

The Dynamic Belowground Ecosystem¹

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INTRODUCTION

Roots comprise the primary interface between plant and soil for uptake of water and nutrients. Much is known about the biochemistry, cell physiology, and membrane physics associated with these important processes (Devlin, 1966; Larcher, 1975; and Pitman, 1976). In this paper we discuss the role of the belowground ecosystem, especially the autotrophic root component, in the structure and function of forest ecosystems. Beyond recognizing roles of anchoring terrestrial plants and uptake of water and nutrients, this component of the forest has been largely neglected in an ecosystem context. In order to focus our discussion on the properties of the belowground ecosystem, we use the term "rhizosphere" to include roots, mycorrhizae, microbes, and rhizophagus invertebrates. Each component of the rhizosphere merits review and speculation as to its own specific roles. However, we have chosen to develop our discussion on the entire subsystem rather than individual components. Many answers to questions we pose about dynamics of belowground subsystems rely on continuing research into detailed processes at organism and community levels.

Roots comprise a substantial portion of forest ecosystems, generally accounting for 15 to 25 percent of total biomass. The range of values reported for individual stands, however, extends from 9 to 44 percent (Santantonio et al., 1977). The greatest amount of root biomass accumulates in temperate old-growth conifer forests (over

200 t/ha, e.g., Rodin and Provdvin (n.d.) in Rodin and Bazilevich, 1967). Broad-leaved and subtropical forest types are characterized by a maximum of 70 to 100 t/ha dry weight of root organic matter (Bazilevich and Rodin, 1968). Regardless of the type of forest, a consistent structural relationship exists between root and shoot across a wide variety of environments inhabited by trees (Fig. 3, Santantonio et al., 1977). Researchers have used this relationship to develop regression equations to estimate the logarithm of root system biomass from the logarithm of stem diameter at breast height. Consistent structural relations have been applied widely to estimate biomass of tree components from easily measured plant dimensions by using these equations, an approach termed "dimensional analysis" by Whittaker and Woodwell (1968, 1971). The proportion of total biomass represented by roots is lowest for forests and ranges up to 90 percent for tundra and certain grasslands. This is because forests accumulate large amounts of woody material aboveground, whereas tundra and grassland communities invest heavily into their structure belowground. Studies of root biomass have been summarized in reviews by Ovington (1962), by Rodin and Bazilevich (1967), and by Santantonio and others (1977).

The most reliable methods of estimating total root biomass usually consist of a combination of excavation and soil coring techniques. Root systems of a limited number of trees are excavated to develop logarithmic regression equations to estimate large structural roots. Soil cores or soil monoliths are taken to estimate small and fine roots on a unit area basis.

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Such a large amount of organic matter, accumulated at considerable metabolic expense, clearly could serve several purposes, such as storage of plant carbohydrates and essential nutrients. The following discussion briefly reviews recent findings on the behavior of belowground ecosystems and suggests some questions yet to be resolved. In particular, seasonal production/turnover of root biomass, role of root processes in nutrient turnover, root exudation, and the significance of belowground dynamics to the energy balance of the forest ecosystems are considered.

Before proceeding further, let us note why understanding the belowground ecosystem is important. Our concept of forest root dynamics incorporates several reasonable but generally untested assumptions. For example, root production has been assumed to be related to shoot production in the same manner as biomass, i.e.,

$$\frac{\text{root production}}{\text{root biomass}} = (k) \frac{\text{shoot production}}{\text{shoot biomass}}$$

Lacking information, the constant (k) has been assumed to equal 1.0. Assumptions such as these have arisen primarily because of technical problems and excessive labor required for research on forest tree roots (Newbould, 1967; Lieth, 1968). Recent progress in this area of study is related to two factors. First, much work emanates from large integrated studies of forest ecosystems such as those initiated as part of the International Biological Program. These studies supported skilled and dedicated technicians necessary to obtain the requisite data. Second, as more became known about the metabolism of forest ecosystems, the potential role of roots in ecosystem function and their energy demands associated with the accumulation and turnover of carbon and other essential elements surfaced as a central link coupling physiological processes and their environmental constraints with ecosystem behavior. Some interesting findings are counter to what has been commonly assumed. A few examples follow.

