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MYCORRHIZAE AND NUTRIENT CYCLING IN NATURAL FOREST ECOSYSTEMS

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SUMMARY

The widespread occurrence of mycorrhizae in nature and their importance in the mineral nutrition of almost all plants has been extensively documented but despite this mycorrhizae have not been included in nutrient cycling studies of forest ecosystems. This neglect may be due to a failure on the part of researchers to recognize the functional differences between mycorrhizae and roots and to the labour-intensive effort needed to study mycorrhizae.

Biomass or surface area of mycorrhizae must be measured before information on ion absorption by mycorrhizae can be applied to forest ecosystems. A full assessment of the importance of mycorrhizae in nutrient cycling also requires data on mycorrhiza production, senescence, and decomposition. Few mycorrhiza studies have provided such data. Consequently, our information on nutrient cycling is derived from fine root (⩽ 5 mm in diameter) data which may or may not include mycorrhizae.

Recent studies have shown that most of the organic input to the decomposition process results from fine root production. Fine root mortality and decomposition is also more important than other mechanisms for returning nitrogen immobilized in vegetation to the soil in both deciduous and coniferous forests. A recently completed study indicates that mycorrhizae account for 50% of the annual throughput of biomass and for 43% of the nitrogen released annually in a Douglas fir ecosystem. These transfers are five times larger than the releases from litterfall or litter decomposition. Clearly, the study of mycorrhizal nutrient cycling is in an embryonic state and considerable additional research is needed.

INTRODUCTION

The widespread occurrence of mycorrhizae in nature and their importance in mineral nutrition of almost all plants has been documented in hundreds of experimental and review papers, as well as numerous books (e.g. Harley, 1969; Hacskaylo, 1971; Marks and Kozlowski, 1973; Sanders, Mosse and Tinker, 1975). Despite this, very little understanding of the contribution of mycorrhizae to nutrient cycling has emerged from the increasing research on the function and productivity of forest ecosystems. This neglect may be due to a failure on the part of researchers to recognize the functional differences between mycorrhizae and roots and to the labour-intensive effort needed to study mycorrhizae. Consequently, most of the information on nutrient cycling in the belowground ecosystem is derived from studies of fine roots (⩽5 mm in diam). Mycorrhizae may or may not be included in these studies (e.g. Ovington and Madgwick, 1959; Duvigneaud and Denaeyer-De Smet, 1970; McQueen, 1973; Edwards and Harris, 1977; Karizumi, 1977; Kimmins and Hawkes, 1978).

The purposes of this review are to examine the impact of mycorrhizae on nutrient cycling in forests and examine the problems inherent in the methods employed in their

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study. The references cited are not intended to be exhaustive, but rather serve as entry points into the larger body of literature.

Broadly defined, mycorrhizae are the result of a mutualistic, symbiotic biotrophy between a fungus (mycobiont) and the absorbing organ of a vascular or non-vascular plant or host (Cooke, 1977). Obscured by this definition is great diversity in nutritional interrelationships, enormous numbers and taxonomic diversity in the fungi and plants involved, and large differences in the morphological and anatomical details of different mycorrhizae.

The following groups of mycorrhizae are commonly recognized on the basis of anatomical and morphological features: ectomycorrhizae, vesicular–arbuscular mycorrhizae, ericaceous, orchidaceous, and ectendomycorrhizae. These groups will not be discussed further since numerous reviews (Harley, 1969; Cooke, 1977; Trappe and Fogel, 1977) have described the associated fungi and plants, plus their occurrence.

MYCOBIONT STRUCTURE

The mycorrhizal association is more extensive than the composite organ resulting from the association between mycobiont and host. In addition to the hyphae intimately associated with the absorbing organ of the host, mycobiont hyphae extend out into the soil either individually or as fascicled strands and rhizomorphs beyond the absorbing zone of the root itself (Bowen, 1973). A *Cenococcum geophilum* Fr. hypha has been traced more than 2 m from a mycorrhiza, with more than 120 lateral branches or fusions formed with other hyphae (Trappe and Fogel, 1977). From 200 to over 2000 individual hyphae were counted emerging from single *Cenoccum* mycorrhizae formed with different host species. The hyphae associated with vesicular–arbuscular (VA) mycorrhizae can extend the phosphate-uptake zone of onions to at least 7 cm from the root surface (Rhodes and Gerdemann, 1975), considerably beyond the 1 to 2 mm zone normally assumed to be the region of phosphate utilization. Sclerotia and reproductive structures are also produced by the mycobiont under certain conditions. Hence a decision to study mycorrhizae only may seriously underestimate the importance of mycorrhizal fungi in nutrient cycling. The different sampling methods required for mycorrhizae, hyphae, and sporocarps, however, vastly increase the effort needed to measure mycobiont biomass and activity.

