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A two-year study of leaf litter decomposition as related to macroclimatic factors and microarthropod abundance in the southern Appalachians

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Chestnut oak *Quercus prinus* L. litter in the southern Appalachian Mountains of the United States decomposes slowly during winter and more rapidly in other seasons. This pattern differed from other studies of litter decomposition in more northern environments where decomposition rates were relatively constant throughout the year or more rapid beneath a winter snow cover. The pattern observed can be approximated by using monthly actual evapotranspiration estimates as a correction factor for the decomposition constant, k, in the commonly-used negative exponential decomposition model.
Mean microarthropod densities increased from a seasonally weighted estimate of 18.2 ind. g^{-1} litter during the first year of decomposition to 73.6 ind. g^{-1} litter during the second year. In spite of this increase, no difference in the rate of weight loss of the litter was observed between the first and second year of the study.

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1. Introduction

Litter decomposition rates are regulated by interactions among litter substrate quality, biota and microclimate (Swift et al. 1979). Recent studies of litter decomposition have emphasized comminution effects of fauna (e.g. Merritt and Lawson 1978), fauna and microbial interactions (Vossbrink et al. 1979, Seastedt and Crossley 1980), and the role of macroclimatic controls and substrate quality (Meentemeyer 1978). Most litter decomposition studies, such as those cited above, have been conducted for one year or less. Litter decomposition studies of longer duration are few and have been primarily concerned with the effects of habitat and substrate quality on decomposition processes (Anderson 1973a, b, Lousier and Parkinson 1976, Fogel and Cromack 1977, McBrayer and Cromack 1980). These longer studies were conducted in north temperate or boreal forests. They reported relatively constant decomposition rates for two years or indicated somewhat reduced rates of decomposition during the second year.

Knowledge of long-term (i.e., longer than the first year) decomposition rates of litter is important in estimating the turnover rate of litter on the forest floor (e.g. Olson 1963). Macroclimatic parameters such as ambient temperature and precipitation are recognized as correlates and regulators of biotic agents of decomposition, at least during the first year (Meentemeyer 1978). The relationship between macroclimate and decomposition rates can occasionally be negated by microclimatic and biotic variables (Whitford et al. 1981). Hence, we hypothesized that the correlation between

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macroclimate and decomposition processes would diminish during the second year of decomposition, when the litter microclimate is more strongly influenced by soil temperature and moisture conditions (e.g. Seastedt 1979).

The objectives of the present study were to document the pattern and annual rate of litter decomposition over two years in a southern temperate forest, and to compare this two-year pattern of weight loss with microarthropod densities and macroclimatic parameters.

2. Methods

Chestnut oak *Quercus prinus* L. leaves were collected from trees during the peak of litterfall in late October 1975, from an oak-hickory forest (Watershed 2) at the Coweeta Hydrologic Laboratory, Macon County, North Carolina. This species was chosen because of its dominance in the forest (ca. 20% of basal area, Day and Monk 1974), and for its slow decomposition rate (Cromack and Monk 1975). Because of slow decomposition, small quantities of leaves could be placed in litterbags (Crossley and Hoglund 1962), with assurance that sufficient material would remain in the bags after two years to assess weight loss and microarthropod abundance. A variable amount of litter (approx. 3 g weighed to the nearest 0.01 g) was placed in preweighed, 10 × 10 cm litterbags (2 mm mesh), reweighed and placed on a single plot of Watershed 2 on 14 November 1975. Four bags were harvested at intervals varying from one to four weeks for two years. One set of bags was harvested immediately after being placed in the field to measure weight loss due to handling. Litter was redried during the process of Tullgren extraction for microarthropods and reweighed. Decomposition rates were calculated by using a single, negative exponential function (i.e., $dN/dt = -kN$, Olson 1963).

