

WOODY LITTER DECOMPOSITION FOLLOWING CLEAR-CUTTING¹

D. T. ABBOTT² AND D. A. CROSSLEY, JR.
Department of Entomology and Institute of Ecology,
University of Georgia, Athens, Georgia 30602 USA

Abstract. Unconfined *Quercus prinus* woody litter of three size classes (0-1, 1-3, and 3-5 cm diameter) was placed on forest floors of a control hardwood watershed and on mesic and xeric sites of a clear-cut watershed at Coweeta Hydrologic Laboratory, North Carolina. Exponential decay coefficients for mass loss on the control were .1524, .1728, and .0912 yr⁻¹ for 0-1, 1-3, and 3-5 cm branches, respectively. Coefficients for 0-1, 1-3, and 3-5 cm branches were .1752, .0756, and .1644 yr⁻¹ on the mesic site and .0456, .0948, and .0377 yr⁻¹ on the xeric site. The effect of site differences on decomposition rate was greater than the effect of diameter, although an inverse relationship between diameter and decay coefficient is suggested. Time in the field, temperature, moisture, and microarthropod abundance also appeared to influence decomposition rate.

Microarthropods dominated the animal community on decaying wood with oribatid mites and collembolans the most numerous. Microarthropod densities were highest on 0-1 cm twigs and lowest on 3-5 cm branches. Microarthropod densities were generally highest on the control, slightly depressed on the mesic site, and greatly depressed on the xeric site. Time in the field and state of decomposition both positively correlated with microarthropod abundance.

Calcium concentration and total calcium exhibited transitory increases but little net change at the end of 1 yr in experimental branches. Total potassium decreased on all sites for 6 mo and for 12 mo on the control and xeric sites, with ≈60% remaining after 1 yr. Total potassium increased rapidly on the mesic site over the last 6 mo and reached 110% of the initial amount. Temperature, moisture, microbes, and microarthropods appeared to control nutrient dynamics.

Woody litter dynamics were more important in terms of nutrient conservation on the clear-cut watershed than on the control and contributed to the resilience of the system. Removal or destruction of woody debris after clear-cutting would decrease the nutrient conservation properties of decaying wood and would probably contribute to watershed output of nutrients.

Key words: clear-cutting; coweeta; decomposition; element cycling; forests; microarthropods; nutrient cycling; nutrient sink; watersheds; woody litter.

INTRODUCTION

Woody litter is a conspicuous element of the forest floor, where it serves various functions such as increasing habitat diversity, enhancing tree seedling survival and functioning as a significant reservoir for some nutrients. Clear-cutting for timber harvest produces, among other things, a pulse of woody input consisting of smaller-sized branches and twigs. Since woody material normally has slow turnover rates (Whittaker et al. 1979), the decomposition rate of woody litter is likely to have profound effects on the recovery of clear-cut forests, especially in the crucial first years when nutrient loss is elevated (Bormann et al. 1968). This paper presents results from a 1-yr study of the initial stages of decomposition for branch and twig litter. Measurements compared twig (0-1 cm diameter) and branch (1-3 cm, 3-5 cm) decomposition on mesic and xeric portions of a recently clear-cut, southern hardwood watershed and an adjacent uncut hardwood control watershed. In addition, microarthropods and other fauna associated with the decom-

posing litter were enumerated. Since arthropods are believed to be instrumental in regulating terrestrial decomposition rates (Crossley 1977, Reichle 1977), this fauna, due to clear-cutting effects, may change woody litter decomposition rates.

The objectives of this research included quantification of (1) rates of mass loss, (2) nutrient dynamics, and (3) microarthropod populations of decomposing woody litter. We hypothesized that each of these would become reduced on the clear-cut watershed due to more xeric conditions on the forest floor resulting from canopy removal (Seastedt and Crossley 1980). Further, we expected that rates would become more retarded on the xeric portions of the clear-cut watershed, in contrast to the mesic areas.

STUDY SITE

Decomposition of *Quercus prinus* L. (Chestnut oak) woody litter was measured on a clear-cut watershed (WS 7) and an adjacent control watershed (WS 2) at Coweeta Hydrologic Laboratory, North Carolina. Both south-facing watersheds have ≈300 m relief with basal elevations of ≈700 m; WS 7 is 59 ha in area while WS 2 is 12.5 ha (Dils 1957).

Soils in both watersheds are composed of Tusquitee

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² Present address: Monsanto Research Corporation, Mound Facility, Miamisburg, Ohio 45342 USA.

stony loam in the lower reaches and Chandler loam elsewhere. The Tusquitee soil is a member of the fine-loamy, mixed, mesic family of humic Hapludults. These soils have formed in loamy colluvium derived from muscovite-biotite schist. The Chandler loam soil is a member of the coarse-loamy, micaceous, mesic family of typic Dystrochrepts. Chandler soils have formed in residuum, weathered from muscovite-biotite schist.