ROLE OF MYCORRHIZAE IN NUTRIENT CYCLING

The enhancement of ion uptake and translocation by mycorrhizal fungi, particularly phosphorus, is well known (Harley, 1969; Bowen, 1973) and a complete discussion is beyond the scope of this paper. The transfer of ^{14}C as well as cations from one mycorrhizal host through a shared mycobiont to an achlorophyllous epiparasite has been demonstrated (Furman and Trappe, 1971) as has the transfer of ^{14}C from one green plant to another via mycobiont hyphae (Reid and Woods, 1969). Mycobionts can also affect other nutrient cycling processes. Mycorrhizal fungi may conserve nutrients against leaching by immobilizing elements in tissue (Trappe and Fogel, 1977). Mycorrhizal growth can also suppress pine litter decomposition (Gadgil and Gadgil, 1971, 1975). Direct nutrient recycling through mycobionts capable of decomposing leaf and other litter materials has also been postulated (Went and Stark, 1968). Environmental and ecological factors controlling ion uptake rates have received scant

attention, severely limiting the application of available information to nutrient cycling studies in natural ecosystems (Nye and Tinker, 1977).

In addition to ion uptake rates, data is needed but unavailable on nutrient content and transfers in the production, senescence, and decomposition of mycorrhizae. Recent reviews of the shedding of plant parts (Kozlowski, 1973) and litter decomposition (Dickinson and Pugh, 1974) only briefly mention mycorrhizae; no measurements of mycorrhiza production or decomposition are cited. Similarly, recent treatments of nutrient cycling in temperate forest ecosystems also fail to include mycorrhizae (Reichle, 1970; Henderson and Harris, 1975; Likens *et al.*, 1977; Whittaker *et al.*, 1979). An understanding of the role of mycorrhizae in these processes is important in understanding withdrawal (immobilization) and release (mineralization) of plant nutrients. The problems inherent in measuring the contribution of mycorrhizae to these processes will be considered in the following sections.

Measurement of mycorrhiza contribution to carbon cycling

Recent studies have shown that the majority of organic input to the decomposition process results from root production (Coleman, 1975; Cox *et al.*, 1977; Fogel and Hunt, 1979). Mortality of fine roots has also been shown to be more important than other mechanisms for returning nitrogen immobilized in vegetation to soil in both deciduous and coniferous forests (Henderson and Harris, 1975; Wells and Jorgensen, 1975). The harvest method, removal of mycorrhizae from soil followed by drying and weighing, is the most direct method for determining the importance of mycorrhizae in these processes. In practice, the harvest method has failed to determine the importance of mycorrhizae due to the arbitrary separation of fine and large roots on the basis of diameter, the upper size limit of fine roots usually ranging from 2 to 10 mm, rather than function. In addition, the methods often used for separating fine roots from soil result in the loss of mycorrhizae in the soil fraction. Roots below 1 to 2 mm in diameter require microscopic examination for identification and hand separation from soil. Many mycorrhizae, ranging in size from 0·5 to 3·0 mm long and 0·15 to 0·6 mm in diameter, were potentially lost, for instance, when McQueen (1968) used a 2-mm screen to separate *Pinus sylvestris* L. (Scots pine) roots from soil. Other researchers have deliberately discarded mycorrhizae before weighing the fine roots (Moir and Bachelard, 1969; Safford and Bell, 1972).

