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LITTER PRODUCTION, DECOMPOSITION, AND NUTRIENT CYCLING IN A MIXED HARDWOOD WATERSHED AND A WHITE PINE WATERSHED

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ABSTRACT

Litter production and decomposition data were obtained for a mixed-hardwood watershed and for a white pine watershed. Litterfall data were obtained for leaves, stems, flowers, acorns, and miscellaneous debris in the hardwood watershed and for needles, stems, and cones in the white pine watershed. Litterfall data obtained included biomass of litter; nitrogen, phosphorus, potassium, calcium, and magnesium contents in litter; and structural organic constituents (lignin, cellulose, and total fiber) of leaf litter. Total annual litter production in the hardwood watershed (1970–1971) was 4369 kg ha^{-1} $year^{-1}$ of which 2773 kg ha^{-1} $year^{-1}$ (64%) was leaf litter. Total annual white pine litter production (1970–1971) was 3253 kg ha^{-1} $year^{-1}$, 98% of which was needle litter in the young stand (planted 1956). Litter decomposition data were obtained for weight loss rate and for loss rates of nutrients. The first-year litter breakdown rate of confined mixed-hardwood leaf litter was $k = -0.70$ $year^{-1}$; the breakdown rate of confined white pine needle litter was $k = -0.46$ $year^{-1}$. Litter decomposition rates of chestnut oak, white oak, white pine, red maple, and dogwood were significantly correlated with senescent leaf carbon-to-nitrogen ratio and sclerophyll index, the sclerophyll index giving a better statistical estimate of decomposition rate.

Nutrient cycling and energy flow are two ecological processes that delineate the structure and dynamics of ecological systems. In terrestrial ecosystems an important set of energy flows and nutrient transfers result from litterfall and from the subsequent decomposition of litter. Litterfall and litter decomposition can be thought of as separate events in terrestrial ecosystems, but such ecological

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processes as energy flow and nutrient cycling permit them to be linked together functionally in an ecosystems context.

Seventy percent of the energy fixed in net primary production in a grazed meadow ecosystem goes directly to decomposer organisms (Macfadyen, 1963). As much as 90% of terrestrial net primary production ultimately is utilized by decomposers (Whittaker, 1970; Odum, 1971). It has been suggested that decomposer organisms may be just as important in aquatic ecosystems as they are in terrestrial ones (Pomeroy, 1970). Litterfall and litter decomposition also account for a substantial portion of internal nutrient cycling in terrestrial ecosystems. In a study of a mesic oak-dominated forest floor, litterfall accounted for approximately 60% (average for the elements phosphorus, potassium, calcium, and magnesium) of internal nutrient input to the forest floor (Carlisle, Brown, and White, 1966a; 1966b).

Biodegradation of litter is a complex process in which microorganisms and soil animals interact synergistically (Crossley, 1970; Witkamp, 1971). Both the microorganisms and soil animals are strongly influenced by such abiotic factors as soil–litter temperature and moisture. Microorganisms predominate in litter decomposition, primarily because they have enzymes capable of biodegrading structural carbohydrates including such complex end products of carbohydrate metabolism as lignin (Witkamp, 1971). As much as 90% of litter materials can be biodegraded by microorganisms (Macfadyen, 1963). Microorganisms are also important in the release and transfer of nutrients bound in the litter (Witkamp, 1971; Stark, 1972; Todd, Cromack, and Stormer, 1973). Soil animals, by interacting synergistically with the microorganisms, function as one set of biological control factors which regulate rates of litter decomposition (Edwards, Reichle, and Crossley, 1970; Ausmus and Witkamp, 1974). In turn these animals are dependent for their nutrition primarily upon the microorganisms they ingest since soil animals lack enzymes necessary to biodegrade all but the simplest forms of structural carbohydrates (Nielson, 1962).

Considerable data exist for litter production and litter nutrients in forest ecosystems, with major review papers summarizing forest-litter data from many different sources (Ovington, 1962, 1965; Olson, 1963; Bray and Gorham, 1964; Rodin and Bazilevich, 1967). For the purpose of facilitating comparison of data from many different ecosystems, total annual litter budgets are preferred; subannual budgets for major litter components usually are available in most recent studies (Carlisle, Brown, and White, 1966b; Sykes and Bunce, 1970; Gosz, Likens, and Bormann, 1972).