The vegetation of both watersheds was comprised of a rich mesic oak-hickory community giving way to a pine-hardwood community on the more xeric ridges. The dominant tree species before cutting on WS 7 was *Q. prinus*, which composed >20% of the basal area. Before the chestnut blight of the 1930's and 1940's *Castanea dentata* L. comprised >30% of the forest basal area. The demise of the chestnut was the major perturbation which occurred in the Coweeta Basin since its acquisition as a research site by the United States Forest Service in 1924. Some selective cutting may have occurred before 1920 on the lower reaches. Winters are mild and summers cool at Coweeta. Mean annual temperature is 13°C; the coldest month is January (3.5°C mean) and the warmest is July (21°C). Precipitation normally varies from 2500 mm annually on the ridges to 1700 mm on the lower elevations with <5% occurring as snow. Further details on the Coweeta Basin can be found in Johnson and Swank (1973).

METHODS

Watershed 7 was clear-cut and marketable sawtimber was logged with a mobile, high-lead cable system in spring and summer 1977. Two plots were established within WS 7; a plot (site 55) with a southeastern aspect and a xeric plot (site 12) on the southwestern face. One south-facing site was established on adjacent WS 2 as a control. Soil and litter moisture for litter, 0–10 cm, and 10–30 cm horizons were estimated gravimetrically by drying at 100°C. Litter was often absent on WS 7.

Chestnut oak branches and twigs (15–30 cm length) of three size classes were cut from living, apparently healthy, trees on WS 7 and taken to the laboratory where their volumes were measured by water displacement. Sixty unconfined pieces each of 0–1 cm and 1–3 cm material, and 40 pieces of 3–5 cm branches were placed in nontouching rows on each study plot, with care taken to insure uniformity of substrate contact. A sampling unit normally consisted of 10 pieces of wood for a size class, although occasionally as few as eight were collected due to losses. Individual branches and twigs were identified by aluminum tags attached with copper wire.

The two smaller size classes were collected every 2 mo while the largest size class was collected every 3 mo. Leftover material not placed in the study plots was dried to constant mass in a forced-air drying oven

TABLE 1. Regression equations for predicting dry mass (grams) from volume (cubic centimetres) for *Quercus prinus* branches. Model $Y = mX + b$.

Diameter class (cm)	<i>m</i>	<i>b</i>	<i>r</i> ²	<i>N</i>
0–1	0.5669	0.4317	.902	41
1–3	0.6061	0.2853	.985	47
3–5	0.6050	–1.4475	.979	14

(50°C). Regressions of dry mass on volume (Table 1) were performed and used to estimate initial dry mass of experimental pieces in the field. Approximately 5 mm thick slices were then removed from the middle and end of each 3–5 cm branch with a coping saw. A knife was used to separate bark from wood. These samples were then redried and weighed to determine tissue composition for both mass and nutrient analyses. These four subsamples from each branch were chopped into 0.5-cm³ blocks before being ground to pass successively a #20 (7.9 meshes/cm) and a #40 (15.7 meshes/cm) screen on a Wiley mill and then were redried.

For elemental analysis, bark subsamples (≈20 mg) and wood subsamples (≈50 mg) were dry ashed (490°C) overnight in prefired and weighed 20-mL crucibles. After cooling, the ashes were dissolved in 20% HNO₃ in two 15-mL steps and stored in 30-mL polyethylene bottles. Secondary standards were prepared in the same manner using United States National Bureau of Standards (NBS) orchard leaves. Samples were analyzed on a flame photometer. Commercially available primary K⁺ and Ca⁺⁺ standards were used. Verification runs were performed utilizing X-ray fluorescence, inductively coupled plasma emission spectrometry, and atomic absorption spectrophotometry. Sample recovery, based on NBS orchard leaves, was estimated at 85% and 95% for K⁺ and Ca⁺⁺, respectively.

Upon collection, each piece of woody litter was carefully picked up, any large pieces of attached debris removed, and then sealed in a plastic bag. Sample bags were stored at 5°C until microscopic examination 24–72 h later. The bags were inflated with CO₂ gas and allowed to sit 1 h before examination to immobilize Collembola and other active animals. The branches were examined under a 40× dissecting microscope and all animals removed and stored in 70% ethanol. All microarthropods were on slides mounted in Hoyer's medium for identification. Microarthropod density was calculated in terms of bark surface area. Microarthropod activity was expressed as:

$$M = \sum_{t=0}^i N_t \cdot T_{(i-t-1)}, \quad (1)$$

where *M* = microarthropod months (=micromonths), *N_t* = number of microarthropods/1000 cm² at time *t*,

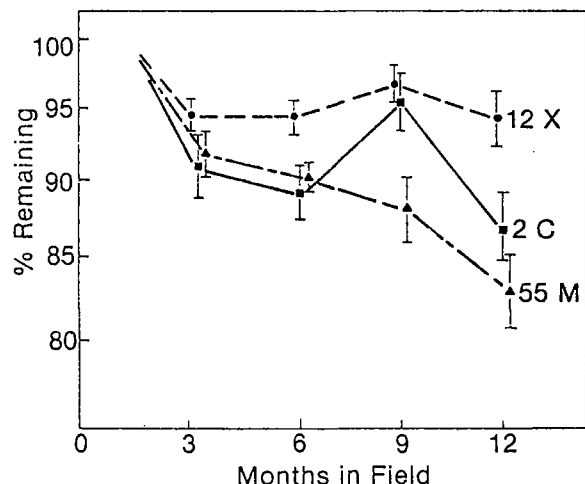


FIG. 1. Mass loss of 3–5 cm *Quercus prinus* branches on a mesic clear-cut site (55 M), a xeric clear-cut site (12 X), and on a mature hardwood control site (2 C) during their initial year in the field. Values are geometric means \pm SE.

and $T_{(t)-(t-1)}$ = the number of months elapsed between measurements. Experimental branches were analyzed for mass and nutrients for the 3–5 cm class.