SEASONAL ACCUMULATION/TURNOVER OF ROOT ORGANIC MATTER

Root biomass of forests is not static. It changes annually and represents a varying proportion of the total biomass during stand development. By far the most dynamic component of root biomass is the fraction defined as "fine roots." No standard definition exists for fine roots. The distinction between fine and large roots is

usually based on an arbitrarily chosen diameter ranging from 1.0 to 10 mm. These roots are distributed in upper soil layers; generally 90 percent are in the top 30 cm. In peat soils, however, the same proportion is in the top 10 cm (Heikurainen, 1957). It has long been known that a seasonal periodicity of root growth is common in woody plants (see reviews by Lyr and Hoffman, 1967; Kozlowski, 1971; Hermann, 1977; and Santantonio et al., 1977). For example, radial growth of woody roots (with secondary xylem thickening) can closely follow the pattern of radial increment growth aboveground (Fayle, 1968). Studies concerned with seasonal periodicity of root elongation, initiation of laterals, and subsequent growth have not clarified whether periods of inactivity reflect physiological or environmentally mediated dormancy. Sutton (1969) concluded that primary growth of roots is probably dominated by environmental conditions. Control probably lies in the interaction of endogenous and environmental mechanisms, but this remains to be demonstrated satisfactorily.

While there is considerable information on the phenology of root growth, there is an insufficient basis for making estimates of root production and turnover. The earliest studies of root production are probably those of Heikurainen (1957) and Kalela (1957). Both studies involved Scots pine (*Pinus sylvestris* L.) in Finland and both reported a modal pattern of rapid growth to peak root biomass in the spring and a gradual decline during the summer to a low of about 50 percent of the peak level. A biomodal peak in root biomass has been reported for an oak woodland in central Minnesota, USA (Ovington et al., 1963) and a stand of European beech (*Fagus sylvatica* L.) in the Solling area of West Germany (Göttche, 1972). In both instances, biomass peaked in spring with a second but lower peak in the fall. Investigations by Harris and others (1978) in a 45-year-old yellow poplar (*Liriodendron tulipifera* L.) stand in east Tennessee also revealed a spring-fall biomodal peak, while for loblolly pine (*Pinus taeda* L.) in North Carolina the modality was less clear with peaks observed in late fall, late winter, and possibly late spring. The year-to-year consistency observed for yellow poplar (Harris et al., 1978) suggests a strong measure of endogenous control. As with root elongation, the correlations of periods of peak biomass with environmental patterns are inconclusive. Current studies of mature Douglas-fir in western Oregon, however, reveal changing seasonal patterns of standing crop of roots <5 mm diam. from one year (moderately dry) to the next (wet) (Santantonio, 1979).

The surprising result of recent studies on seasonal dynamics of fine roots is the large flux of organic matter which is involved -- large in an absolute sense as well as relative to other organic matter fluxes of forest ecosystem (Harris et al., 1975). Using a coring device, Harris and others (1978) sampled a yellow poplar forest stand intensively over a two-year period. The lateral root biomass of yellow poplar showed considerable variation in the smaller root size classes (Fig. 1). Small roots within this forest were characterized by a peak in late winter (1 March), a minimum in mid-May, a second peak in mid-September, and a minimum in early winter (December to January). This pattern appears to be consistent among successive years. Based on summation of positive seasonal differences between minimum and subsequent peak biomass, net root biomass production was 9.0

t/ha, with a net annual turnover (translocation and sloughing) of equal magnitude. This value of net annual small root production is 2.8 times larger than mean annual aboveground wood production determined for the study area from allometric equations and periodic (1965 to 1970) dbh inventory (Sollins et al., 1973).