In this paper we compare nutrient cycling from litter production and litter decomposition in a mixed-hardwood ecosystem with the same nutrient-cycling processes in an adjacent white pine (*Pinus strobus* L.) watershed in the southern Appalachians. We also compare indexes of foliage-litter substrate quality obtained from the two different vegetation types and discuss nutrient cycling implications of foliage-litter nitrogen and phosphorus levels in the context of carbon allocation to such substrates as lignin and cellulose.

RESEARCH AREAS

The two forest watersheds used in this study are located within the U. S. Forest Service Coweeta Hydrologic Laboratory, Franklin, N. C. The two field sites were chosen such that litter production and litter decomposition in a mixed-hardwood ecosystem could be compared and contrasted with corresponding litter dynamics in a white pine ecosystem. The mature mixed-hardwood stand, designated by the U. S. Forest Service as watershed 18, is 12.5 ha in area. The white pine stand, planted in 1956, is 13.5 ha in area and was designated as watershed 17. Broad environmental differences between the two watersheds are minimized in that they have similar slopes, aspects, altitudinal ranges, soils, and precipitation and are contiguous for approximately one-half their vertical distances (Kovner, 1955; Johnson and Swank, 1973).

MATERIALS AND METHODS

Square traps 0.5 m on a side were used for hardwood leaf litter, flower litter, and debris. To make all traps equal regardless of ground slope, we placed each trap on wooden legs and leveled each with a spirit level during installation. The traps were checked periodically thereafter. Thirty of the litter traps were placed at random in the hardwood watershed in the fall of 1969. Acorn litter was collected from 20 60-cm by 60-cm cloth-bottomed deadfall traps.

White pine needles were collected in 200-cm by 15-cm aluminum troughs used in a throughfall study of watershed 17 (Best, 1971). Nineteen of these troughs were used; 10 were located in one random transect and 9 were located in another random transect through the watershed.

During the fall periods, leaf and needle litter were collected at approximately 2-week intervals. Since some of the white pine needles became lodged in branches, additional litter collections were made at intervals throughout the year. No hardwood collections were made in winter because little leaf litter remained on the trees after December. Beginning in late spring and continuing through the summer at monthly intervals, flower litter and debris were collected in the hardwood watershed.

Stem and branch litter were collected from 18 10-m by 10-m ground plots in the hardwood stand. During the summer of 1970, the total accumulated standing crop of woody litter was estimated. Within each plot, two 2-m by 2-m subplots, located on opposite diagonal corners of the large plots, were used to collect stem litter less than 2.5 cm in diameter. In the whole plot, woody litter 2.5 cm or greater in diameter was collected. American chestnut logs and branches were excluded from the standing crop totals since they represented litter input from a catastrophic event in the watershed. The following year collection was made of all woody litter that had fallen into the plots.

In the summer of 1970, 10 3.33-m by 3.33-m woody-litter plots were set up in the white pine stand; collections were made in the summer of 1971. Most of the dead branches remain on the trees. Consequently woody-litter input to the forest floor is as yet relatively unimportant for the white pine stand. Woody-litterfall data from the ground plots of both watersheds were corrected to a horizontal area basis for average slopes of 53% in both watersheds. This permitted comparison of woody litter from the ground plots with litter-trap data on a common basis.

Data for first-year leaf-litter breakdown of single species were obtained during two consecutive 1-year periods, beginning in the fall of 1969. Single tree species for which leaf-litter decomposition data were obtained included chestnut oak (*Quercus prinus* L.), white oak (*Quercus alba* L.), red maple (*Acer rubrum* L.), and flowering dogwood (*Cornus florida* L.) in the hardwood watershed and eastern white pine in the pine stand. The four species used for deciduous-litter breakdown were chosen to give a range of decomposition rates and to represent the more important species groups producing leaf litter within the system. In the hardwood stand additional leaf-decomposition data were obtained for mixed-species leaves in litter bags.

