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Microarthropods in decaying wood from temperate coniferous and deciduous forests

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With one figure

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1. Introduction

Decaying wood represents a large source of energy and nutrients in many forest ecosystems (GRIER & LOGAN, 1977; SWIFT, 1977 a; VOGT *et al.*, 1982; HARMON *et al.*, 1986), and provides both a substrate and a food resource for a diverse assemblage of fauna (ELTON, 1966). Invertebrates assist in the decomposition of wood in a manner similar to that observed in the decomposition of foliar litter (e. g. AUSMUS, 1977; SWIFT, 1977; SEASTEDT, 1984). Relatively little is known about the fauna inhabiting decaying wood. FAGER (1968) reported on species composition and relative abundance of arthropods on natural and artificial logs. HARMON *et al.* (1986) summarized the patterns of decaying wood use by macroarthropods, while WALLWORK (1976), ABBOT *et al.* (1980) and ABBOT & CROSSLEY (1982) documented population densities and effects of microarthropods found on decaying branch litter during the initial stages of decay. However, population densities of microarthropods in larger pieces of decaying wood or in wood in advanced stages of decay have not been quantified.

The present study measured the densities of microarthropods in tree stems (boles) of various stages of decay from a coniferous forest in the northwestern U.S. Numbers of microarthropods in different factions or different types of wood (e. g. sapwood vs heartwood) were recorded, and a list of mite (Acari) species was prepared. These results were compared with published information on microbial respiration and decomposition dynamics of this wood (SOLLINS *et al.*, 1987). A less extensive data set was also collected at two additional sites, a coniferous forest site in the Rocky Mountain region, and a riparian forest site found in the tallgrass prairie biome. Densities of microarthropods from these samples were compared with similar results from samples obtained from the forest floor of these sites. These findings allow us to generalize about patterns of microarthropod abundance in decaying wood.

2. Study sites and methods

Three sites were used to measure microarthropod population densities in decaying wood. The primary site was located in a mature Douglas-fir (*Pseudotsuga menziesii*®) forest at the H. J. Andrews Forest in the Cascade Mountains of Central Oregon. Nutrient dynamics and wood decay rates at this site have been reported in detail by SOLLINS *et al.* (1980, 1987). The site (called High 15 in the 1987 report) had an average temperature of 8 °C on an annual rainfall of 2150 mm. A second site was located in a grand fir (*Abies grandis*®) forest at the University of Montana Biological Station, located about 1100 km east of the Oregon site in western Montana. The Montana forest also had an average temperature of 8 °C, but rainfall averaged only 556 mm. Decaying boles of Douglas fir trees were sampled for microarthropods at both sites. Boles of a few other species of trees were also sampled for microarthropods. Both sites

had typical mor soils, with a 1–2 cm litter layer of decomposing conifer needles and fine woody debris. The third site was located in a riparian forest in northeastern Kansas, a bur oak (*Quercus macrocarpa*) forest described by KILLINGBECK (1986) and ABRAMS (1986). Temperature averaged 13°C and rainfall averaged 835 mm at this largely grassland site. Decaying boles of bur oak and hackberry (*Celtis occidentalis*) were sampled. The forest soil in the deciduous was a classic mull type formed, in part, by extensive earthworm activity. Small amounts of raw litter occurred over a rich A horizon.

Wood was classified into decay classes according to the procedure detailed by TESKA & CROMACK (1980) and HARMON *et al.* (1986). The age since the death of the tree could be established for some of the samples by analysis of tree-ring growth increments of living and dead trees. However, for wood in advanced stages of decay, this analysis was not possible. The use of decay classes therefore provided a means of standardizing decay characteristics of the wood so that measurements such as microarthropod population densities could be compared. Briefly, decay class I is essentially solid wood with intact bark. Decay class II is similar but shows softening of the sapwood. Decay class III has structurally sound heartwood but shows discoloration and evidence of mycorrhizal invasion. Decay class IV has rotten heartwood that breaks into small, blocky pieces, and decay class V has soft, powdery heartwood. Only fragments of outer bark and heartwood remain in decay classes IV and V; inner bark and sapwood have disappeared. All age classes were sampled in Oregon. Montana and Kansas samples were restricted to decay class IV and V boles that could be sampled with a coring tool. The Montana samples were subdivided into surface heartwood (top 5 cm) and subsurface heartwood (5 cm or deeper within the bole). The boles in Kansas were not large; only surface samples were taken.