Other experimental data on ecosystem carbon metabolism for the same *Liriodendron* forest study area corroborate the existence of a large, annual belowground allocation of carbon. Estimated net photosynthetic influx and soil-litter carbon efflux yield an amount of unaccounted carbon input to soil equivalent to 7.5 tons organic matter per hectare (Harris et al., 1975; Edwards and Harris, 1977). For temperate deciduous forests, the common assumption that belowground primary production is a fraction of aboveground primary production proportional

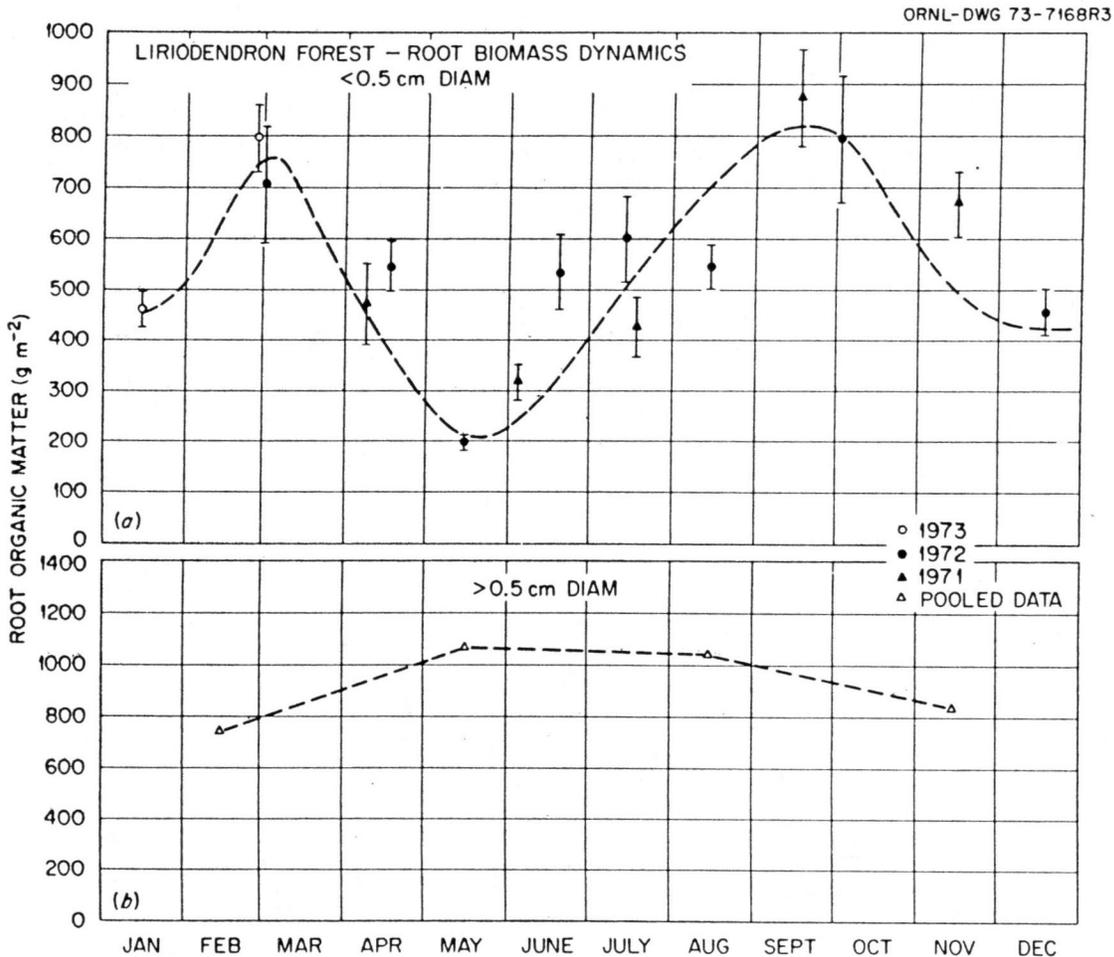


Figure 1. Seasonal distribution of lateral root biomass in a *Liriodendron* forest for (a) roots $< 5\text{ mm}$ diam. and (b) roots $> 5\text{ mm}$ diam. ($\bar{x} \pm 1\text{ SE}$). Net biomass production and turnover were calculated from differences in pool size through the year. Based on monthly summary of core data, no consistent pattern of biomass dynamics could be detected for roots $> 5\text{ mm}$ diam.

to biomass pool size would lead to an underestimate of total annual root production.

