiracaroidea and Euphthiracaroidea and ten of the endophage species found in the litterbags. Relatively undecomposed petioles from the superficial litter had not been colonized while well-decomposed petioles were also empty, though many held burrows with fecal pellets. Colonized petioles generally contained one or two animals. Unidentified oribatid immatures, fecal pellets and microarthropod eggs were found in excavations in oak leaf-planes though it was unclear whether microarthropods had made excavations or had moved into preexisting ones. Live immatures and numerous casts from deutonymph and tritonymph molts of the most abundant endophage, *Cepheus* sp. nr. *corae*, were very abundant in the fresh oak litter. They were consistently found clinging to the outside of leaf-veins protruding on the leaf underside. Immatures of *Cepheus* were also common in the extractions from the bags. *Cepheus* may be excavating chambers in the leaf-plane where it thickens near the veins, rather than burrowing in the leaf's woody tissues.

Discussion

Decomposition

The first factors one might consider to account for a change in decomposition rate from one year to the next are differences in environmental factors and differences in litter quality. In this case, the concordance in mass loss between cohorts for litter types other than oak is evidence that relevant environmental conditions did not differ substantially between the periods during which they decomposed. Collections were made from the same trees in both years, controlling for variation in quality due to genotype and microclimate. C:N ratio, the most common measure of litter quality, was nearly identical in the two oak cohorts.

The rise in endophage numbers in oak litter from the first to the second year, coupled with the observations of endophage activity in the litter, is evidence that an increase in endophage activity was responsible for the acceleration of decomposition. The importance of endophages in the structural changes in litter has been well documented. Fossil evidence indicates that endophagous oribatid mites were important decomposers in the Paleozoic before insects joined the wood-boring functional group (Labandeira et al., 1997). Modern records of endophage activity most commonly document Ptyctima species transforming pine needles into packets of fecal pellets (Ponge, 1991 and references therein). Bal (1970), in a micromorphological study of decaying red oak, found *Rhysotritia minima* (Berlese) mining within the 'ribs and branches' of red oak leaves.

The direct effect of microarthropod respiration on decomposition, calculated from microarthropod biomass and metabolic rates, is quite modest, ranging from 1.5 to 10%. The oribatid component of that small figure was estimated, in one temperate wood-