Data for litter breakdown of single species were obtained using decimeter square fiber glass litter bags (Crossley and Hoglund, 1962), each containing approximately 2.5 g of leaves. In the deciduous stand the integrated decomposition rate was obtained for mixed-hardwood leaves confined in the large, 0.125 m^2, litter bags each containing approximately 40 g of deciduous leaves. In addition to the larger size, a different bag design was used for the mixed-litter bags to permit easier entry of soil animals. The upper half of each large bag was made of 2.54-cm-mesh nylon netting, while the lower half was fine 2-mm-mesh nylon to inhibit loss of small leaf fragments from the bag. The decimeter-sized fiber glass litter bags used for single-species leaves from chestnut oak, white oak, red maple, and dogwood and needles of white pine were all 1-mm mesh.

Litter bags were removed from the field at approximately monthly intervals. The bags were weighed to determine percentage weight loss from original samples before the samples were ground in a Wiley mill for nutrient analysis.

Litter weight loss was quantified for single-species and for mixed-deciduous litter bags using the exponential decay model of Olson (1963). Nutrient loss rates from mixed deciduous litter were also quantified using the same approach.

Leaves, other small litter, and woody litter were air-dried for storage where practical or dried at 50°C when wet litter or green leaves were collected. Leaves that were to be used for decomposition studies were air-dried only to prevent possible chemical changes that might affect decomposition. For nutrient analyses, including nitrogen, litter was dried at 70°C. All final dry-weight biomass calculations were made on litter subsamples dried at 70°C. Samples were oven-dried at 50°C for analysis of organic constituents of litter. Nutrient analyses included determinations of sodium and the following major elements: nitrogen, phosphorus, calcium, potassium, and magnesium.

A micro-Kjeldahl technique was used for nitrogen determinations. Micro-Kjeldahl procedures were those of the Soil Testing and Plant Analysis Laboratory of the Agronomy Department, University of Georgia, as given in their 1971 laboratory manual (*Laboratory Procedures for the Analysis of Soils, Feed, Water, and Plant Tissue*). All other elements were determined by direct-reading spark-emission spectroscopy (Jones and Warner, 1969). Analyses for the percentage of acid-detergent fiber (cellulose and lignin) and non-cell-wall plant material followed the methods of Van Soest (1963, 1966, and 1967). The sclerophyll index was calculated following the method of Loveless (1961). Since the sclerophyll index as originally proposed uses the ratio of crude fiber to crude protein × 100, crude fiber was estimated (Ellis, Matrone and Maynard, 1946) as total acid-detergent fiber × 0.64. Crude protein was calculated (Loveless, 1961) as percent nitrogen × 6.25. The percentage of carbon in leaf litter used for decomposition studies was estimated from the percentage lignin content in leaves using a regression given by Van Soest (1963).

To analyze for changes in nitrogen and total fiber, we harvested green leaves in August from several of the more important tree species in the hardwood stand and from the white pine stand. To analyze nutrient differences between senescent leaves and needles, we collected additional leaf samples in mid-October. For comparative purposes we have included a few values for western coniferous and deciduous species.

RESULTS AND DISCUSSION

Results are given as annual budgets of nitrogen, phosphorus, calcium, potassium, and magnesium in litterfall and biomass of different hardwood and white pine litterfall components in Tables 1 and 2. The leaf-litterfall category in the hardwood watershed does not include litter from shrubs, such as *Kalmia latifolia* L., *Rhododendron maximum* L., or herbaceous litter. Such litter was estimated (Day, 1971) to total 370 kg ha^{-1} year^{-1}. Herbaceous leaf litterfall was not estimated in the white pine stand; ground cover was sparse, however, owing to the closed canopy.

Total litter production in the hardwood watershed was 4369 kg ha^{-1} year^{-1}, which is within the lower 95% confidence interval of the annual litter production, totaling 4800 ± 548 kg ha^{-1} year^{-1} for 11 other North American warm temperate deciduous forests (Bray and Gorham, 1964). Hardwood-litter production was only 14% greater than the mean annual litter production of 3730 ± 260 kg ha^{-1} year^{-1} in 67 cool temperate deciduous forests (Bray and Gorham, 1964). In an oak-dominated British forest with a similar rainfall regime as Coweeta, on soils of low nutrient status, a total annual litter budget of 3858 kg ha^{-1} year^{-1} was observed (Carlisle, Brown, and White, 1966a). On calcareous soils in Meathop Wood, Great Britain, an average total litter production of 5130 kg ha^{-1} year^{-1} was reported (Sykes and Bunce, 1970).