The results from yellow poplar are not an extreme example. While the number of studies is limited, a sufficient range of forest ecosystem types is represented to indicate that the large flux of organic matter belowground is a general property of forest ecosystems. In mature (70-170 yrs), natural stands of Douglas-fir in western Oregon, Santantonio (1979) has found that seasonal patterns and ratios of live-to-dead roots (<5 mm diam.) distinctly differ between wet and dry sites (Figs. 2 and 3). Accounting for quantitative changes in live and dead fine roots from one month to the next, root growth, mortality, and decomposition from March 1977 to March 1978 were estimated. Root growth was 8.5, 10.2, and 10.1 t/ha for wet, moderate, and dry sites, respectively; root mortality was 10.9, 12.2, and 13.1 t/ha, respectively; and root decomposition was 12.3, 12.5, and 18.4 t/ha, respectively.

In another study of 40-year-old Douglas-fir stands, Keyes (1979) found a contrasting pattern in biomass of roots <2 mm diameter between "good" and "poor" sites. On the good site, no seasonal pattern was apparent (mean of 2.5 t/ha), while on the poor site there was a modal pattern

with a late-spring peak (8.3 t/ha in June) and a November minimum (2.1 t/ha). Keyes did not separate live and dead roots, but he observed rapid appearance and disappearance of root tips, suggesting rapid turnover even on the good site where no seasonal pattern was observed.

McGinty (1976) found no seasonal pattern of fine root biomass in a mixed hardwood watershed at Coweeta (western North Carolina). McGinty suggested that the absence of a seasonal pattern might reflect niche differentiation belowground, but he did not separate living and dead root components. McGinty indicated there may be a "root capacity" for a mature forest-soil combination -- as the forest matures, net root production equilibrates with root mortality. While McGinty's study did not provide a conclusive estimate of primary production of roots, growth into filled trenches represented a fine root production of 6.0 t/ha/yr. Given the standing pool of roots, <25 mm of 27 t/ha, this suggests a turnover time of 4 to 5 years. His measured decay rates for roots would support a turnover time at least as rapid as proposed.

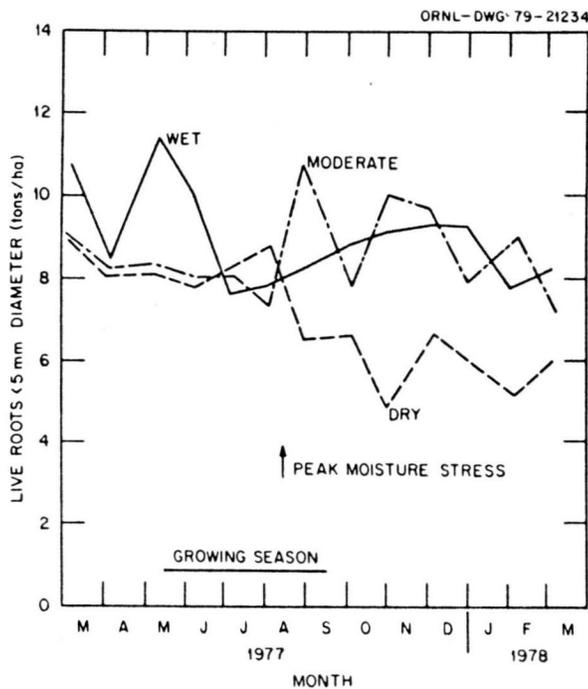


Figure 2. Seasonal fluctuations of live fine roots of Douglas-fir on three sites. Standard errors of estimate are approximately equal to ± 1.0 t/ha.