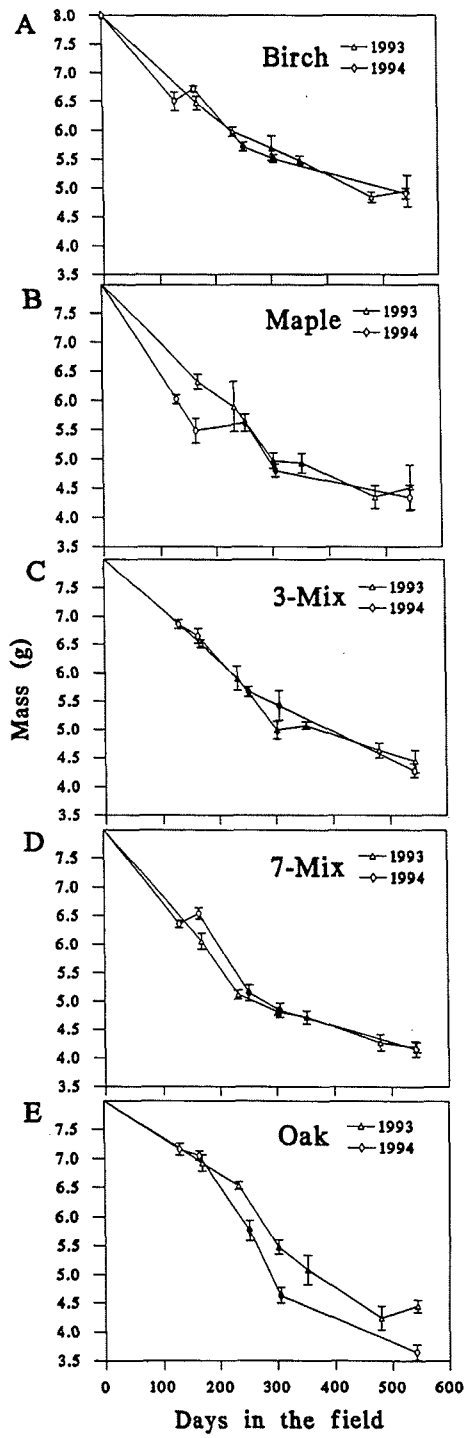

Figure 1. Mass-loss over 18 months from 1993 and 1994 litterbags of each litter type: (A) yellow birch, (B) sugar maple, (C) mix of birch, maple and red oak, (D) mix of seven litter types, (E) red oak. Filled symbols denote the four litterbag collections from which endophage data were derived. Data are means and standard errors. N=6 bags per date for birch, maple and oak and N=12 bags per date for the two mixed litters.

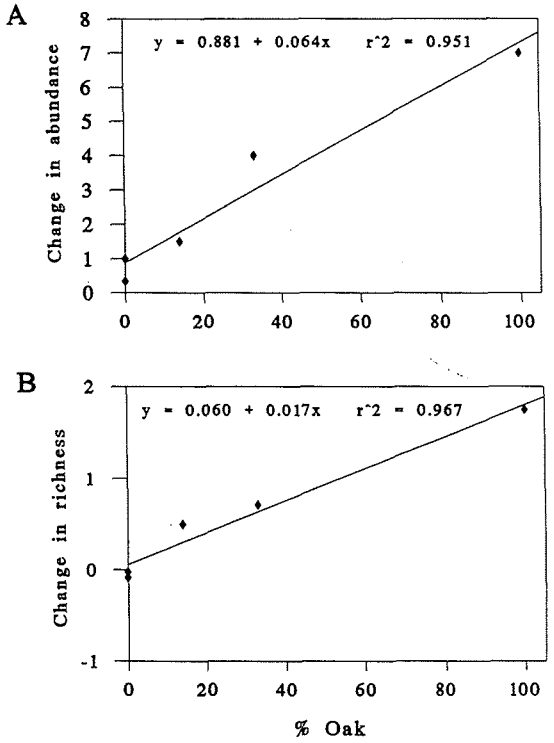

Figure 2. Regression of: (A) the mean change in endophage abundance and (B) the mean change in endophage richness (number of species per bag) from the first to the second litter cohort for each of the five litter types against the proportion of oak leaves in the litter treatments: oak=100%, 3-Mix=33%, 7-Mix=17%, birch and maple=0%. N=12 bags per year for birch, maple and oak and N=24 bags per year for the two mixed litters.

land study, to be 45% (Petersen and Luxton, 1982). Substantial microarthropod contributions to mass loss are primarily through facilitation of microbial activity.

Endophage activity in broad-leaf litter should facilitate microbial activity in both the petiole and leaf plane. Animals penetrating the interior of the petiole and leaf mesophyll spread inoculum within the substrate and, through comminution, expose new substrate for microbial colonization. The transformation of petioles and veins into chambers of fecal material also increases their moisture holding capacity. The litter layer undergoes dramatic fluctuations in moisture and periodic drying is a critical limitation to microbial growth (Dix, 1984). Such patches of increased moisture retention might serve as refugia from desiccation for fungal mycelia from which they can recolonize the leaf plane more rapidly when conditions become favorable again.

While the numbers of animals extracted from bags appears quite low to have had a strong impact on de-

composition, the actual numbers of endophages in oak were undoubtedly much higher. The rarity of juvenile endophages in extractions and the presence of endophages in dry litter inspected after extraction are indications that extraction efficiency of Tullgren funnels for these mites is poor. It is particularly low for juveniles, who, because of their higher abundances and exclusively burrowing habit, should be responsible for more burrowing activity than the adults. Efficiency is also probably reduced in litter types with microhabitats suitable for burrowing, like red oak, since animals in burrows are less likely to be extracted than animals mobile in the open litter. In spite of these drawbacks, the abundance of extracted animals is still useful as a proportional measure of the actual populations active in the litter.