Mass loss was calculated as the difference between measured final dry mass and predicted initial dry mass from the dry mass on volume regressions of the calibration branches. Other methods of estimating volume of decayed wood were investigated. Volume can be estimated by measuring length and diameter at several points and using either the formula for a cylinder or a right frustum for calculations. We found this approach to be inferior for small material. Another approach is to measure displacement of sand or water after paraffin impregnation. This approach is tedious and can potentially interfere with subsequent nutrient analyses. Our approach avoided these problems, although it would not be suitable if change in volume during decomposition was a desired parameter. Advantages of our technique include not having to dry the wood before placement in the field, and thus altering its decomposition rate, and not chemically altering the wood after recovery, a desirable situation for nutrient analyses. Exponential decay coefficients were calculated by fitting the mass loss data to the model:

$$Q_t = Q_0 e^{-kt}, \quad (2)$$

where Q_t = mass at time t , Q_0 = initial mass, and k = the annual exponential (base e) decay coefficient. Nutrient analyses were restricted to the 3–5 cm material, where one bark and one wood sample were taken from both the end and middle of each branch and then analyzed on the flame photometer (two replicates per sample, 928 measurements of experimental material, and 112 of calibration branches for each K^+ and Ca^{++} , plus one NBS orchard leaf sample per five samples).

TABLE 2. Annual exponential decay coefficients for woody litter by size class and site. Values are k 's (yr^{-1}) in the expression e^{-kt} .

WS/site, treatment	Diameter class (cm)			Mean k
	0–1	1–3	3–5	
2, Uncut control	.1524	.1728	.0912	.1388
7/55, Clear-cut mesic	.1752	.0756	.1644	.1384
7/12, Clear-cut xeric	.0456*	.0948	.0377	.0594
Mean k	.1244	.1144	.0978	

* Regression slope not different from zero at .05 probability level.

RESULTS

Mass loss for 3–5 cm *Q. prinus* branches on each site was significantly different from zero (Fig. 1) (ANOVA, $P < .05$). Analysis of variance indicated a significant site effect ($P < .05$); therefore separate regressions of dry mass remaining were required for each site. With the exception of samples taken at 9 mo, the control WS 2 and the mesic clear-cut site 55 displayed similar patterns of mass loss, with greatest losses occurring during the first and last sampling intervals.

Among 0–1 and 1–3 cm material, only 0–1 cm twigs on xeric site 12 failed to yield a significant regression of mass loss on time (ANOVA, $.10 < P < .05$). Table 2 summarizes mass loss for all sizes and sites examined when fit to the exponential model. The block experimental design allowed averages to be calculated across both site and size class. Decay coefficients for the control and mesic sites are the same when averaged across size classes but were much reduced on the xeric clear-cut site. Soil moisture (percent dry mass, 10–30 cm depth) was higher on the mesic site than on the xeric site on every sampling date (average for year = 45% on site 55; 32% on site 12). Moisture differences were apparent for litter and 0–10 cm soil, but more variable. The other side of the block design comparison, the relationship between decay coefficient (averaged across sites) and diameter of woody material (Fig. 2) appears to be inversely linear.

With respect to bark : wood ratios (Fig. 3), the mesic site and control again showed similar behavior, with the greatest difference occurring at 9 mo. Neither site differed significantly from the initial condition throughout the year. Xeric site bark : wood ratios increased over the initial condition at 3, 6, and 9 mo. At the end of 1 yr none of the sites differed either from each other or from the initial condition.

Nutrient analyses

Calcium concentrations in wood (Fig. 4) and bark (Fig. 5) differed greatly. Calcium concentrations in wood on the mesic site showed a modest ($\approx 20\%$) but steady increase over a year, while the control (with the exception of the anomalous 9-mo sample) showed a slight decrease through time. Calcium in xeric site