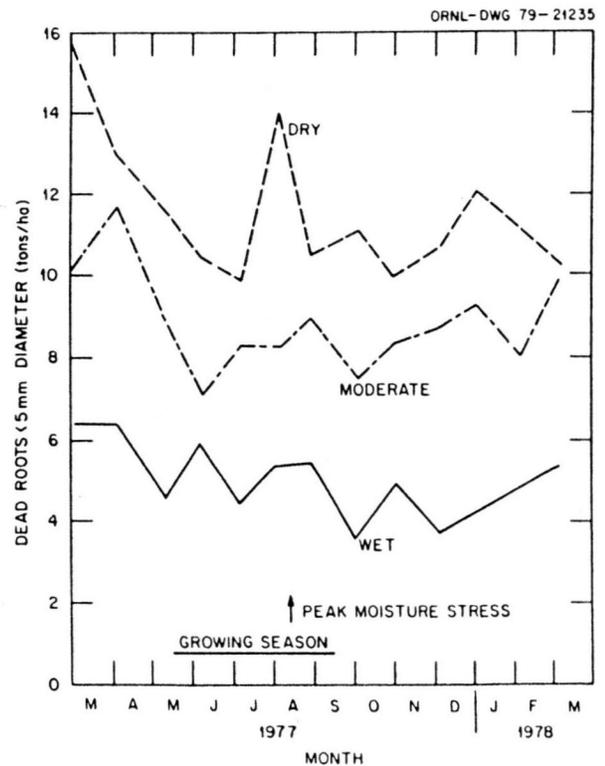


Figure 3. Seasonal fluctuations of dead fine roots of Douglas-fir on three sites. Standard errors of estimate are approximately equal to ± 1.0 t/ha.

McGinty's large size cut-off (25 mm) vastly underestimates the dynamics of fine roots (<5 mm) or absorbing roots (<1 mm). Thus his estimates of production and turnover should be considered conservative.

McClougherty (1980) studied fine root production and turnover in a red pine plantation (54 yrs old) and a natural mixed hardwood stand in southern New England. Root production in the pine plantation was 4.1 t/ha; mortality was 4.3 t/ha. Based on CO₂ evolution attributable to root organic matter decay (an equivalent of 0.7 t/ha) and estimates of herbivore consumption (0.8 t/ha), 2.8 t/ha were transferred to soil organic matter. A similar pattern of fine root dynamics was observed in the natural hardwood stand. Production was 5.3 t/ha; mortality was 4.2 t/ha; CO₂ loss was only 0.9 t/ha; herbivore consumption was 0.3 t/ha; transfer to soil organic matter was 3.0 t/ha. While these results are in contrast with other studies cited here which suggest prompt (~1 yr) turnover of root organic matter, these findings are consistent with the general accumulation of organic matter in northern temperate forest soils.

Another recently completed study in *Abies amabilis* forests in the Pacific Northwest region (Grier et al., ms. in prep.) further strengthens the case for large throughput of organic matter belowground. Net primary production above- and belowground was studied in 23-year-old and 180-year-old stands. Total organic matter (aboveground plus belowground) in the two stands was 77 and 585 t/ha, respectively. Belowground net production was 9.9 and 11.7 t/ha, respectively, with root detritus production amounting to 8.1 and 11.0 t/ha, respectively. Aboveground production was 6.5 t/ha in the 23-year-old stands and 4.6 t/ha in the 180-year-old stands.

Recent studies in coniferous forests have shown that a significant fraction of the small root turnover is comprised of mycorrhizal roots (Fogel and Hunt, 1979; Grier et al., ms. in review). The relative contributions of mycorrhizal and non-mycorrhizal roots to root turnover in deciduous forests is presently unknown.

The large accumulation of root organic matter is a seasonal phenomenon. The net annual accumulation of structural root organic matter (not to be confused with fine root production) is much smaller and can best be described as a ratio of total aboveground and belowground biomass times the net annual aboveground production. What, then, is the fate of seasonal fluxes of organic matter belowground? Most of this material is promptly metabolized by soil heterotrophs (Edwards and Harris, 1977).

Analysis of total and proportional efflux of CO₂ from the soil surface (Edward and Harris, 1977) and experimental measurements of root decay rate (W. F. Harris, unpub. data) corroborate the prompt metabolism of root detritus. Similar findings (Kanazawa et al., 1976; McGinty, 1976; Persson, 1978, 1979; Santantonio, 1979; and Keyes, 1979) all point to prompt disappearance of fine root organic matter. We are thus left with the following generalization: the soil of temperate coniferous and deciduous forest ecosystems annually receives an input of root organic matter equal to or much greater than the input from any other source; this organic matter is promptly metabolized by heterotrophs.