Converting mycorrhiza or root tip numbers to biomass requires an estimate of fragment or root tip weight. Unfortunately, such estimates are rare and consequently many published estimates of mycorrhiza numbers cannot be converted to biomass. Mycorrhizae produced by different hosts and different mycobionts on the same host may vary in weight depending on size, extent of branching, and thickness of associated mantle. Radiata pine (*Pinus radiata* D. Don) mycorrhizae have been reported to weigh $4{\cdot}3 \times 10^{-5}$ g dry wt per fragment (Marks, Ditchburne and Foster, 1968) and Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] mycorrhizae $19{\cdot}7 \times 10^{-5}$ g dry wt per fragment (Fogel and Hunt, 1979).

The difficulties associated with excavating and processing mycorrhizae favour the development of indirect methods for estimating their biomass. Unfortunately, no correlation has been found between quantities of fine and coarse roots or between root weight and diameter (McQueen, 1968). Even if equations were developed, experience with coarse roots indicates that the applicability of such equations is

probably limited to similar sites and conditions. Total coarse root biomass per given area tends to vary more than the root biomass of an individual tree, depending on stand age, density, and soil moisture (Karizumi, 1977).

The labour intensive effort needed to separate mycorrhizae from soil necessitates some knowledge of mycorrhiza distribution in designing an efficient sampling scheme. Spatial variation of fine roots (0·4 to 3 mm in diameter) within *Pinus radiata* stands has been shown to be independent of the proximity of pine stems (Moir and Bachelard, 1969). Similarly, Santantonio (1974) found little or no correlation between weight of 0·3 to 10 mm broad roots and distance of the sample point from the centre of a sample tree in a 450 year old *Pseudotsuga menziesii* stand.

Table 1. *Vertical distribution of carbon, hyphae, mycorrhizae, and sclerotia with soil depth at Dinner Creek, Oregon in September 1977 (Fogel and Hunt, 1979)*

Depth (cm)	% Total			
	Carbon	Hyphae	Mycorrhizae	Sclerotia
10	42	36	53	42
30	22	32	32	42
50	10	20	14	11
70	21	9	1	6
90	6	4	0	0

Numerous studies have shown that numbers of mycorrhizae, root tips, and absorbing roots decrease with increasing soil depth at rates dependent on soil aeration and fertility (Marks *et al.*, 1968; McQueen, 1968, 1973; Meyer and Göttsche, 1971; Hermann, 1977; Fogel and Hunt, 1979). In a 120 year old beech (*Fagus sylvatica* L.) forest, 75·5 % of the root tips were found in the F and H layers of the forest floor (Meyer and Göttsche, 1971). McQueen (1968) reported that 63·4, 84·0 and 57·1 % of the absorbing roots (mycorrhizae and unsuberized non-mycorrhizal roots) were present in the top 12 to 16 cm of 10 to 105 year old Scots pine and mixed pine–beech stands. No mycorrhizae were found in the forest floor of a 50 year old Douglas fir stand subject to prolonged summer drought (Table 1); 53·4 % of the mycorrhizae occurred in the top 20 cm of the mineral soil (Fogel and Hunt, 1979). Ectomycorrhizae have been found at depths of 1 to 3 m; VA mycorrhizae at 1·4 to 2·2 m (Trappe and Fogel, 1977).

Distribution of mycorrhizae may be correlated with that of organic matter. Harvey, Larsen and Jurgensen (1976) report that 95 % of active mycorrhizae are associated with organic material in a 250 year old Douglas fir–larch stand. Five percent of all active mycorrhizae occur in the top 38 cm of mineral soil, 66 % in the humus, 21 % in decayed wood, and 8 % in charcoal.

The few published estimates of mycorrhiza biomass (Table 2) are difficult to compare due to differences in separation methods, phenological status of the stand at sampling, stand types, depth of soil sampled and whether active or total mycorrhiza weights are reported. The total standing crop of Douglas fir ectomycorrhizae in the top 15 cm of soil (Fogel and Hunt, 1979), for instance, is three to eight times greater than that reported for radiata pine (Marks *et al.*, 1968). The difference in these standing crop estimates may be due to the smaller size of pine mycorrhizae or to the greater stem density of the Douglas fir stand.