TABLE 1

HARDWOOD WATERSHED 18: ANNUAL LITTERFALL BUDGET FOR BIOMASS AND MACRONUTRIENTS FOR 1970–1971

Category	Leaves	Stems ≤2.5 cm diameter	Stems >2.5 cm diameter	Acorns: Cups	Acorns: Shells	Acorns: Kernels	Flowers	Debris*	Total
Biomass,†									
kg ha^{-1} year^{-1}	2773 ± 305	706 ± 88	306 ± 145	122	120	171	6.2 ± 2.5	165 ± 37	4369
% of biomass	63.5	16.2	7.0	2.8	2.7	3.9	0.1	3.8	100.0
Macronutrients,‡ kg ha^{-1} year^{-1}									
Nitrogen	23.57	3.89	1.35	0.49	0.54	1.71	0.13	2.20	33.87
Phosphorus	3.48	0.62	0.25	0.11	0.10	0.26	0.01	0.22	5.03
Potassium	13.00	0.57	0.20	0.90	0.40	2.19	0.05	0.76	18.07
Calcium	34.11	5.57	1.73	0.43	0.41	0.15	0.03	2.16	44.49
Magnesium	6.10	0.10	0.01	0.02	0.00	0.07	0.02	0.23	6.55

*Debris category includes such fine litter fragments as bud scales, lichen fragments, and insect frass.

†Figures given are mean ±95% confidence interval of the mean.

‡Calculated as the product of average biomass, in kilograms per hectare per year, and percentage nutrient concentration on a dry-weight basis.

TABLE 2

WHITE PINE WATERSHED 17: ANNUAL LITTERFALL BUDGET FOR BIOMASS AND MACRONUTRIENTS FOR 1970–1971

Category	Needles	Stems*	Pine cones	Total
Biomass, kg ha^{-1} year^{-1}	3184 ± 293	38.5 ± 14.0	30.6 ± 8.1	3253
% of biomass	97.9	1.2	0.9	100.0
Macronutrients, kg ha^{-1} year^{-1}				
Nitrogen	26.27	0.16	0.11	26.54
Phosphorus	3.66	0.03	0.03	3.72
Potassium	5.32	0.10	0.12	5.54
Calcium	19.08	0.11	0.003	19.19
Magnesium	2.71	0.002	0.000	2.71

*Most dead stems remained attached to the trees.

Total annual litter production in the white pine watershed was 3253 kg ha^{-1} year^{-1}, considerably less than the mean annual litter production of 5425 ± 950 kg ha^{-1} year^{-1} in 8 other North American warm temperate coniferous forests (Bray and Gorham, 1964). However, the white pine needle-litter production of 3184 ± 293 kg ha^{-1} year^{-1} does not differ significantly from annual needle-litter production, averaging 3640 ± 510 kg ha^{-1} year^{-1} in 10 North American warm temperate coniferous forests (Bray and Gorham, 1964). North American warm temperate forests average 37% nonneedle litter, while cool temperate forests average 23% (Bray and Gorham, 1964). On this basis, the white pine watershed at Coweeta could average 4500 to 5000 kg ha^{-1} year^{-1} total annual litter production when mature. Needle-litter production did not differ significantly from white pine needle production, averaging 3386 ± 375 kg ha^{-1} year^{-1} for three stands located in the northeastern United States (Chandler, 1944).

Comparing the nutrient budgets of these three northeastern white pine stands with data in Table 2 shows that the former were cycling 26% more nitrogen, 10% more potassium, 54% more magnesium, nearly the same quantities of calcium, and 46% less phosphorus. Comparison of total annual litterfall nutrient budgets in Tables 1 and 2 shows the hardwood stand was cycling more potassium, calcium, and magnesium in litterfall than the white pine stand. The appreciably greater amounts of potassium, calcium, and magnesium being cycled by the hardwood ecosystem than by the white pine watershed are consistent with other reports (Chandler, 1944; Ovington, 1962; 1965); temperate hardwood ecosystems generally cycle more cations than coniferous ecosystems with similar productivities. In the present case, total litterfall and nutrient return in litter are substantially less in the white pine watershed.