Information on root biomass dynamics of tropical forests is extremely limited. However, one recent study suggests that for certain tropical forest types, production of root organic matter also may be large with turnover equally rapid, similar to the general pattern emerging from analysis of temperate forests. Jordan and Escalante (1979) observed significant root growth activity at the soil surface in "tierra forme" (never flooded) forests growing on oxisols in the Amazon Territory of Venezuela. The surface growth appeared to be in response to litterfall. Roots (<6 mm) grew around fallen litter but were subsequently sloughed as the "captured" litter decayed. This growth amounted to 117 g/m²/yr, a flux equivalent to 12 percent of aboveground detritus inputs. Such a response may represent a highly developed adaptation to the lower available nutrients in highly weathered tropical soils.

Before leaving the subject of root organic matter dynamics, we should mention the dynamics of larger structural roots (≥ 5 mm diameter). Generally, this organic matter component is much more stable, certainly not exhibiting significant seasonal or even annual dynamics. However, it would be incorrect to consider this a static pool. Again, evidence is sparse, but Kolesnikov (1968) observed that a cyclic renewal of large structural roots occurs during the development of a forest stand. One cannot pass up the speculation that a physiological balance might exist within individual forest trees, causing this main structural component to shift so that the fine root structure continually invades "new" areas of its soil habitat. Whether this speculation will withstand closer observation, and what the controlling factors and mechanisms might be, remain to be answered.

ROOT ORGANIC ACCUMULATION DURING STAND DEVELOPMENT

During forest stand development, the amount of root organic matter increases on an absolute basis, but the proportion of the total biomass as root organic matter decreases. Patterns of root/shoot ratio between deciduous and coniferous forests vary (Rodin and Bazelivich, 1967). Generally, coniferous forests reach an equilibrium root/shoot ratio earlier in stand development (i.e., at a lower total biomass) than is the case for deciduous forests.

THE SIGNIFICANCE OF ROOT DYNAMICS TO ELEMENT INPUTS TO SOIL AND ELEMENT CYCLING

Much more limited than our knowledge of root organic matter dynamics is our knowledge of the role of root production/turnover (sloughing) to element cycling. Of course, some assumptions about root element content can be used to estimate the flux of elements to the soil. McGinty's (1976) work begins to place the contribution of roots in perspective. In oak-hickory and eastern white pine forests of Coweeta, North Carolina, roots comprised 28 percent of the forest biomass but contained 40 percent of plant nutrients in hardwoods and 65 percent of plant nutrients in pines. Thus, this dynamic root component is a nutrient-rich substrate. Roots can return nutrients to the soil in several ways: death and decay, exudation and leaching, and, indirectly, when consumed by grazers.

Studies of leaching and exudation from roots are likewise limited. In a northern hardwood forest ecosystem, Smith (1970) has found root exudation (during growing season) to account for 4 kg/ha of carbon, 8 Kg K/ha, and 34.2 kg Na/ha for three principal tree species (*Betula alleghaniensis*, *Fagus grandifolia*, and *Acer saccharum*). Although the techniques employed (modified axenic culture) risk introducing artifacts, a considerable potential for contribution of elements to the soil via exudation exists.

Direct exudation of mineral nutrients to the soil may be of minor significance, however, in comparison to the role of low molecular weight organic acids contained in root oxidation. This small loss of reduced carbon may have a major effect on pH regulation in the rhizosphere and nitrogen metabolism of the plant (Sollins et al., 1979), and the oxalate as a product of fungal metabolism as well as higher plants could have a significant effect on weathering of soil minerals, especially the availability of phosphorus to plants (Graustein et al.,

1977; Cromack et al., 1979). Results thus far implicate a complex control system in which forest trees exert a strong influence over their chemical environment suggestive of a high degree of co-adaptation.

Radiotracer studies with ^{134}Cs have shown that over 50 percent of ^{134}Cs in roots of tagged yellow poplar seedlings was transferred to culture solutions in less than 7 days (Cox, 1972). Sandberg and others (1969) estimated that during one growing season 75 percent of ^{137}Cs transferred by yellow poplar seedlings grown in sand was due to exudation-leaching. In their analysis of a cesium-tagged yellow poplar forest, Waller and Olson (1967) considered root exudation leaching processes as important pathways of cesium transfer to soil based on concentration of ^{137}Cs in soil at various depths. If *in situ* processes of Cs are comparable to those of the chemical analog, potassium, large quantities of K could be transferred to soil annually by leaching-exudation processes.