Quantitative estimates of microarthropods from wood and litter and soil were obtained by high-gradient extraction methods (MERCHANT & CROSSLEY, 1970; SEASTEDT & CROSSLEY 1978). A known volume of wood was obtained with a 5 cm diameter circular hole-cutter or coring tool and placed inside 5 cm diameter × 5 cm deep aluminum canisters. They were placed on a 16-unit extractor for one week or until the wood was thoroughly dried. Extractions were made inside a walk-in cooler with an ambient temperature of 5°C. Initial low recovery of microarthropods from wood samples extracted with this procedure was attributed to the low relative humidity inside the cooler. To correct this problem, the extractor was placed inside large plastic bags. These procedures increased the relative humidity of the apparatus and extractions appeared more efficient. Preliminary samples were not used in subsequent analyses. Wood samples were examined under the dissecting scope following extraction, as no microarthropods found. We suspect, however, that a number of species were not collected with the high-gradient extractor (WALTER *et al.*, 1987). Initial moisture content of wood samples was never lower than 30% by mass and no correlation was observed between population densities of microarthropods and moisture content of the wood. Wood samples from Oregon were obtained in winter and summer. A preliminary analysis indicated no density differences attributable to season, and results were therefore combined. Montana and Kansas samples were obtained only in summer.

Microarthropods were examined under a dissecting scope and sorted into broad taxonomic groupings using the procedure of SEASTEDT & CROSSLEY (1981). The oribatid mites from Montana were identified only to family level. No attempt was made to elucidate the taxonomic composition of the samples from Kansas. A subset of the Oregon samples, consisting of collections made from each decay class, was examined in more detail to provide information on the composition of the mite fauna. These samples were sorted into „morphotypes" under a dissecting scope, and representatives of each type were mounted on a slide and examined with a phase-contrast microscope. Adult specimens differing in morphological characters were given different code numbers, and a „species list" was prepared from these results. This list is undoubtedly an underestimate of the number of mite species found in decaying wood. Voucher specimens were deposited in the Dept. of Entomology Museum at Oregon State University.

3. Results and discussion

3.1. Microarthropod population densities in wood of varying stages of decay

Microarthropod populations in decaying wood collected at the Oregon site exhibited extremely large variation in sample population densities both within and among decay classes. This variation is greater than that observed in litter and soil and reflects the fact that structurally sound wood houses few microarthropods. Populations occurred in regions of microbial activity or cavities created by wood-boring arthropods (e. g. AUSMUS, 1977). As expected, microarthropods in Oregon samples were found only in outer portions of wood during the initial stages of decay (figure 1). Outer and inner bark housed the most microarthropods during the initial stages of decay, and numbers were highest in sapwood during intermediate stages of decay. All of the inner bark and sapwood disappears after about 40 years of decay. Heartwood initially contained no microarthropods in decay class I samples and microarthropod numbers increased through the decomposition process (figure 1). Expressed on a volume basis, population desities in heartwood were not statistically different in decay classes III to V (One-way Anova, $p > .10$). SOLLINS *et al.* (1987) found few relationships between decay class of Douglas fir boles and respiration rate by microbes in

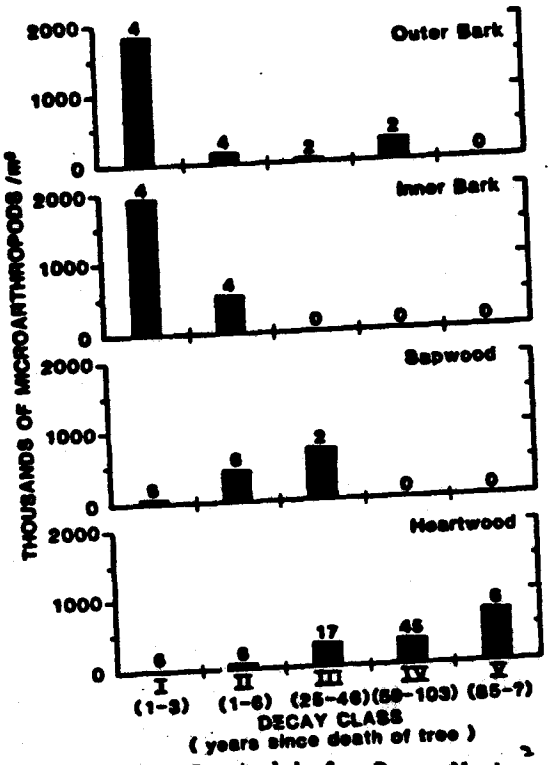

Fig. 1. [illegible] in decaying boles from Oregon. Numbers over bars indicate sample size for each type and decay class of wood. Zeros indicate that the type of wood was no longer present in that age class.

this wood. Peak values occurred in decay class II logs, but values were not statistically different from older decay classes. Moisture and nutrient content (% of mass) progressively increased with decay class, and SOLLINS *et al.* (1987) believed that microbial biomass increased with the age of the decaying wood.