Macroclimate parameters measured at the Coweeta Hydrologic Laboratory included temperature and precipitation data obtained by U.S. Forest Service personnel. These data were converted to monthly estimates of actual evapotranspiration (AET) by the procedure of Thornthwaite and Mather (1955). AET is a measure of both available energy and moisture; hence, the parameter is a useful index of potential macroclimatic control of biotic processes (Meentemeyer 1978). If monthly AET affects monthly decomposition rates, then the fraction of observed monthly AET divided by the average monthly AET, multiplied by an appropriate expression of the decay constant, k, should express this relationship. Since decomposition is a cumulative process, we evaluated the relationship by expanding the computational formula for the negative function described above to:

$$\ln(N_t) = \ln(N_o) - (\sum_0^t AET/\text{total } AET \times k)$$

where: N_t = percent of weight remaining at time t,
t = days of decomposition,
N_o = percent of initial weight (100% – handling loss),
$\sum_0^t$ AET = cumulative AET from time 0 to time t,

total AET = sum of AET values observed over entire study period, and k = decomposition constant for study period (–0.628).

Microarthropods collected by Tullgren extraction of litter were sorted into broad taxonomic groupings: suborders for mites (Acarina), and order for other arthropods. Less abundant groups were combined for analysis. Spiders, pseudoscorpions and centipedes were termed the predator group. Protura, Symphyla, Pauropoda, Diplopoda and a number of orders of insects were grouped as miscellaneous arthropods. This last group was dominated by fungivores and detritivores, but did include a few predaceous insect taxa. Data on microarthropod abundance were calculated on the basis of number of individuals per gram of litter. Microarthropod data were pooled into quarter year (94-day) intervals to present short-term environmental effects from obscuring seasonal trends in microarthropod densities. Means were calculated from data treated with a natural log transformation. This proce-

Tab. 1. Decomposition rates for chestnut oak litter confined in litter bags, Coweeta Hydrologic Laboratory, North Carolina, 1975–1977. Decomposition constant (k) = single component negative exponential model, percent remaining = $-e^{-kt}$. r = correlation with negative exponential model.

Parameter	Total (2yr)	First year	Days 0–120 only	Days 120–365 only	Second year	Days 365–485 only	Days 485–731 only
Decomposition							
Constant k (yr^{-1})	–0.314	–0.293	–0.152	–0.426	–0.387	0.139	–0.573
% loss (yr^{-1})	27.0	24.6	14.1	34.9	32.1	+14.9	43.6
r	0.86	0.90	0.76	0.85	0.55	0.10 (ns)*	0.48
sample size	117	67	32	35	50	15	35

*ns = not significant, other all r values significant at $p < 0.05$.

dure tended to normalize the data as well as homogenize the variances (Gerard and Berthet 1966), but the geometric means thus calculated were lower than the arithmetic means.

3. Results

3.1. Litter decomposition

Litter harvested on day 0 of the study indicated handling losses averaging 4.25%. These handling losses were incorporated into the negative exponential model by setting weights at day 0 to 95.75%, instead of 100%. Least squares regression (log weight on time) estimated that chestnut oak leaves lost 24.6% of their initial weight during the first year on the forest floor and lost 32.1% of the remaining weight (or 24.2% of initial weight) during the second year (Tab. 1). The actual data points have been plotted to illustrate the pattern of decomposition and emphasize the increasing variability in the weight loss of individual litter samples through the course of the study (Fig. 1). This increasing variability is attributed to the cumulative effects of microhabitat variation (Fogel and Cromack 1977).

First year decomposition patterns in the southeastern United States have been described as "three component curves" (Olson and Crossley 1963, Croom and Ragsdale 1976). Weight loss is initially rapid in autumn (component 1), then slows to near zero in winter (component 2) then again increases in spring and summer (component 3). This pattern is evident in our results, and has been observed in other one-year litterbag studies at Coweeta (Seastedt 1979). Decomposition rates during the second year exhibited a "two component curve". The initial period of rapid weight loss was lacking, and little or no decomposition occurred during winter, followed by more rapid decomposition in subsequent seasons.

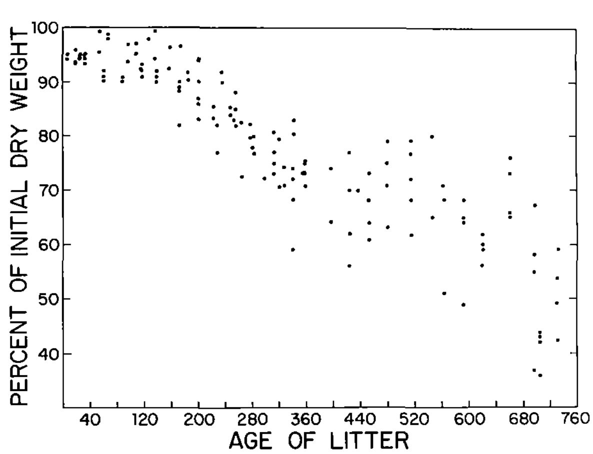

Fig. 1. Percent of initial dry weight of chestnut oak litter contained in litterbags in relation to the length of time (days) on the forest floor. Day 0 was 14 November 1975.