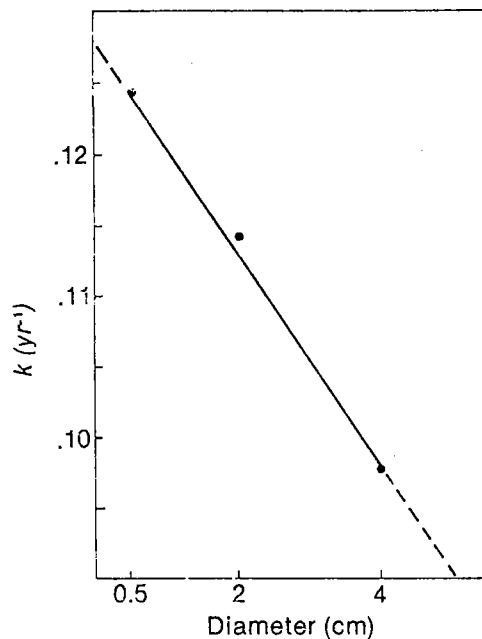


FIG. 2. Relationship between annual exponential decay coefficient and diameter of *Quercus prinus* woody litter. Model: $k = .1287 - .0076x$ (cm), $r = -.998$, $N = 3$.

branches displayed two sharp decreases in concentration and two increases, with the concentration down 37% at the end of a year. For the most part calcium concentrations in bark were an order of magnitude or more higher than in wood.

Potassium concentrations in bark (Fig. 6) and wood (Fig. 7) differed from each other much less than did calcium. In both tissues potassium concentrations behaved most similarly on the control and xeric sites,

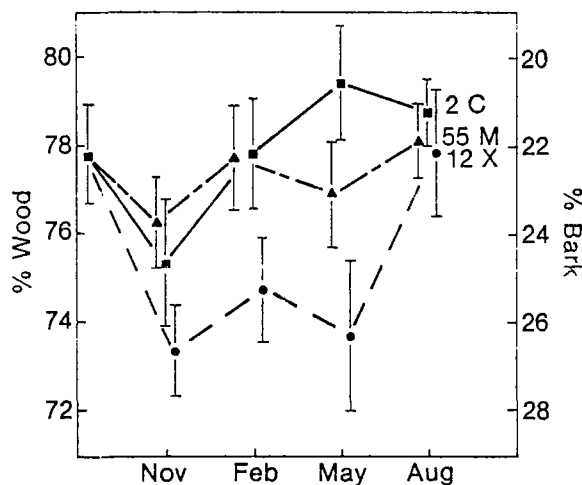


FIG. 3. Bark:wood ratios for 3-5 cm *Quercus prinus* branches on sites 12 and 55 in WS 7, and control WS 2. Abbreviations as in Fig. 1. Values are means \pm SE.

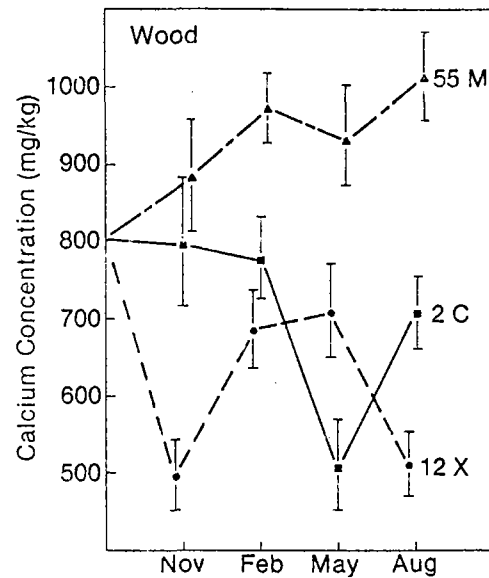


FIG. 4. Calcium concentrations in woody tissue of 3-5 cm *Quercus prinus* branches on sites 12 and 55 in WS 7, and control WS 2. Abbreviations as in Fig. 1. Values are geometric means \pm SE.

although concentrations in xeric site material were usually reduced relative to the control. In wood concentrations fell on all sites for 6 mo and continued to fall on the control and xeric sites over the entire year. Potassium in mesic site wood rose rapidly in concentration over the last 6 mo and exceeded the initial concentration after a full year in the field. Concentrations of potassium in bark on the control and xeric sites appeared to oscillate about a 25% reduction, while levels increased in mesic site bark over the last 6 mo.

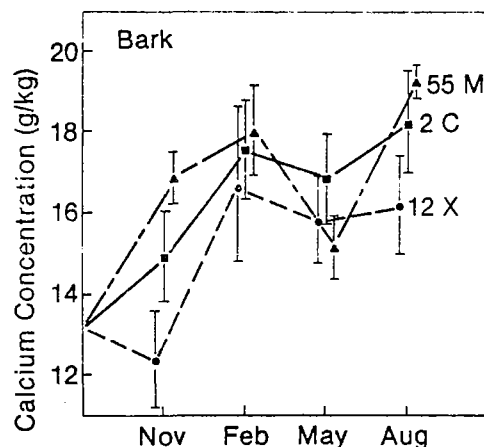


FIG. 5. Calcium concentrations in bark tissue of 3-5 cm *Quercus prinus* branches on sites 12 and 55 in WS 7, and control WS 2. Abbreviations as in Fig. 1. Values are geometric means \pm SE.