Litter from the reproductive materials and fine debris in the hardwood watershed had equal or higher percentage concentrations of all macronutrients, except calcium, as did deciduous leaf litter. Branch litter contained smaller nutrient concentrations than deciduous leaf litter. Flower litter, which was mostly from oaks, and miscellaneous debris contained relatively more macronutrients, except potassium, than did acorns. Partitioning the acorns into component parts permitted the nutrient quality of the kernels to be assessed. Acorn production in 1970 to 1971 was heavy and totaled 9.4% of total litterfall biomass. Three years of acorn production in an oak-dominated forest in Great Britain averaged 2.5% of total litter (Sykes and Bunce, 1970). Although no acorns were collected at Coweeta during the subsequent year, production seemed noticeably less.

Total litter nutrient input budgets in throughfall and litterfall are given in Table 3. Data are for potassium, calcium, magnesium, and sodium in both the hardwood and the white pine stands. Both watersheds are cycling nearly similar amounts of nutrients in throughfall, but they differ substantially in quantities

TABLE 3

COMPARISON OF LITTERFALL AND THROUGHFALL NUTRIENT BUDGETS BETWEEN HARDWOOD AND WHITE PINE STANDS FOR 1970–1971

Nutrient budgets, kg ha^{-1} $year^{-1}$	K	Ca	Mg	Na*
Hardwood				
Annual litterfall, total	18.07	44.49	6.55	0.009
Annual throughfall, total†	30.50	8.10	3.10	8.600
Total annual budget	48.57	52.59	9.65	8.609
Annual litterfall, % of total	37.2	84.6	67.9	0.1
White pine				
Annual litterfall, total	5.54	19.19	2.71	0.002
Annual throughfall, total†	30.50	6.30	2.00	7.20
Total annual budget	36.54	25.49	4.71	7.202
Annual litterfall, % of total	15.2	75.3	57.5	0.03

*Sodium concentration is 2 ppm in hardwood litter and 0.5 ppm in white pine litter.

†From Best (1971).

and in total proportions of nutrients contributed by litterfall. In terms of absolute amounts and percentage contribution by litterfall to the total nutrient budgets, the deciduous system has more elements in litterfall relative to throughfall than is the case for the white pine stand.

When the total nutrient budgets in the hardwood watershed are compared with those of a mesic oak-dominated forest in Britain (Carlisle, Brown, and White, 1966b) for the elements potassium, calcium, and magnesium, it is seen that the percentages contributed by litterfall in the Coweeta hardwood stand are all greater by an average of 22%. Total amounts of potassium and calcium cycled at Coweeta in both throughfall and litterfall also are greater by 20%, while 27% more total magnesium was cycled in their system. Sodium budgets are very different in the two deciduous forests, with nearly seven times more total sodium being cycled in the British oak woodland. Although detailed budgets are not given in Table 1, actual sodium content of litter in the British system (Carlisle, Brown, and White, 1966b) was three orders of magnitude greater than that of the hardwood litter at Coweeta.

In Table 4 the data for organic constituents in leaves show several trends. Most senescent leaves have higher total fiber and lignin but lower nitrogen and phosphorus than do leaves in the mid-growing season. For purposes of comparison with deciduous species, we had to take composite samples of all age classes of needles or leaves to obtain a representative sample for foliar nutrient and organic analyses.

It has been hypothesized that foliar sclerophyll indexes above 100 to 150 indicate a vegetation that is adapted to growing on phosphorus-deficient sites (Loveless, 1961; 1962). Species growing on such sites generally have lower protein content than vegetation with adequate phosphorus available (Loveless, 1961; 1962). Although there is some question as to when in the season to sample green leaves for sclerophyll determinations, very early season values probably would be misleading owing to higher nitrogen and phosphorus content and lower fiber content. When mid-August values for green hardwood leaves at Coweeta are compared, all sclerophyll indexes are high, indicating a sclerophyllous vegetation. All conifer species compared, including those from the western United States, have high sclerophyll indexes. Red alder and snowbrush are included as examples of nitrogen-fixing species. Nitrogen-fixing species might have low sclerophyll indexes simply because they have a readily available source of nitrogen, even in soils of low phosphorus availability. American chestnut survives at Coweeta only as stump sprouts.