Once mycorrhizae have been separated from the soil, determination of the mycobiont portion of mycorrhiza biomass is extremely difficult. The initimate physical association concomitant with Hartig net formation in ectomycorrhizae precludes separation of mycobiont and host tissue. After sonication in a pectinase solution, cortical cells are still trapped in the Hartig net; it is possible to separate the stele by this method, however (Fogel, unpublished). Harley (1971) estimated by dissection that the mycobiont comprises about 40 % of the total dry wt of beech ectomycorrhizae. Dissection underestimates mycobiont weight since the contribution by the Hartig net hyphae cannot be determined. Another, albeit tedious, approach is measuring the cross sectional area of host and mycobiont and multiplying by the specific gravity of each component. Still another possible method is to assay for 'fungal chitin' and then convert to mycobiont biomass (Ride and Drysdale, 1972; Swift, 1973; Hepper, 1977). This latter approach has recently been shown to be of limited value in estimating biomass of aquatic Hyphomycetes due to the dependence of the conversion factor on the age of the mycelium and lowered oxygen concentration (Sharma, Fisher and Webster, 1977). Lack of a hyphal mantle and the intracellular penetration of host cells by the mycobiont in VA mycorrhizae compound these problems.

Table 2. *Standing crop of mycorrhizae in different forests*

Species and location	Stand age (years)	Sample depth (cm)	Stems ha^{-1}	Standing Crop ($kg\ ha^{-1}$)	Separation method	Source
Pseudotsuga menziesii						
Oregon, USA	50	15	1626	4421 to 11333	0·5 mm screen	Fogel & Hunt, 1979
	50	100	1626	9762 to 25032	0·5 mm screen	Fogel & Hunt, 1979
Pinus radiata						
Australia	42	15	296	1433	0·5 mm screen	Marks *et al.*, 1968
Fagus sylvatica						
?	120	87	—	2522*	handsort ?	Meyer & Göttsche, 1971
Pinus sylvestris						
France	10	32·5	26875	989†	2 mm screen	McQueen, 1968
P. sylvestris–Fagus sylvatica France	65	26	2200	1380†	2 mm screen	McQueen, 1968
	105	32	1400	2720†	2 mm screen	McQueen, 1968
Pinus sylvestris						
Sweden	20	30	1100	50–380‡	2 mm screen	Persson, 1978

* Live roots only ?
† Mycorrhizae plus unsuberized roots
‡ Roots less than 1 mm in diameter.

Identification and quantification of mycobiont hyphae in soil and sporocarps are also severely hampered by available techniques. The hyphae of some mycobionts, i.e. *Cenococcum geophilum*, are very distinctive and easily differentiated from hyphae of other species in quantitative measurements using the Jones–Mollison soil agar thin-film or membrane filter techniques (Hansen, Thingstad and Goksoyr, 1974; Nagel-de Boois and Jansen, 1971). The hyphae of most mycobionts are not distinctive, however, and one may have to resort to immunofluorescent identification of selected species Schmidt *et al.*, 1974; Malajczuk, McComb and Parker, 1975).

Techniques for quantifying sporocarp production are presented in Richardson (1970) and Fogel (1976, in press). Many presumed mycobionts have been identified (Trappe, 1962, 1971), although proving that a fungus is mycorrhizal may require

isolation of the fungus from mycorrhizae or sporocarps and resynthesis of mycorrhizae under aseptic conditions (Hacskaylo, 1953).

MEASUREMENT OF MYCORRHIZA PRODUCTION

One measure of the rate of mychorrhiza production is the change in biomass over a given period, but its accurate measurement presents even greater problems than measuring biomass. The longer the period between two sampling events, the greater the chance of missing rapid oscillations in biomass. Other errors result from biomass losses due to respiration, mycophagy, translocation of materials, exudation, and mortality. All of these losses have not been measured simultaneously under field conditions, nevertheless, the harvest method has been used to measure biomass change or production and turnover of fine roots and ectomycorrhizae.

Production of fine *Liriodendron tulipifera* L. and *Pinus taeda* L. roots ($\leqslant$ 5 mm diameter) has been calculated by summing the differences between seasonal maximum and minimum root biomass measurements. Differences between maximum and minimum root biomass within a season were used to estimate root weight loss due to root sloughing and translocation since no acceptable method of separating live from dead roots was felt to exist. Net fine root biomass production of an 80 year-old *Liriodendron* stand was 9000 kg ha^{-1}, net annual turnover was of equal magnitude (Harris, Kinerson and Edwards, 1977). Net root production of a 14 year-old *Pinus taeda* stand was 8600 kg ha^{-1} with an equivalent net annual turnover. Longevity of fine roots in both stands appeared to be no longer than one year. Decomposition of root organic matter in the *Liriodendron* stand accounted for 42 % of the total soil carbon efflux and was 2 to 2·8 times greater than the efflux resulting from litter decay (Edwards and Harris, 1977).