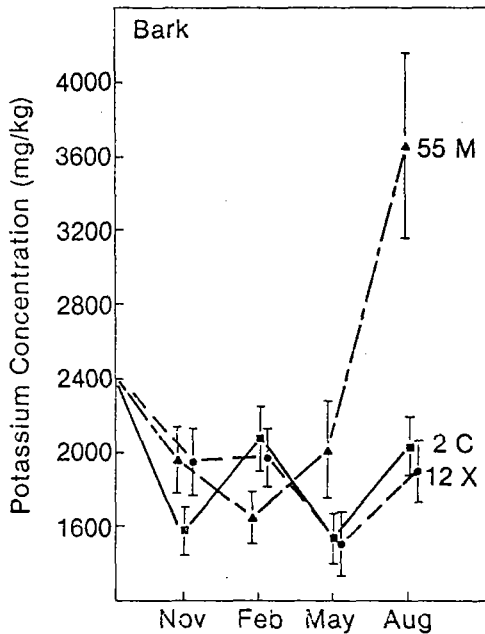


FIG. 6. Potassium concentrations in bark tissue of 3-5 cm diameter *Quercus prinus* branches on sites 12 and 55 in WS 7, and control WS 2. Abbreviations as in Fig. 1. Values are means \pm SE.

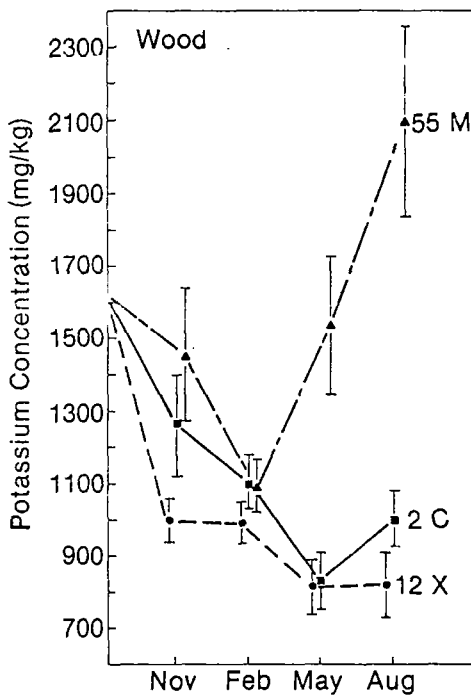


FIG. 7. Potassium concentrations in wood tissue on 3-5 cm *Quercus prinus* branches on sites 12 and 55 in WS 7, and control WS 2. Abbreviations as in Fig. 1. Values are means \pm SE.

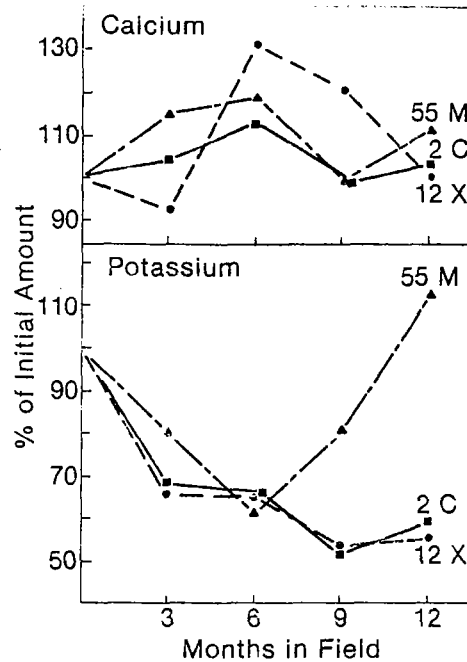


FIG. 8. Percent of initial amount of calcium and potassium remaining in 3-5 cm *Quercus prinus* branches on sites 12 and 55 in WS 7, and control WS 2. Abbreviations as in Fig. 1.

By combining mass loss data, bark : wood ratios, and nutrient concentrations it was possible to calculate the total amount of calcium and potassium contained in entire branches (Fig. 8). Although temporary increases in calcium did occur, at the end of 1 yr only the mesic site exceeded initial content (Wilcoxon signed-ranks test $P < .05$). Potassium content decreased in the control ($k = .535$, $r^2 = .73$, $P < .01$) and xeric site ($k = .556$, $r^2 = .78$, $P < .01$) branches all year and on the mesic site for 6 mo. During the last 6 mo mesic site branches contained more potassium than branches from other sites (Mann-Whitney U test, $P < .001$) and at 12 mo exceeded initial content (Wilcoxon signed-ranks test $P < .01$). Control and xeric site potassium contents were fit to a simple negative exponential model with decay coefficient of $.54 \text{ yr}^{-1}$.

Microarthropods

The mesofauna of decaying *Q. prinus* branches were dominated by the microarthropod groups Acari (mites) and Collembola (springtails). Meso- and macroarthropods were virtually absent, as were nematodes and annelid worms. Insect larvae (mostly Cecidomyiidae) became evident only late in the study. Richness, diversity, and numbers showed a general increase throughout the study. No clear successional patterns were discerned. The most abundant group was Cryptostigmata, which have been described elsewhere (Abbott et al. 1980).