Evidence has been presented that a phosphorus content below 0.3% is associated with a lower protein content and a high sclerophyll index (Loveless, 1961; 1962). Most phosphorus values for green leaves in the species listed in Table 4 were less than 0.2%, except yellow poplar and Douglas fir, and all were below 0.3%.

Sclerophyll vegetation occurs in both wet and dry habitats (Loveless, 1962). Phosphate deficiency is characteristic of acid soils in areas of high rainfall

TABLE 4

REPRESENTATIVE SPECIES DATA FOR FOLIAGE ORGANIC-MATTER QUALITY

Species	Location	% N	% P	% total acid detergent fiber	% lignin	Sclero-phyll index
Chestnut oak (G)*	Coweeta, N. C.	2.0	0.18	32.8	12.6	168
Chestnut oak (S)		1.2	0.12	48.3	25.5	430
Scarlet oak (G)	Coweeta, N. C.	1.8	0.16	31.0	15.5	177
Scarlet oak (S)		0.9	0.12	34.8	16.7	397
White oak (G)	Coweeta, N. C.	2.0	0.17	26.0	9.1	132
White oak (S)		1.0	0.12	38.2	17.2	390
Mixed hickory (G)	Coweeta, N. C.	2.1	0.18	33.7	9.2	165
Mixed hickory (S)		1.2	0.16	42.9	16.9	351
Red maple (G)	Coweeta, N. C.	1.5	0.16	29.3	9.4	200
Red maple (S)		1.2	0.14	30.0	12.7	260
Yellow poplar (G)	Coweeta, N. C.	2.0	0.20	29.3	7.2	146
Yellow poplar (S)		1.0	0.12	41.1	14.6	443
Dogwood (G)	Coweeta, N. C.	2.0	0.18	22.4	3.5	115
Dogwood (S)		1.4	0.14	21.1	3.9	160
American chestnut (G)	Coweeta, N. C.	1.9	0.18	30.3	7.6	163
American chestnut (S)		1.0	0.10	32.8	8.8	354
White pine (G)	Coweeta, N. C.	1.4	0.17	38.8	16.4	296
White pine (S)		0.9	0.11	54.3	31.0	617
Douglas fir (G)	Corvallis, Ore.	1.0	0.27	28.3	16.5	309
Douglas fir (S)		0.5	0.26	38.6	24.1	815
Ponderosa pine (G)	Flagstaff, Ariz.	0.8	0.14	32.4	16.1	414
Engelmann spruce (G)	Logan, Utah	0.6	0.07	27.4	13.3	510
Red alder (G)	Blue River, Ore.	2.5	0.23	11.9	6.0	49
Red alder (S)		2.1	0.16	19.4	9.5	94
Snowbrush (G)	Blue River, Ore.	2.0	0.13	15.7	6.1	80
Snowbrush (S)		0.81	0.06	21.0	10.0	265

*All samples represent mean values of composite samples taken from at least five different individual trees, except Ponderosa pine and Engelmann spruce. G = mid-growing season, S = senescent.

(Salisbury, 1959); Coweeta watersheds are situated in a region of high rainfall, and considerable weathering of the older Appalachian land surface has occurred (Kovner, 1955). Return of phosphorus in litterfall averages 0.11% concentration on a dry-weight basis, based on total litterfall biomass and total amount of phosphorus given in Table 1. The white pine stand is cycling an equally low level of phosphorus in litterfall (Table 2). The critical level is 0.2% for phosphorus immobilization in decomposing litter (Alexander, 1961). Phosphorus values in decomposing litter at Coweeta are all less than 0.2%, showing that this element would tend to be immobilized by microbial organisms. First-year phosphorus loss of 34% from mixed-hardwood leaf litter was considerably lower than the first-year weight loss of 50% (Cromack, 1973). Further evidence of phosphorus deficiency in Coweeta soils comes from experimental data with these soils in which American sycamore (*Platanus occidentalis* L.) seedlings lacking mycorrhizae show phosphate-deficiency symptoms when grown in greenhouse containers (Best, Marx, and Monk, 1974); presence of mycorrhizal symbionts would permit survival and reproduction of tree vegetation in the infertile soils characteristic of Coweeta. Phosphorus-cycling levels remain low enough to indicate that the vegetation would have the high sclerophyll indexes observed.