Very few data are available to compare return of elements to the soil via aboveground and belowground processes. Table 1 summarizes a comparison for an extensively studied yellow poplar forest at Oak Ridge, Tennessee (Cox et al., 1978). In this analysis, consumption was assumed to be 10 percent of root detritus. Root detritus turnover was estimated by the large residual CO_2 efflux from soil unaccounted for after litter decomposition and autotrophic root respiration were subtracted from total soil CO_2 efflux.

In this example (Table 1), annual return of elements to soil by root processes was three times the combined aboveground inputs (including atmospheric) for K and at least 1.5 times aboveground inputs for N. Of the total (aboveground and belowground) return to soil, root processes accounted for turnover of 70 percent of organic matter, 62 percent of N, and 86 percent of K. Some additional fraction (here assumed to be about 10 percent of the total estimated detrital flux) was transferred to soil consumer pools.

Estimates of total herbivory on roots do not exist. Root-feeding nematodes and various larval stages (e.g., cicada) might be principal consumers (Ausmus et al., 1978). Assuming consumption as 10 percent of the estimated turnover may be high for temperate forests. Schauer mann (1977) reported that rhizophagous Curculionidae consumed 81×10^3 kcal/ha/yr and comprised 12 percent of the biomass of soil invertebrates. Assuming comparable consumption rates per unit weight among all soil invertebrates, total consumption might approach 800×10^3 kcal/ha/yr. In Schauer mann's beech forest

study, Curculionidae consumption was 0.1 percent of net primary production (presumed to be aboveground only). Edwards (in Auerbach, 1974, p. 86) estimated the total energy consumed by invertebrates to be 2 percent of total amount fixed annually. Thus, evidence to date points to a small absolute flux of energy by consumption of root (or aboveground) biomass. Despite the small absolute role of consumers, we cannot dismiss their importance to the functioning of forest ecosystems. Schauermann regarded the Curculionidae as accelerators of the mineralization processes because of physical damage to roots and effects of their feces on microbial decomposition. He found that 87 percent of energy turnover in the rhizophagous larval population occurred between August and April -- a period generally coincident with high root turnover. Waldbauer (1968) reported a similar pattern for many insect populations.

SIGNIFICANCE OF ROOT SLOUGHING TO FOREST ENERGY BALANCE

Odum (1969) suggested a strategy of increasing conservation of nutrients in element cycling during forest ecosystem development. The mechanism leading to a closed cycle for nitrogen could be root sloughing and subsequent microbial mineralization. In temperate, deciduous forests at Oak Ridge, Tennessee, biomass and nitrogen accumulate in roots during periods favorable for growth (summer) or just preceding growth (late winter); and winter growth occurs largely at the expense of stored photosynthate. During periods unfavorable for growth (fall-winter) or when aboveground energy demands are high (spring-early summer canopy development), root biomass is sloughed, thus reducing the total energy demand on the temperate forest system at a time when reserves are seasonally depleted and/or plant requirements for carbon are high elsewhere (e.g., canopy development).

Table 1. Annual aboveground and belowground organic matter and element returns to soil in a yellow poplar (*Liriodendron tulipifera* L.) stand¹

	Biomass	Nitrogen	Potassium
	kg/ha	kg/ha	kg/ha
<u>Aboveground</u> ²			
Dryfall/wetfall	...	7.2	3.6
Canopy leaching	...	2.3	29.4
Litterfall	3,310	42.2	10.0
Total aboveground return	3,310	51.7	43.0
<u>Belowground</u> ³			
Root transfer processes ⁴			
Death and decay	6,750	76	128
Consumption	750	9	14
Exudation-leaching	128
Total belowground return	7,500	85.0	270
Total return to soil	10,810	136.7	313

¹From Cox et al., 1978.

²Aboveground data from Edwards and Shanks (unpub. data); chemical determinations were made on fallen material.

³Root biomass estimates from a *Liriodendron* stand (>80% *Liriodendron*).

⁴Exudation-leaching data are extrapolated from seedling studies of Cox (1975), assuming equivalent behavior of Cs and K. Element losses via root sloughing are based on amount of sloughed biomass times mean root N content; element flux via consumption assumed to be 10 percent of total belowground return.