Persson (1978) used a similar approach in measuring the seasonal changes in fine root ($\leqslant$ 1 mm in diam.) biomass in a 15 to 20 year-old *Pinus sylvestris* stand. Production was equal to the summation of increments (positive differences) in biomass plus necromass. The resulting annual production of fine roots (biomass plus necromass) was 1830 kg ha^{-1}, at least twice that of annual litter fall. Inclusion of shrub fine roots in the production estimate boosted root production to four times that of litter fall. The cumulative annual total for *P. sylvestris* necromass was 1210 kg ha^{-1}, a throughput or 'die-back' of 66 %. Similar values of 80 to 92 % have been reported for European beech (Göttsche, 1972), 40 % for *Pseudotsuga menziesii* (Santantonio, in press), 42 % for *Liriodendron* (Edwards and Harris, 1977), 90 % for *Juglans* (Bode 1959), and 48 % for *Quercus* woodland (Ovington, Heitkamp and Lawrence 1963).

Santantonio (in press) has estimated growth, mortality, and decomposition of fine Douglas fir roots ($\leqslant$ 5 mm in diameter) by balancing transfers between live root, dead root, and soil organic matter pools to allow for the observed amounts of live and dead fine roots collected at each sampling period. He showed that simply summing biomass increments or decrements over time results in underestimates of 30 to 60 % in root growth, 50 to 70 % in mortality, and 50 to 65 % in decomposition.

The standing crop and turnover of mycorrhizae, fungal hyphae, sclerotia, and sporocarps in a 50 year old Douglas fir stand has recently been reported by Fogel and Hunt (1979). Standard harvest techniques were used to collect samples at monthly intervals. Biomass change or throughput was calculated by summing the significant differences in annual or seasonal maximum and minimum standing crops for a component. Turnover time was calculated by dividing the maximum monthly standing

crop by the total annual throughput for each component. Mycorrhizae (Table 3) accounted for 50 % of annual biomass throughput. Mycorrhiza throughput was five times greater than the litter fall or litter decomposition throughputs. Mycorrhiza die-back was 58 % of the maximum monthly standing crop, well within the range reported for fine roots.

Table 3. *Biomass and throughput of ecosystem components in a young Douglas fir ecosystem at Dinner Creek, Oregon from 1976–1977 (Fogel and Hunt, 1979)*

	Standing crop, kg ha^{-1}	Percentage total s.c.	Throughput, kg ha^{-1}	Percentage total throughput
Total aerial	258128	58	2817	9
Roots	49289	11	ND*	—
Mycorrhizae	25023	6	14611	50
Forest floor	19034	4	3032	10
Total fungi	9885	2	9214	30
Soil organic matter	87600	20	ND	—
Total stand	448959	101	29674	99

* ND, no data.

Mycorrhizae die-back results from senescence accompanied by decomposition of all or portions of mycorrhizae. Senescence has been attributed to stresses imposed on tree root systems by drought, periodic high water tables, extreme soil temperatures defoliation, rhizophagy, parasitism, over-fertilization, and in some instances by internal hormonal control (Redmond, 1955; Lyr and Hoffman, 1967; Head, 1973; Reynolds, 1974). Apparently the change in dry wt of excised mycorrhizae during their decomposition in the field has not been studied, but direct observation of apple roots 1 to 1·5 mm in diameter indicates that roots disintegrate a short time after senescence (Head, 1973). Annual throughput values of 40 to 90 % for fine roots and mycorrhizae of a variety of trees in different climatic regions suggest that fine roots and mycorrhizae only persist for 1 to 3 years. Ectomycorrhizae, however, have been reported to persist from several months to as long as 8 years (Trappe and Fogel, 1977). Mean longevities of 4 years for pine ectomycorrhizae and 6 to 7 years for fine roots have been reported by Orlov (1968). Similar longevities of 3 to 10 years for roots under 1 to 5 mm in diameter have been reported for Scots pine (Lyr and Hoffman, 1967). The discrepancy in the estimates of ectomycorrhiza longevity might be explained by the shedding of the lateral branches and the persistence of the central axis for several years. The large annual throughput of mycorrhizae in forests clearly indicates that mycorrhizae are more important in carbon cycling than commonly believed and deserve more study.