High sclerophyll indexes are associated with lower foliage ash contents (Loveless, 1962). One general implication of this work is that ecosystems which are characterized by highly sclerophyllous vegetation (possibly due to phosphorus deficiency) are cycling smaller quantities of total nutrients, as reflected by ash content, than is the case for vegetation with low sclerophyll indexes (Monk, 1966). When comparative sclerophyll data become available from many of the temperate ecosystems for which litter nutrient data exist, then a better judgment can be made concerning the relationship between nutrient cycling in the system and the sclerophyll indexes of their characteristic vegetations. Assessment of the role of mycorrhizal symbionts in permitting survival and reproduction of tree vegetation in soils of low fertility is also needed.

Decomposition and nutrient-loss-rate data were obtained for both hardwood and white pine litter. On the basis of sets of litter bags put out in two consecutive years, first-year decomposition data for single species in both watersheds showed the following exponential weight loss rates: $k = -0.46$ year^{-1} for white pine, $k = -0.61$ year^{-1} for chestnut oak, $k = -0.72$ year^{-1} for white oak, $k = -0.77$ year^{-1} for red maple, and $k = -1.26$ year^{-1} for dogwood. A mixture of hardwood leaves contained in large litter bags had an annual exponential loss rate of $k = -0.70$ year^{-1}, or in terms of percentage weight loss, 50% weight loss occurred during the first year. By contrast, white pine averaged only 37% weight loss during the first year. The slowest decomposing hardwood species was chestnut oak, which averaged 46% weight loss during the first year. Dogwood, the fastest decomposing hardwood species, averaged 68% weight loss during first-year decomposition.

Release of nutrients during first-year decomposition showed that nitrogen, phosphorus, and calcium tended to be immobilized, while magnesium and potassium were lost at greater rates than weight. The mixed-hardwood litter lost only 12% nitrogen during the first year, and there was no significant loss of nitrogen from white pine litter. Mixed-hardwood litter had a carbon-to-nitrogen ratio of 62 : 1, while white pine had a carbon-to-nitrogen ratio of 58 : 1;

carbon-to-nitrogen ratios appreciably greater than 30 : 1 result in increasing immobilization of nitrogen in the microbial populations' decomposing litter (Alexander, 1961).

Mixed hardwood litter lost 34% of phosphorus during the first year of decomposition, in contrast to a 50% weight loss; an indication that partial immobilization of phosphorus occurred. In white pine there was no significant loss of total phosphorus in first-year decomposition, but the weight loss was 37%. As indicated previously, the probable reason for the appreciably lower loss rate of phosphorus compared to weight loss from decomposing litter was the low level of phosphorus (0.12%) in foliage litterfall of both watersheds. The critical level at which phosphorus is immobilized in organic material is 0.2%.

Calcium loss rate was also less than the weight loss of the deciduous litter, e.g., a 29% first-year loss of calcium compared to a 50% weight loss. There was no significant loss of calcium from white pine litter during the same period. Evidence exists that litter- and soil-inhabiting fungi can concentrate substantial amounts of calcium (Stark, 1972; Todd, Cromack, and Stormer, 1973), quantities perhaps sufficient to result in partial immobilization of this nutrient in litter. Macronutrient quantities of calcium as well as other cations, such as potassium and sodium, can be used by fungi to neutralize oxalic acid, which is a low-energy waste product of carbohydrate metabolism in fungi (Foster, 1949). Oxaloacetic acid, a key intermediate in respiratory metabolism, is hydrolyzed to oxalic acid and acetate by oxaloacetate hydrolase in fungi (Burnett, 1968). The common metabolic production of this acid would result in substantial demand of cations, such as calcium, in the production of oxalate salts (Foster, 1949).