3.2. Population densities in decayed wood versus densities in forest litter and soil

Microarthropod numbers in wood of decay classes IV and V sampled in Montana were not statistically different from population densities observed in similar samples from Oregon. Population densities of microarthropods from the Montana decaying wood were compared similar estimates obtained from the top 5 cm of litter and soil of adjacent forest floor (table 1). These results indicate that decaying wood is a relatively poor substrate for microarthropods. Two types of samples from wood were compared to litter samples; surface wood represented the outer 5 cm of heartwood and included moss adhering to the wood. Microarthropod population densities in the outer 5 cm of wood were about half of those numbers observed in forest litter and soil. Collembolans and prostigmatid mites were the only 2 groups exhibiting statistically different population densities, but trends were similar for all groups. Microarthropod population densities in subsurface wood were almost an order of magnitude lower than those observed in litter and soil. Fewer numbers were observed for all groups, with mesostigmatid mites and collembolans exhibiting the largest difference in population densities. Microarthropod population densities in the subsurface wood were also significantly less than those observed in the surface 5 cm of decaying wood.

Most of the Kansas wood samples were from the surface 5 cm of decaying class IV and V logs. Microarthropods obtained from Kansas samples were less abundant than those found on surface wood from Montana, but generally more abundant than those found on Montana subsurface wood (table 2). The top 5 cm of litter and soil of the Kansas deciduous forest also housed about half of the population densities of microarthropods observed in the coniferous forest soil. This difference is characteristic of microarthropod population densities observed in mor and mull-type surface soils (ANDERSON, 1975). Even in a mull soil, however a comparison of population of microarthropods in wood versus those in litter and soil indicate that decayed wood remains an inferior substrate, with overall densities in wood about half those observed on the forest floor.

Table 1. Population densities of Montana microarthropods in decayed surface heartwood (Classes, IV and V) (outer 5 cm), subsurface wood (>5 cm from log surface) and forest litter + soil.

Microarthropod group	Thousands of individuals/m³		
	surface wood (n = 8)	subsurface wood (n = 17)	litter and soil (n = 15)
Acarina[2])	2,170 (1,690–2,630)	601 (456–688)	3,910 (2,950–4,510)
Cryptostigmata (Oribatida)	1,290 (651–1,950)	395 (309–447)	2,260 (1,680–2,640)
Prostigmata (Actinedida)	408 (187–598)	199 (85–232)	1,360 (856–1,620)
Mesostigmata (Gamasida)	169 (53–248)	17 (4–20)	319 (228–376)
Collembola	135 (88–179)	45 (18–53)	620 (452–712)
Total Microarthropods[2])	2,340 (1,830–2,830)	655 (497–750)	4,830 (3,540–5,200)

Note: Values are arithmetic means with 95 % conf. limits for geometric parentheses.[1])

[1]) Wood samples are from decay classes IV and V. Litter and soil samples were taken from the top 5 cm of the forest floor, but have been converted to numbers/m³ for comparison with wood samples.
[2]) Includes groups not tabulated separately.

Table 2. Population densities of Kansas microarthropods from outer 5 cm of decayed heartwood and from the top 5 cm of the forest floor.

Microarthropod group	Thousands of individuals/m³	
	wood (n = 16)	forest floor (n = 24)
Acarina[1])	1,040 (768–1,208)	1,510 (1,130–1,600)
Cryptostigmata (Oribatida)	472 (304–556)	757 (491–831)
Prostigmata (Actinedida)	154 (87–183)	629 (472–682)
Mesostigmata (Gamasida)	410 (208–493)	123 (42–105)
Collembola	158 (13–332)	369 (215–391)
Total microarthropods[1])	1,280 (974–1,480)	2,630 (1,580–2,220)

Note: Values are arithmetic means with 95 % conf. limits for geometric means in parentheses.
[1]) Includes groups not tabulated separately.