Nitrogen contained in sloughed organic matter is conserved as part of the soil detritus by those microbial processes which immobilize it.

The cyclic pattern of photosynthate accumulation in a deciduous forest and the sustained productivity, which is in part dependent on available N, are closely coupled through activities of soil microbes on a large systematically replenished substrate rich in nitrogen. In this respect, continuous maintenance of living roots in temperate forests would impose energy limitations on detritivores by reducing periodic influx of nitrogen-rich root organic matter, because this flux represents 70 percent of total detrital input. While data from other deciduous systems are scarce, we hypothesize that evolution of temperate forest species has favored mechanisms which contribute to systematic return of elements and organic matter through belowground sloughing. Sloughing, therefore, stabilizes biogeochemical cycles of potentially limiting elements in an environment typified by seasonally limited photosynthate availability. As illustrated in Table 2, carbon (energy) is rapidly metabolized within the ecosystem and lost (as CO_2). Essential elements, on the other hand,² are retained effectively

because of the interactions of autotrophs and decomposers.

The energy expenditure to forest ecosystems represented by root sloughing is high. In the yellow poplar forest at Oak Ridge (Harris et al., 1975; Edwards and Harris, 1976), Edwards (in Auerbach, 1974) estimated that lateral root growth, sloughing, and maintenance respiration accounts for 44.8 percent of the total energy fixed annually in photosynthesis (1.88×10^3 kcal/m²). Root sloughing, with subsequent microbial immobilization, offers a particularly attractive mechanism to explain retention of essential elements in the uptake zone. In another context, maintenance and development of a fertile soil requires significant input of energy (contained in organic matter). For the yellow poplar forest, energy requirements for maintenance of soil are on the order of 66 percent of the energy fixed annually by photosynthesis (roots + 21% allocation to leaves). Many of man's activities which reduce both energy fixed photosynthetically and/or energy input to soil are most severely manifested by degradation of the soil with respect to humified soil organic matter and fertility. The energy inputs to soil (dominated in temperate forests by root

Table 2. Comparison of turnover times for carbon, nitrogen and calcium in temperate deciduous forests (Tennessee)¹

Component	Turnover time (yrs) ²		
	Carbon	Nitrogen	Calcium
Soil	107	109	32 ³
Forest biomass ⁴	155	88	8
Litter (O1 + O2)	1.12	<5	<5
Total ⁵	54	1,815	445
Decomposers	0.01	0.02	?

¹From O'Neill et al., 1975.

²Carbon data based on carbon metabolism of yellow poplar forest (Harris et al., 1975; Reichle et al., 1973); nitrogen data based on nitrogen budget for mixed deciduous forest (Henderson and Harris, 1975); calcium data based on calcium budget from a *Liriodendron tulipifera* forest (Shugart et al., 1976).

³Turnover time based on available Ca and assumes all losses of Ca from soil are from the pool of available Ca.

⁴Considers aboveground biomass pool. Cyclic renewal of structural roots (Kolesnikov, 1968) would lower turnover time. Tree mortality estimated from permanent plot resurvey (3-year interval) and likely underestimates the mortality rate over the duration of a forest generation.

⁵Total calculated as sum of elements in living and dead components of the ecosystem; element loss based on sum of all losses from ecosystem.

sloughing) contribute to maintenance of soil fertility.

A number of areas require additional study. First, the pattern of belowground detritus contributions needs to be determined for additional forest types, especially forests of extreme climates. The large photosynthate requirements for maintenance respiration of forests combined with a large annual sloughing of root organic matter may limit forest growth in climates severely limiting photosynthate production. In this same vein, the influence of stresses (whether natural or of anthropogenic origin such as air pollutants) on photosynthate translocation needs to be examined in mature forests in order to evaluate forest response to perturbations. The decay of root organic matter occurs rapidly. Are there biochemical changes in sloughed roots that promote decomposability or alter the behavior of fungal symbionts generally associated with the rhizosphere? Answering these and other questions about the dynamic belowground component of forest ecosystems will provide an exciting challenge to forest ecology for the next several years.

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