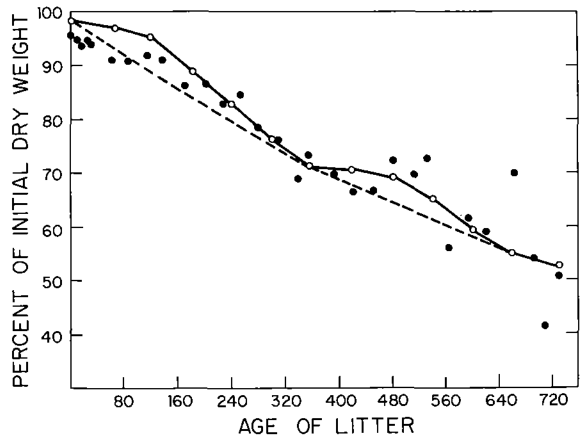

Fig. 2. Average percents of initial weight of chestnut oak litter (solid circles) compared with a negative exponential model (dashed lines) and an AET-modified negative exponential model (open circles connected by solid line).

3.2. Decomposition in relation to actual evapotranspiration rates

The Coweeta basin is characterized by mild winters and cool summers, with ample rainfall occurring in all seasons (Johnson and Swank 1973). In the present study moisture deficits (rainfall minus potential evapotranspiration) occurred only in April and July 1976, and again in July 1977. AET values ranged from a low of 3 mm in January 1977 to a high of 115 mm in August of the same year. AET estimates for the first year of study (November 1975 – October 1976) were 706 mm versus 705 mm for the second year of decomposition. Thus, cumulative AET was very similar for each of the two years of the study, and Meentemeyer's (1978) AET model would predict almost identical decomposition rates for the two years.

Patterns of decomposition produced by the negative exponential model and the negative exponential model modified by AET values were compared with empirical results (Fig. 2). In general, the AET-modified model produced a "two component", inverse sigmoid curve per year with some slight irregularities introduced by using the actual monthly AET values. The correlation coefficients for both models with the data points are the same ($r = 0.86$), and both models exhibit "lack of fit" characteristics (i.e., values are consistently higher or consistently lower than the observed means) during much of the first year. Obviously, the slope of the negative exponential model does not exactly describe the pattern of decomposition in the southern Appalachians. Modifying the expression by use of an AET correction factor better describes the pattern of decomposition, but it fails to describe the initial rapid loss in litter weight. Otherwise, the modified AET model mimics the deviations of the observations from the simple negative exponential model.

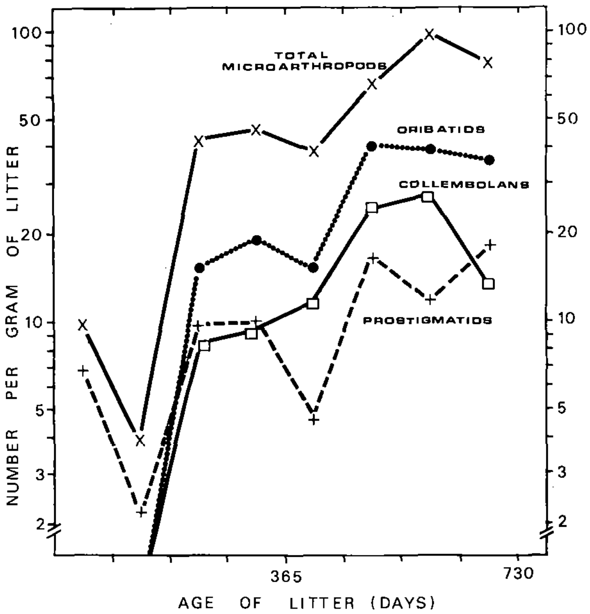

Fig. 3. Patterns of microarthropod abundance on chestnut oak litter contained in litterbags. Sample sizes and significant differences between quarter-year estimates are reported in Tab. 2.