Many faunal groups active in decomposition were not documented in this study. It examined only the oribatid mites, which, in total abundance, did not differ between the years for any litter type. We cannot, therefore, rule out altogether, the possibility of oak-specific responses in other taxa contributing to the change in mass-loss. However, the significant loss in petiole density is unambiguously the work of burrowers. The clear affiliation of endophages with oak microhabitats and the match between the slow life histories of endophagous species and the lag-time in the shift in decomposition implicate endophages as drivers of the mass-loss changes.

Endophage populations

Among the endophagous species on the site there is no doubt variation in the degree to which oak petioles are habitat. Roughly half of the endophagous species identified from the site were found in the litterbags. Of these, the adults of three species and the juveniles of two endophagous groups were observed in oak leaves. Berg (1991) censused the species of the endophagous families Phthiracaridae and Euphthiracaridae and observed a range of specialization from those exclusively in wood to those divided between wood and litter. In this experiment, buried small woody debris is abundant on the site and undoubtedly present in every plot.

The endophages' specificity for oak among the litter types is due to the oak's substantial and stable woody microhabitats relative to those in other litter types. Endophages in foliar litter burrow in parenchymatic tissues surrounded by epidermal sheaths (Gourbière et al., 1985; Lions and Gourbière, 1988). The woody components of birch leaves are too narrow to support the burrowing of most species. While the petioles and veins of some maple leaves can be of suitable size for burrowing, the sheath around the petiole is lost quite early in decomposition. Unsheathed petioles represent a less suitable microhabitat probably because they are more susceptible to desiccation and may offer less protection from predation.

While adult oribatid mites are heavily scleritized, eggs and soft-bodied juveniles are more vulnerable to predation. Estimates of survivorship to adulthood for oribatid mites are 10% (Schatz, 1983), and 12% (Norton, 1985 citing Mitchell, 1977). The amount of suitable material for oviposition and juvenile development is likely to be a strong determinant of endophage abundance.

The year long lag-time before the correlation of endophage abundance with the abundance of oak litter appears is consistent with the long-lived adult stages and long generation times and of oribatid mites. One endophagous species has been shown to live for more than 3 years (Webb, 1989) and adult longevities of one to two years may not be uncommon in temperate soils (Norton, 1994). In temperate regions, endophagous species initiate 1–3 generations each year (Luxton, 1981 and references therein) and development times from egg to adult of a year or more are most likely the rule (Norton, 1985). Populations in this study initiated at least two generations during the experiment. In the first year's litter, the adults extracted from the bags would have been those that matured in pre-treatment litter and buried woody debris. Only in the second year would higher rates of oviposition and juvenile survival due to abundance of petioles in oak litter have manifested in higher adult populations.

Implications for effect of disturbance and decomposition

If the selection of the endophage functional group by woody litters seen in this study is a general phenomenon, then endophage activity is an intrinsic factor in their decomposition rates in undisturbed situations. Endophages, though, are characterized by low population growth rates and limited dispersal capacity and are thus slow to recover from disturbances. Those disturbances that remove woody microhabitats, such as burns, can take years to recover their endophage populations (Crossley et al., 1998; Webb 1994). Scheu and Schulz (1996), in a survey of stages of secondary succession, note the strikingly slow development

of the oribatid community after cessation of cultivation relative to the recovery of other soil groups. Studies of oribatid species composition at boundaries between woodlands and disturbed areas (Sgardelis and Usher, 1994; Borcard 1995) have shown that endophages are not present in disturbed areas even when there are adjacent source populations. The finding of Hunt et al. (1988), that pine needles decomposed substantially faster in their native habitat than in an adjacent meadow site, could be a reflection of restricted endophage distribution.

Given the low resilience of these populations, faunal disturbance may have long-term repercussions for decomposition. A previous study at the Coweeta Hydrologic Lab is suggestive of such a link. Oribatid densities fell markedly in response to clear-cutting of a deciduous site, most likely due to extreme litter temperatures (Seastedt and Crossley, 1981). Eight years later, oribatid densities in the cut area were still only 54% of densities of undisturbed forest (Blair and Crossley 1988) and decomposition rates of all litter types remained depressed, most markedly that of oak. The authors hypothesize low microarthropod populations as the cause of the reduced decomposition rates.

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