Potassium and magnesium loss rates were greater than weight loss rates for both mixed-hardwood litter and white pine litter. Potassium loss during the first year for hardwood litter was 83%, while potassium loss was 82% from white pine litter. Magnesium loss was 77% from mixed hardwood litter and 68% from white pine. It has been shown that ^{137}Cs (an analogue of potassium) loss rates were greater than weight loss rates for three deciduous species (Witkamp and Frank, 1969). In another study the loss rate of ^{134}Cs was also considerably greater than the weight loss rate of white oak (Witkamp and Crossley, 1966). Potassium is known to be significantly concentrated by both the vegetative and sporocarp portions of fungi-inhabiting litter (Stark, 1972; Todd, Cromack, and Stormer, 1973). In contrast to calcium, which tends to form insoluble calcium oxalate crystals in such vegetative structures of fungi as hyphae and rhizomorphs, potassium is readily translocated in fungi where it is accumulated in sporocarps (Stark, 1972). Although potassium oxalate can be formed, it is much more soluble than calcium oxalate and would tend to be lost by leaching when excreted by hyphae. Potassium is more easily leached from litter than any other essential cation (Cromack, 1973). Magnesium was not significantly accumulated by fungi in litter substrates at Coweeta (Todd, Cromack, and Stormer, 1973), indicating a lesser use rate for the element than for potassium. Magnesium also is not as easily leached from litter as potassium (Cromack, 1973), in part because it is less easily displaced from cation exchange sites in litter substrates than is potassium.

Weight-loss regressions were calculated from exponential loss rates of white pine, chestnut oak, white oak, red maple, and dogwood (as previously mentioned) and the chemical properties of the senescent leaves of those trees. Two simple linear regressions were calculated using the exponential weight loss rates of the species as the dependent variables and the carbon-to-nitrogen ratios and sclerophyll indexes of senescent leaves of these species (Table 4) as independent variables. The linear regression of exponential weight loss rate (y) and carbon-to-nitrogen ratio (x) is

$$y = -1.92 + 0.026x \qquad (n = 5, r = 0.86, p = 0.06) \tag{1}$$

The data for the carbon-to-nitrogen ratio in senescent leaves of the five species used in Eq. 1 were: white pine, 58.0 : 1; chestnut oak, 42.2 : 1; white oak, 48.3 : 1; red maple, 39.2 : 1; and dogwood, 31.8 : 1. The linear regression of the exponential weight loss rate (y) and sclerophyll index (x) is

$$y = -1.34 + 0.001x \qquad (n = 5, r = 0.90, p < 0.05) \tag{2}$$

Comparison of the two regressions shows that the sclerophyll index of senescent foliage is a statistically better variable with which to assess leaf decomposition rate than is the senescent leaf carbon-to-nitrogen ratio.

The sclerophyll index incorporates information about organic-matter quality for decomposition in terms of such structural compounds as cellulose and lignin, as well as crude protein nitrogen. The carbon-to-nitrogen ratio itself does not indicate the nature of the carbon substrate. Alexander (1961) presents evidence from the work of others (Fuller and Norman, 1943; Peevy and Norman, 1948; Pinck, Allison, and Sherman, 1950) that litter decomposition rates may be better predicted by knowing lignin content than by knowing the carbon-to-nitrogen ratio. The present data on sclerophyll index, which incorporates lignin and cellulose as total acid detergent fiber, plus a linear regression relating species lignin content to decomposition rate (Cromack, 1973), support his basic hypothesis (Alexander, 1961).

A possible consequence of sclerophylly not considered by Loveless (1961; 1962) was that leaf-litter decomposition rates would be less in those species with high sclerophyll indexes. As discussed previously, he established relationships between high leaf sclerophyll indexes and low leaf levels of phosphorus, nitrogen, and ash. In forest ecosystems characterized by cycling low levels of nitrogen and phosphorus, the sclerophyll index can be considered an index to slower organic matter decomposition rates and release rates of such nutrients as nitrogen and phosphorus.

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Errata:

1. page 617, second paragraph, last sentence. Change ..."three orders of magnitude greater" to "two orders of magnitude greater".

2. page 617, next to last paragraph: Delete Douglas-fir from the last sentence.

3. In table 4, page 618, reduce all phosphorus values by 1/3 for western coniferous, western deciduous and western broadleaf evergreen species. All eastern deciduous and coniferous species values for P are correct.

4. page 620, second paragraph, last sentence: The Alexander, 1961 reference was left out in referring to critical level at which P is immobilized in organic material.