3.3. Microarthropod abundance

Microarthropod numbers per gram of leaf litter increased with litter age (Fig. 3). Initial colonizers included mostly prostigmated mites, particularly species of the family Tydeidae (Crossley and Hoglund 1962). Prostigmatids declined during the second quarter of the first year and thereafter composed less than 25% of the total fauna. Oribatid mites (Cryptostigmata) dominated the fauna after the first half year, and from the third quarter of the first year to the end of the study oribatid mites, total acarines and total microarthropod densities showed no significant seasonal changes in densities (Tab. 2). Other groups, including collembolans, mesostigmatid mites, the predator group and the miscellaneous group, did not reach maximum densities until the second year of study. Overall, annual weighted geometric means for total microarthropods averaged 18.2 and 73.6 ind. g^{-1} litter for year 1 and year 2, respectively. Thus, microarthropods were much more numerous on chestnut oak litter during the second year.

4. Discussion

Chemical components of litter such as carbohydrates, proteins, cellulose and lignin decompose at different rates, and litterbag studies measure the net loss of all of these components (Minderman 1968). A nearly universal phenomenon reported in decomposition studies is the initial rapid loss of litter weight followed by a slower rate of decomposition. This initial weight loss is attributed to the leaching of soluble litter materials that occurs in the presence or absence of microflora and fauna (Witkamp and Crossley 1966, Croom and Ragsdale 1976, Vossbrink et al. 1979). Continued decomposition of litter after the loss of soluble components is primarily the result of biotic processes (e.g. Vossbrink et al. 1979). McBrayer and Cromack (1980) reported that litter decomposition in a Minnesota forest continued through winter beneath snow. Litter temperatures remained at or above freezing throughout much of the period of snow cover. Their study supported earlier work by Stark (1973), who reported that decomposition was most rapid during winter in a Jeffrey pine *Pinus jeffreyi* Grev. and Balf. system in Nevada. There, moisture restraints during summer inhibited decomposition while winter temperatures, ameliorated by a snow cover, did not have an equally adverse effect. In the southern Appalachians, however, decomposition was significantly slowed during winter, and was not measurable during the second winter of the study (Tab. 1). Snow seldom remains on the ground for more than

Tab. 2. Microarthropod densities (number·g^{-1}) on chestnut oak litter confined in litter bags, Coweeta Hydrologic Laboratory, North Carolina, 1975–1977. (Values are geometric means). Study initiated 14 November 1975.

Arthropod taxa	Maximum age of litter (yr) (Sample size)							
	0.25 (21)	0.50 (12)	0.75 (10)	1.0 (10)	1.25 (16)	1.50 (3)	1.75 (8)	2.0 (13)
Total Acarina	9.0 B*	3.1 A	29.8 C	34.9 C	22.6 C	65.2 C	58.9 C	62.7 C
Cryptostigmata	1.2 A	0.7 A	13.9 B	19.2 B	15.5 B	40.3 B	39.5 B	35.8 B
Prostigmata	6.9 B	2.1 A	9.5 BC	10.0 BC	4.6 AB	16.9 BC	11.9 BC	18.2 C
Mesostigmata	0.1 A	0.2 AB	2.6 CD	4.1 D	1.1 BC	6.9 D	5.7 D	4.1 D
Collembola	0.9 A	0.4 A	8.6 B	9.1 B	11.6 BC	24.3 BC	26.1 C	13.5 BC
Predators	0.0 A	0.1 A	0.1 AB	0.2 AB	0.0 A	0.5 C	0.2 BC	0.2 BC
Miscellaneous	0.1 A	0.2 AB	0.4 ABC	0.6 BC	0.4 ABC	2.7 D	2.2 D	1.0 C
Total arthropods	9.9 B	3.9 A	42.9 C	46.1 C	38.2 C	93.6 C	98.4 C	78.4 C

*Means followed by different letter(s) are significantly different from other means of the same taxon (Duncan Multiple Range Test, $p < 0.05$).