Table 3. Composition of Acari in wood of varying stages of decay.

Group	Identification	Number of specimens in decay class					All samples
		I	II	III	IV	V	
Cryptostigmata	*Phthiracarus sp.*	–	–	–	1	–	1
	Microzetes sp.	–	–	7	5	11	23
	Euphthiracarus sp.	–	1	–	–	–	1
	Parhypochthonius sp.	1	–	–	10	7	18
	Brachychthoniidae, *Gen. sp.*	–	–	–	1	–	1
	Eupochthonius sp.	–	–	–	–	3	3
	Gymnodamaeidae, *Gen. sp.*	–	–	1	–	–	1
	Gryposcramarus sp.	–	–	3	–	–	3
	Cultroribula bicultrata ■, ■	–	–	51	–	–	51
	Cultroribula sp.	–	1	1	–	–	2
	Carabodes sp.	–	–	–	1	3	4
	Tectocepheus sp.	–	–	–	1	7	8
	Oppiella nova ■, ■	4	3	359	16	5	387
	Oppia sp.	–	1	1	–	–	2
	Oppiidae, *Gen. sp.*	–	–	5	–	1	6
	Suctobelba sp.	3	9	–	2	24	38
	Oripodidae, *Gen. sp.*	1	–	–	–	–	1
	Scheloribates sp.	–	2	36	–	6	44
	Ceratozetidae, *Gen. sp.*	–	–	–	–	1	1
	Oribatella sp.	–	1	–	–	–	1
	Parachipteria sp.	–	4	4	–	–	8
	Galumnidae, *Gen. sp.*	–	1	–	–	–	1
Prostigmata	*Bichimaelia sp.*	–	–	1	1	4	6
	Alicorhagiidae, *Gen. sp.*	–	1	–	–	10	11
	Lordalychidae, *Gen. sp.*	–	–	2	–	8	10
	Nanorchestes sp.	1	–	3	1	9	14
	Labidostommatidae, *Gen. sp.*	–	–	–	1	–	1
	Eupodes sp.	–	–	1	2	11	14
	Eupodidae, *Gen. sp.*	–	–	3	1	5	9
	Rhagidiidae, *Gen. sp.* A	–	–	–	8	5	13
	Rhagidiidae, *Gen. sp.* B	–	1	3	1	–	5
	Tydeidae, *Gen. sp.*	–	–	–	1	–	1
	Cyta sp.	–	–	1	–	–	1
	Scutacaridae, *Gen. sp.*	1	6	–	–	2	9
	Tarsonemidae, *Gen. sp.*	–	–	1	–	–	1
	Tarsocheylidae, *Gen. sp.*	–	3	4	–	1	8
	Stigmaeidae, *Gen. sp.*	–	–	1	–	–	1
Mesostigmata	Digamasellidae, *Gen. sp.*	3	2	5	9	–	19
	Ologamasidae, *Gen. sp.*	3	–	2	3	–	8
	Zerconidae, *Gen. sp.* A	–	5	1	–	–	6
	Zerconidae, *Gen. sp.* B	–	–	–	–	1	1
	Polyaspidae, *Gen. sp.*	8	10	22	3	–	43
	Uropodidae, *Gen. sp.*	–	1	1	–	–	2
	Unidentified	–	–	1	–	2	3
Astigmata	Acaridae, *Gen. sp.*	2	2	30	–	1	35
Total "species"		10	18	26	19	21	44
Number of samples examined		11	10	11	7	4	43

Table 4. Adult oribatids found in 8 samples of sub-surface decaying wood and litter from a grand fir forest in western Montana.

Family	Litter		Decaying wood	
	number	[%] of total	number	[%] of total
Palaeacarida	7	1.4	–	–
Phthiracaridae	3	0.6	–	–
Euphthiracaridae	2	0.4	35	16.0
Brachychthoniidae	25	5.1	–	–
Damaeidae	13	2.7	2	0.9
Liacaridae	13	2.7	–	–
Eremaeidae	7	1.4	–	–
Camisiidae	1	0.2	–	–
Nothridae	1	0.2	1	0.5
Nanhermannidae	1	0.2	1	0.5
Eremaeidae	7	1.4	–	–
Carabodidae	10	2.1	8	3.7
Tectocepheidae	16	3.3	21	9.6
Autognetidae	2	0.4	2	0.9
Astegistidae	1	0.2	–	–
Oppiidae	232	47.7	46	21.0
Suctobelbidae	120	24.7	96	43.8
Oribatulidae	13	2.7	3	1.4
Oribatellidae	6	1.2	–	–
Achipteriidae	4	0.8	2	0.9
Carstoniidae	1	0.2	2	0.9
Galumnidae	1	0.2	–	–
Total adults	486	100	219	100