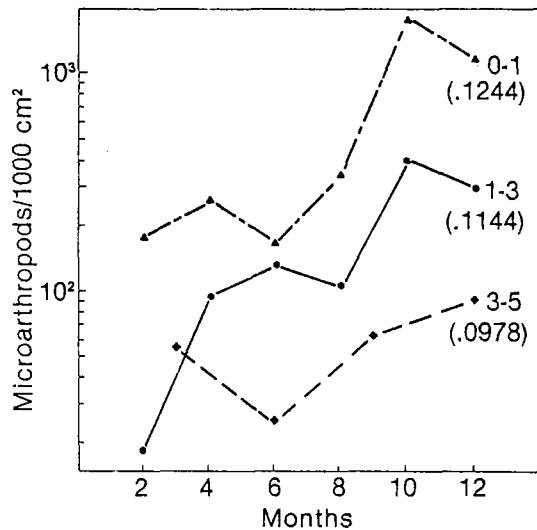


FIG. 9. Numbers of microarthropods per 1000 cm² surface area found on 0-1, 1-3, and 3-5 cm diameter *Quercus prinus* woody litter. Decay coefficient is in parentheses.

Several patterns became evident when microarthropod abundance on decaying branches and twigs was examined. When density is plotted by size class across sites (Fig. 9) an inverse relationship appears. Because of extremely skewed frequency distributions (the best fit was a negative binomial) only mean numbers are shown. No transform was found which adequately normalized the data. There also appears to be a relationship between microarthropod density and decay coefficient. Abundance also tends to increase with time. Microarthropod abundance is also affected by

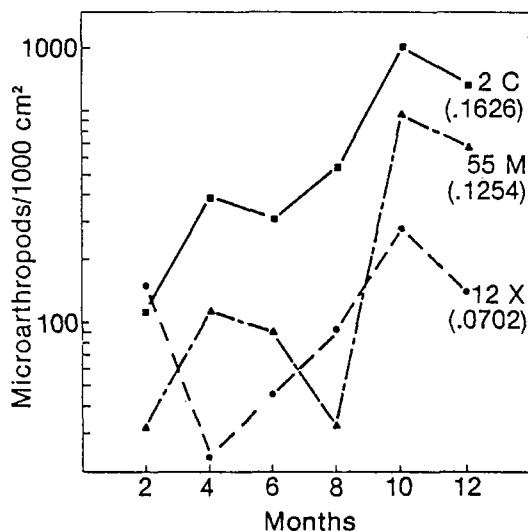


FIG. 10. Numbers of microarthropods per 1000 cm² surface area of 0-1 and 1-3 cm *Quercus prinus* twigs for sites 12 and 55 in WS 7, and WS 2. Abbreviations as in Fig. 1. Decay coefficient is in parentheses.

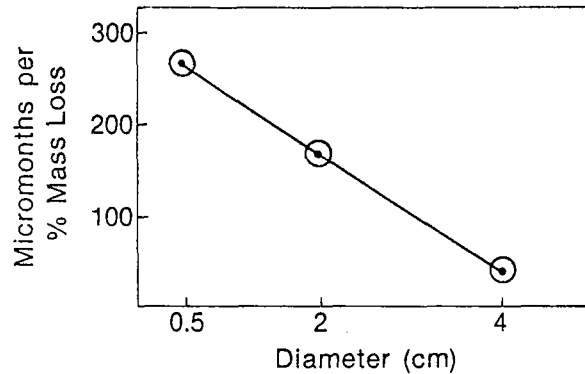


FIG. 11. Relationship between the number of microarthropod months ("micromonths") associated with each percent mass loss, and diameter of *Quercus prinus* woody litter.

site (Fig. 10). The control site was clearly more favorable to microarthropods, although high densities were attained on the mesic site late in the study. Again, microarthropod density, time, and state of decomposition appear to be related. Fig. 11 illustrates the negative linear relationship between microarthropod activity and diameter when adjusted for the effects of mass loss.

DISCUSSION

Mass loss

Quercus prinus twigs and branches lost mass at rates 2.5 times slower than *Q. prinus* leaf litter (Seastedt and Crossley 1981). Decay rates appear to be highly influenced by microclimatic factors such as moisture and temperature. Low moisture levels and high temperatures in the lethal range for mites (Madge 1965, Abbott et al. 1980) inhibit wood decay. Diameter of branch material also appears to have an effect, with larger size classes taking longer to decay. This relationship was hypothesized by Harris et al. (1972) to be curvilinear (otherwise large logs would not decay at all), but a simple linear relationship, although not strongly supported by this study, does adequately describe this phenomenon over the range of size classes in this study. The decay rates measured here are similar to those found by Swift et al. (1976) for oak and other hardwoods in England. Our rates are lower than some literature values (e.g., Gosz et al. 1973). The high rates in that study were attributed to physical processes, such as the falling off of bud scales. Since terminal growth (green) was avoided in this study, and since no large bark:wood ratio changes were observed, the decay rates reported here are more likely to represent true decomposition and less likely to represent physical removal. The decomposition rates of wood and bark reported by Fogel and Cromack (1977) are lower than those reported here, and may be explained by their use of litterbags or the generally dry summers found at their study site. The differences be-

tween the results of various studies may be due to species differences, although the only distinctions found thus far have been those separating hardwoods and softwoods (Gosz et al. 1973). The very low rates reported by Grier (1978) are likely due to very large diameter (>40 cm) of the material examined, if the diameter-decay rate relationship proves to be valid. The rapid initial mass losses reported here are probably the result of using fresh material in which microbial utilization of easily decomposable nonstructural carbohydrates had not been inhibited by drying (Hulme and Shields 1970). From examination of the bark : wood ratios it would appear that this easily decomposable material is in the woody tissue and not the bark. This contention is supported by the work of Fogel and Cromack (1977), who found bark to be highly refractory.