several days at a time, although frosts are frequent. Thus, litter is exposed to a wide range of temperature and decomposition is inhibited by this environmental regime. The warm, moist growing season of the southern Appalachians allows decomposition rates above those observed in more northerly or drier environments. The net result of these interactions between environment and litter chemical content is a "three component" decomposition curve pattern during the first year of decomposition (i.e., rapid loss of soluble components followed by slow decomposition in winter followed by rapid weight loss), and a "two component" decomposition curve observed during the second year and perhaps thereafter. The failure of the AET-modified, negative exponential function to mimic the three component curve could be partially corrected by recognizing "readily decomposable" and "recalcitrant" fractions of the fresh litter and employing a two component negative exponential model (e.g. Bunnell and Tait 1974, Lousier and Parkinson 1976). Since we lacked litter chemistry data, such a model was not attempted here.

Microarthropod densities are initially low in first-year litter during winter and early spring. Evidently the arthropods' ability to move into fresh litter is not a factor. Total microarthropod densities were significantly larger in the first quarter of the year than during the second quarter. Rather, low moisture content (Wiegert 1974) or the polyphenol content and/or absence of suitable microflora in the litter (Anderson 1975) likely inhibited colonization by microarthropods. Densities increase in older litter and remain fairly constant during the second year. Leaf drop in autumn buries one-year old litter; thus, environmental extremes in temperature and moisture are ameliorated. While microarthropods remain in older litter during the second winter, feeding activities apparently cease. Renewed decomposition is not observed in second year litter until about April (Fig. 1). If the effects of microarthropods on the annual rate of litter decomposition are roughly proportional to faunal densities, then faunal impacts are much more significant during the second year of decomposition. However, the annual rates of decomposition of one and two year old chestnut oak litter were very similar. Additional two-year decomposition studies conducted during the same years at Coweeta indicated that other litter species decomposed at a somwehat slower rate during the second year. Assuming a more favourable microclimate (i.e., less temperature variation and warmer winter temperatures, Seastedt 1979) and more detrital feeders, then equal or lower second-year decomposition rates can be attributed to poorer substrate quality. Data from Coweeta indicate higher lignin concentrations in older litter (Cromack 1973), and similar findings of changes in substrate quality have been reported elsewhere (e.g. McBrayer and Cromack 1980). A large number of studies have correlated lignin concentrations with decomposition rates (e.g. Meentemeyer 1978). Results from our study in a southern temperate forest are similar to those studies conducted in more northern environments; annual rates of litter decomposition do not differ appreciably between first and second years of decomposition. Decomposition rates do vary seasonally in the southern Appalachians, and this variation is attributed to large seasonal variation in AET. While the actual causal factors of decomposition are changing over time, the sum of the interactions appears to be nearly constant; hence, macroclimatic factors such as AET are strongly correlated with first and second-year decomposition rates of litter.

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References

Anderson, J. M. 1973a. The breakdown and decomposition of sweet chestnut *Castanea sativa* Mill. and beech *Fagus sylvatica* L. leaf litter in two deciduous woodland soils. I. Breakdown, leaching and decomposition. – Oecologia (Berl.) 12: 251–274.

– 1973b. The breakdown and decomposition of sweet chestnut *Castanea sativa* Mill. and beech *Fagus sylvatica* L. leaf litter in two deciduous woodland soils. II. Changes in the carbon, hydrogen, nitrogen and polyphenol content. – Oecologia (Berl.) 12: 275–288.

– 1975. Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. – J. Anim. Ecol. 44: 475–495.

Bunnell, F. L. and Tait, D. E. N. 1974. Mathematical simulation models of decomposition processes. – In: Holding, A. J., Heal, O. W., MacLean, S. F. Jr, and Flanagan, P. W. (eds). Soil organisms and decomposition in tundra. IBP tundra biome steering committee, Stockholm. pp. 207–225.

Cromack, K., Jr. 1973. Litter production and decomposition in a mixed hardwood watershed and a white pine watershed at Coweeta Hydrologic Station, North Carolina. – Ph.D. Diss. Univ. Georgia, Athens. 160 p.

– and Monk, C. D. 1975. Litter production, decomposition and nutrient cycling in a mixed hardwood watershed and a white pine watershed. – In: Howell, F. G., Gentry, J. B. and Smith, M. H. (eds). Mineral cycling in southeastern ecosystems. ERDA symposium series CONF 740513, NTIS, Springfield, VA. pp. 609–624.