3.3. Species composition the mites (Acari) in wood

The microarthropod fauna of decaying wood in Oregon is dominated by oribatid mites, both in terms of total numbers and numbers of species abundance (table 3). A total of 44 species of mites were identified from 43 wood samples from Oregon, half of which were species of Cryptostigmata.

15 species of prostigmatid mites were represented, along with at least 6 species of mesostigmatid mites and at least one species of astigmatid mite. A general trend towards increased numbers of species from decay class I to decay class III was evident. Trends beyond decay class II may be obscured by variable sample size. The fauna was dominated by relatively few species. *Opiella nova*, *Cultroribula bicultrata*, *Suctobelba sp.* and *Schelorobates sp.* were the dominant oribatid mites. A polyaspid mite was the abundant mesostigmatid mite, while no single family dominated the Prostigmata. None of the above-mentioned species or families are considered wood-feeders by LUXTON (1972) or KRANTZ (1978). Of these groups, only oribatid mites are particulate feeders, and gut contents of the above species contained mostly fungal hyphae. Those species that did appear to ingest large quantities of wood included *Microtritia sp.*, *Parhypochthonius sp.* and a third species whose fecal pellets were observed in the samples but was not, itself, collected. This last oribatid mite, an undescribed species of *Epilohmannia* (R. A. NORTON, personal communication), was unique for its relatively large size and bright red fecal pellets. The color of the pellets was presumably due to the presence of large amounts of heartwood in the feces. However, specimens of this species were collected only from Tullgren extractions of wood and were not obtained from those samples reported

here. Thus, those species that appear to directly feed upon decaying wood composed a minor component of the microarthropod fauna found in this substrate.

Oribatid mites found in Montana decaying wood were compared to those found in forest litter and soil (table 4). Two results are evident. First, the wood fauna was depauperate in species compared to a similar number of litter and soil samples, and second, the dominant species found in wood are generally the same species that dominante the fauna of litter and soil. *Oppiella nova* was abundant from both substrates, as was *Suctobelba sp.* However, species of Brachychthoniidae were abundant in litter and soil, but were not found in wood. This finding is consistent with the Oregon results, where only one specimen of *Brachychthonius sp.* was found in 43 samples. Species that had ingested large quantities of wood included only species of Euphthiracaridae, a subdominant group common to both the Montana and Oregon samples. Notably missing from the Montana samples were *Parhypochthonius sp.* and Cultroribula bicultrata. Otherwise, the composition of the wood fauna appeared quite similar at the level of resolution used in this study. While neither the Oregon or Montana data are to be considered an exhaustive list of the oribatids present in wood, the results suggest that the dominant arthropods found in decaying wood are relatively small species of oppiid and suctobelbid mites, which also dominante the litter and soil fauna (e. g., table 3 and ABBOTT *et al.*, 1980).

4. Discussion

Quantitative but taxonomically-crude data such as ours may overgeneralize about the apparent minimum roles of specialized oribatids in the decay processes of wood. R. A. NORTON (pers. communication) suggests that burrowing oribatid mites such as the phthiracarids and xenillids are common and important in the physical breakdown of fungus-invaded wood. The effects of microarthropods on microbial processes, in conjunction with physical fragmentation, have been hypothesized to be relatively more important in recalcitrant substrates such as wood (SEASTEDT, 1984). Nonetheless, the numerical patterns shown in fig. 1 indicate that heartwood is an attractive substrate for modest densities microarthropods only in the latter stage of decay. High variability in numbers of microarthropods per sample found in this study corresponded with high variability in microbial respiration reported by SOLLINS *et al.* (1987). Wood is apparently a more heterogenous habitat for decomposers and associatd fauna than is litter and soil.