Nutrient dynamics

Calcium is a relatively immobile element in decomposing organic matter. Often calcium concentration increases as the organic matrix in which it is imbedded decays. For this reason total amounts of calcium, rather than concentrations, must be examined. After 1 yr the total amount of calcium in branches on all sites was virtually unchanged. However, since transient increases in calcium did occur, it would be preferable to interpret the data as net balances, with active inputs and outputs in approximate equilibrium. Since bark contains most of a branch's calcium, total budgets are very sensitive to accurate estimations of the contribution of bark to total mass; thus interpretations of calcium dynamics must be conservatively viewed as tentative.

Unlike calcium, potassium is highly mobile and subject to leaching. Microbes usually have higher nutrient concentrations than the substrates upon which they are found (Stark 1973, Swift 1977) and are capable of penetrating wood and accumulating nutrients before any change in substrate mass can be detected (Healey and Swift 1971). Fig. 12 represents the causal vectors we believe to be responsible for changes in potassium and calcium content of woody material. If both bark and wood lost potassium due to leaching at equal rates, then changes in potassium content should follow the dashed diagonal lines. Immobilization or uptake of potassium by microbes in either bark or wood should cause a deflection from the theoretical leaching pathway. Equal microbial activity in both tissues could cause the observed (e.g., mesic site 55) changes to follow the leaching pathway, but would tend to retard or reverse the speed and/or direction of movement along the leaching pathway. The strong deflection on xeric clear-cut site 12 may be a result of a restriction of microbial activity to bark tissue followed by a general lack of activity, in which case the resultant movement parallels the leaching pathway. There may have been some translocation of calcium from wood to bark

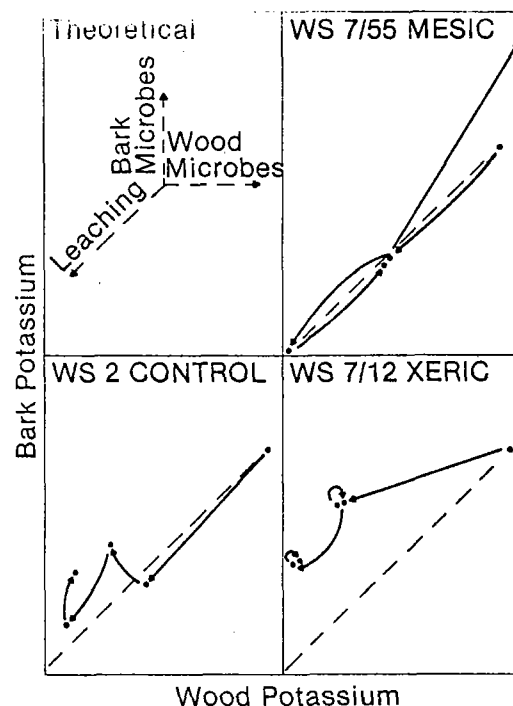


FIG. 12. Observed potassium dynamics in *Quercus prinus* woody litter and theoretical vectors of possible causal factors. Dashed diagonal lines represent probable leaching pathways. Note two-dimensional axes.

on this site as well. Potassium levels in throughfall under tree debris on the clear-cut were elevated (W. T. Swank, *personal communication*). If the greater mass loss on the mesic site (relative to the xeric site) is an indication of greater microbial activity, then it is possible that the observed increase in potassium content was due to microbial uptake and immobilization of throughfall potassium. The failure of wood on the control watershed to increase at a similar rate may be a result of the much lower potassium levels found in throughfall on the control. Decomposing woody litter can thus act as a significant nutrient sink where conditions are favorable for microbial activity and can help reduce potential system losses of nutrients.

Microarthropods

Leaf litter in a hardwood forest at Coweeta has ≈ 400 microarthropods/1000 cm² surface area (Gist 1972, Day 1973). Late in the study, microarthropods on the two smaller size classes of woody litter were just as abundant as leaf litter populations and were still increasing on the 3–5 cm material. In undisturbed forests woody litter fall is dominated by material <3 cm in diameter (Christensen 1977, 1978). The greater abundance of microarthropods on the smaller material at Coweeta may be a result of selection on the animal's part for material most like that which normally occurs. This preponderance of animals on the smaller material

would be even greater if numbers were expressed on a volume- or length-of-branch basis rather than a surface-area basis, as smaller twigs have relatively more bark surface area. Additionally, the increasing abundance of cecidomyiid larvae on the generally depressed xeric site may be an indication that white rot (fungal dominated) is occurring here to a greater extent than brown rot (bacterial dominated) (Wallwork 1976).