Croom, J. M. and Ragsdale, H. L. 1976. Dynamics of cesium-134 and biomass in treated and untreated turkey oak leaf litter bags. – In: Adriano, D. C. and Brisbin, I. L., Jr. (eds). Environmental Chemistry and Cycling Processes. ERDA-CONF 760429, NTIS, Springfield, VA. pp. 700–708.

Crossley, D. A., Jr. and Hoglund, M. P. 1962. A litterbag method for the study of microarthropods inhabiting leaf litter. – Ecology 43: 571–573.

Day, F. P. and Monk, C. D. 1974. Vegetation patterns on a southern Appalachian watershed. – Ecology 55: 1064–1074.

Fogel, R. and Cromack, K., Jr. 1977. Effect of habitat and substrate quality on douglas-fir litter decomposition in western Oregon. – Can. J. Bot. 55: 1632–1640.

Gerard, G. and Berthet, P. 1966. A statistical study of microdistribution of Oribatei (Acari). II. The transformation of the data. – Oikos 17: 142–149.
Johnson, P. L. and Swank, W. R. 1973. Studies of cation budgets in the southern Appalachians of four experimental watersheds with contrasting vegetation. – Ecology 54: 70–80.
Louiser, J. D. and Parkinson, D. 1976. Litter decomposition in a cool temperate deciduous forest. – Can. J. Bot. 54: 419–436.
McBrayer, J. F. and Cromack, Jr., K. 1980. Effect of snowpack on oak-litter breakdown and nutrient release in a Minnesota forest. – Pedobiologia 20: 47–54.
Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. – Ecology 59: 465–472.
Merritt, R. W. and Lawson, D. L. 1978. Leaf litter processing in floodplain and stream communities. – In: Johnson, R. R. and McCormick, J. F. (eds). Strategies for protection and management of floodplain wetlands and other riparian ecosystems. Gen. Tech. Rep. WO-12, U.S.D.A. Forest Service, Washington, D.C. pp. 93–105.
Minderman, G. 1968. Addition, decomposition and accumulation of organic matter in forests. – J. Ecol. 56: 355–362.
Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. – Ecology 44: 322–331.
– and Crossley, Jr., D. A. 1963. Tracer studies on the breakdown of forest litter. – In: Shultz, V. and Klement, A. W., Jr. (eds). Proceedings of the first national symposium on Radioecology. Reinhold, N.Y. pp. 411–416.
Seastedt, T. R. 1979. Microarthropod response to clear-cutting by cable logging in the southern Appalachians: Effects on decomposition and mineralization of litter. – Ph.D. Diss. Univ. of Georgia, Athens. 122 p.
– and Crossley, Jr., D. A. 1980. Effects of microarthropods on the seasonal dynamics of nutrients in forest litter. – Soil Biol. Biochem. 12: 337–342.
Stark, N. 1973. Nutrient cycling in a Jeffrey Pine Ecosystem. – University of Montana Press, Missoula. 389 p.
Swift, M. J., Heal, O. W. and Anderson, J. M. 1979. Decomposition in terrestrial ecosystems. – Studies in Ecology Volume 5. University of California Press. 372 p.
Thornthwaite, C. W. and Mather, J. F. 1955. The water balance. – Publications in Climatology 8: 1–96.
Vossbrink, C. F., Coleman, D. C. and Wooley, T. A. 1979. Abiotic and biotic factors in litter decomposition in a semi arid grassland. – Ecology 60: 265–271.
Whitford, W. G., Meentemeyer, V., Seastedt, T. R., Cromack, K. Jr., Crossley, D. A. Jr., Santos, P., Todd, R. L. and Waide, J. B. 1981. Exceptions of the AET model of litter decomposition in deserts and a clear-cut forest. – Ecology 62: 275–277.
Wiegert, R. G. 1974. Litter bag studies of microarthropod populations in three South Carolina old fields. – Ecology 55: 94–102.
Witkamp, M. and Crossley, D. A. Jr. 1966. The role of microarthropods and microflora in breakdown of white oak litter. – Pedobiologia 6: 293–303.

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