The diversity of the microarthropod fauna in wood is depauperate compared to that found in forest litter and soil. We found only 22 species of oribatid mites inside of decaying wood compared to 51 species found in coniferous litter by WALTER (1985) at a slightly lower elevation site. ABBOTT *et al.* (1980) reported over 60 species of oribatids from North Carolina on forest litter and freshly-fallen wood stems. FAGER (1968) reported 55 species of mites in decaying logs, but only 26 species of oribatids were observed. An examination of an equal number of wood and litter samples from Montana produced twice as many species from the litter samples. Fauna restricted to decaying wood appear to be few; perhaps *Microtritia sp.*, *Gehypochthonius sp.* and *Epilohmannia n. sp.* represent such species. However, samples taken of forest litter and soil often contain small fragments of decaying wood (e. g. ANDERSON, 1978; SEASTEDT *et al.*, 1980). Thus, we should expect to see species restricted to feeding on decayed wood to be present in such samples, but in reduced numbers compared to samples containing only wood. Hence, just as WIEGERT (1974) reported that the litter fauna is a subset of a more diverse soil fauna, the fauna of decaying wood may also be considered a subset of the forest floor fauna. The most numerous species found in decaying wood, members of the Oppiidae and Suctobelbidae, are also the most numerous species found in litter and soil. The dominant role of microarthropods in wood decomposition, as indicated by the feeding habits of the dominant mite species, involves fungivory. Fungi first colonize the wood. These microbes are then grazed by microbivores which allows the wood substrate to be recolonized by the same of different microbes, including bacteria (e. g. SWIFT, 1977 b). A portion of the microarthropod fauna may also be feeding on other mycophagous invertebrates (WALTER, 1987). The grazing and recolonization cycle is repeated many times over before the substrate is mineralized. At the risk of belaboring the

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Microarthropod population densities in large woody debris increase during the decay process. Maximum densities were about 2×10^5 individuals per m^3 of wood, but remained 2–10 times lower than population densities found in an equivalent amount of litter and soil from either coniferous or deciduous forests. Oribatid mites are the most abundant microarthropods in wood. Specie diversity of all microarthropod groups is lower in decaying wood compared with species numbers in litter and soil. The dominant species in wood appear to be mycophagous; the number of wood-feeding microarthropods compose a small minority of both species and numbers of fauna found in decaying boles.

Key words: coniferous forest, decay, deciduous forest, population density, microarthropods, mites, Oribatids, species diveristy, wood.

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obvious, this cycle in wood is much slower than that observed in decaying foliage, as evidenced both by measurements of microbial activity and mass loss (HARMON *et al.* 1986; SOLLINS *et al.* 1977) and by low microarthropod densities.

A second, albeit smaller trophic pathway also exists in wood. A subset of the fauna, represented in our samples by species of the family Euphtiracaridae and *Parhypochthonius sp.*, does directly ingest wood. Whether or not these species have a gut flora capable of digesting cellulose remains somewhat controversial (e. g. LUXTON, 1972, 1979). Our data indicate that wood of later decay classes is preferred, suggesting that these species are actually feeding on the microflora contained on the wood. Nonetheless, these fauna do affect the structural integrity of the wood and may, in fact, be responsible for modifying the physical properties used in determining the decay class of the wood. Wood of decay class V, for example, is largely made up of fecal pellets. Once the wood is converted to fecal pellets, decomposition may be increased due to enhancement of surface area (e. g. KITCHELL *et al.*, 1979), and these pellets become substrate for further microbial and microbivore activity.

5. Zusammenfassung

[Mikroarthropoden in rottendem Holz von Nadel- und Laubbäumen der gemäßigten Zone]

Die Besatzdichte von Mikroarthropoden in Holz nahm während der Rotte von Baumstämmen zu. Bezogen auf das Volumen (des belebten Substrates) betrug die Besatzdichte im rottenden Holz nur 1/10 bis 1/2 der Besatzdichte in den oberen Streu- und Boden-Schichten (von 0–5 cm u. Fl.) der Nadel- oder Laubwälder; die Ursache dafür ist vermutlich das für Mikroarthropoden relativ nährstoffarme Substrat.

Oribatiden sind die am zahlreichsten vertretene Tiergruppe im rottenden Holz; die meisten Arten dieser Gruppe sind vermutlich microphytophag. Holzfressende Mikro-Arthropoden sind die wenigsten Arten und die geringste Zahl der Individuen.

Schlüsselwörter: Nadelwald, Laubwald, Holz-Abbau, Rotte, Besatzdichte, Abundanz, Diversität, Mikro-Arthropoden, Acari, Oribatei.

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