The relationship between microarthropod abundance and decay rate (abundance can account for up to 60% of the variance in mass remaining) suggests a causal relationship. Microarthropod months, a cumulative measure of activity, gives slightly better correlations with decay rate. Although abundance is highest on the smallest material, microarthropods appear to be more effective in causing decay on the larger material. Microarthropods are known to be effective inoculators, and may affect microbial growth rates and species composition through grazing. It would appear that woody litter decomposition is an interactive effect of both microbes and microarthropods. Unfortunately, both microbes and microarthropods respond similarly to climatic variables such as moisture and temperature; thus it is difficult to isolate effects. It appears that the climatic variables affecting decomposition rates may do so through their effects on microarthropods and the microarthropod-microbes interaction.

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LITERATURE CITED

- Abbott, D. T., T. R. Seastedt, and D. A. Crossley, Jr. 1980. The abundance, distribution and effects of clearcutting on Cryptostigmata in the Southern Appalachians. *Environmental Entomology* 9(5):618-623.
- Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. *Science* 159:882-884.
- Christensen, O. 1978. The dynamics of wood litter fall in a Danish oak forest. *Natura Jutlandica* 20:155-162.
- . 1977. Estimation of standing crop and turnover of dead wood in a Danish oak forest. *Oikos* 28:177-186.
- Crossley, D. A., Jr. 1977. The roles of terrestrial saprophagous arthropods in forest soils: current status of concepts. Pages 49-56 in W. J. Mattson, editor. *The role of arthropods in forest ecosystems*. Springer-Verlag, New York, New York, USA.
- Day, F. B., Jr. 1973. Primary production and nutrient pools in the vegetation on a Southern Appalachian watershed. Dissertation. University of Georgia, Athens, Georgia, USA.
- Dils, R. E. 1957. A guide to the Coweeta Hydrologic Laboratory. United States Department of Agriculture, Springfield, Virginia, USA.
- Fogel, R., and K. Cromack, Jr. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. *Canadian Journal of Botany* 55:1632-1640.
- Gist, C. S. 1972. Analysis of mineral pathways in a cryptozoan foodweb. Dissertation. University of Georgia, Athens, Georgia, USA.
- Gosz, J. R., G. E. Likens, and F. H. Bormann. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. *Ecological Monographs* 43:173-191.
- Grier, C. C. 1978. A *Tsuga heterophylla*-*Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Canadian Journal of Forestry Research* 8:198-206.
- Harris, W. F., G. S. Henderson, and D. E. Todd. 1972. Measurement of turnover of biomass and nutrient elements from the woody component of forest litter on Walker Branch watershed. Memo Report 72-146, Eastern Deciduous Forest Biome, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Healey, I. N., and M. J. Swift. 1971. Aspects of the accumulation and decomposition of wood in the litter layer of a coppiced beech-oak woodland. Pages 417-430 in *Proceedings of the Fourth Colloquium of the Zoology Committee of the International Society of Soil Sciences* 14-19 September, Dijon, France. *Annales de Zoologie—Ecologie Animale (numéro hors-série)* 1971. Institut National de la Recherche Agronomique, Paris, France.
- Hulme, M. A., and J. K. Shields. 1970. Biological control of decay fungi in wood by competition for non-structural carbohydrates. *Nature* 227:300-301.
- Johnson, P. L., and W. T. Swank. 1973. Studies of cation budgets in the southern Appalachians in four experimental watersheds with contrasting vegetation. *Ecology* 54:70-80.
- Madge, D. S. 1965. The effects of lethal temperatures on Oribatid mites. *Acarologia* 7:121-130.
- Reichle, D. E. 1977. The role of soil invertebrates in nutrient cycling. In U. Lohm and T. Persson, editors. *Soil organisms as components of ecosystems*. *Ecological Bulletin (Stockholm)* 25:145-156.
- Seastedt, T. R., and D. A. Crossley, Jr. 1981. Microarthropod response following cable logging and clear cutting in the Southern Appalachians. *Ecology* 62(1):126-135.
- Stark, N. 1973. Nutrient cycling in a Jeffrey Pine Ecosystem. University of Montana Press, Missoula, Montana, USA.
- Swift, M. J. 1977. The roles of fungi and animals in the immobilization and release of nutrient elements from decomposing branch-wood. In U. Lohm, and T. Persson, editors. *Soil organisms as components of ecosystems*. *Ecological Bulletin (Stockholm)* 25:193-202.
- Swift, M. J., I. N. Healey, J. K. Hibberd, J. M. Sykes, U. Bampoe, and M. E. Nesbitt. 1976. The decomposition of branch-wood in the canopy and floor of a mixed deciduous woodland. *Oecologia* 26(2):139-149.
- Wallwork, J. A. 1976. The distribution and diversity of soil fauna. Academic Press, New York, New York, USA.
- Whittaker, R. H., G. E. Likens, F. H. Bormann, J. S. Eaton, and T. G. Siccama. 1979. The Hubbard Brook ecosystem study: forest nutrient cycling and element behavior. *Ecology* 60:203-220.