Contribution of mycorrhizae to nutrient cycling

The harvest method can be extended to estimate the importance of mycorrhizae in cycling nutrients other than carbon by measuring nutrient concentrations in ecosystem components (mycorrhizae, foliage, etc.) and transfer rates between components (litterfall, decomposition, etc.). A major assumption of this approach is that the nutrient content of components is the same as that of throughput and that withdrawal

Table 4. *Published values for the concentration of elements in fine roots and mycorrhizae of trees (modified from Kimmins and Hawkes, 1978)*

Species and location	Age, years	Diameter, mm	Percentage concentration N	P	K	Ca	Mg	Reference
Picea abies								
South Sweden	55	<5	0·33	0·03	0·10	0·13	0·03	Nihlgård, 1972
Picea glauca (Moench) Voss and *Abies lasiocarpa* (Hook.) Nutt.								
British Columbia, Canada	230	<6·4	2·03	0·24	0·38	0·53	0·11	Kimmins & Hawkes, 1978
Picea abies								
northern taiga, Russia	200	1–5	1·29	0·08	0·22	0·31	0·12	Marchenko & Karlov, 1962
northern taiga, Russia	200	<1	1·22	0·14	0·26	0·44	0·17	Marchenko & Karlov, 1962
forest tundra, Russia	200	1–5	1·50	0·06	0·17	0·24	0·09	Marchenko & Karlov, 1962
forest tundra, Russia	200	<1	1·72	0·09	0·10	0·24	0·18	Marchenko & Karlov, 1962
Picea excelsa Link								
Russia	200	<1	1·22	0·01	0·26	0·44	0·17	Rodin & Basilevich, 1967
Pinus sylvestris								
Britain	40	<5	0·97	0·12	0·32	0·18	0·06	Ovington & Madgwick, 1959
Pseudotsuga menziesii								
Oregon, USA	450	<5	0·62	0·10	0·17	0·69	—	Santantonio, 1974
Oregon, USA	50	2–5	0·54	0·10	0·20	0·50	0·07	Fogel, unpublished
Oregon, USA	50	<0·6*	0·62	0·15	0·21	0·11	0·02	Fogel, unpublished
Oregon, USA	50	<0·6†	1·61	0·26	0·95	0·06	0·12	Fogel, unpublished
Fagus sylvatica								
South Sweden	90	<5	0·67	0·08	0·32	0·15	0·06	Nihlgård, 1972
Quercus robur L.								
Voronezh Forest, Russia	50	<0·3	—	0·01	4·16	0·71	0·22	Rodin & Basilevich, 1967
Voronezh Forest, Russia	50	1 to 0·3	—	0·08	0·72	0·56	0·22	Rodin & Basilevich, 1967

* Mixed mycorrhizae washed in water.

† Tuberculate mycorrhiza of *Rhizopogon vinicolor* Sm. with cortex removed, not washed in water.

of nutrients before senescence of components is negligible. This assumption may not be valid since decreases in nitrogen, phosphorus, and potassium concentrations prior to abscission have been shown in conifer needles (Millar, 1974). Similar decreases in mycorrhiza nutrient levels have not been reported but large seasonal fluctuations in root carbohydrate reserves and nitrogen levels have been observed. Laing (1932) noted that the seasonal variation in starch content of young, active Norway spruce (*Picea abies* (L.) Karst.) roots differed from that in older roots. Krueger and Trappe (1967) reported large seasonal differences in the starch and sugar content of Douglas fir roots, but little variation was found in crude fat or protein concentrations. Kozlowski and Winget (1964) estimated from girdling experiments that only about 2% of the phloem-translocated carbohydrate reserve in 8 year old *Pinus resinosa* Ait. originated in roots. The girdling experiment suggests that carbohydrate reserves in roots are used for root growth, not shoot growth. In a recent study arginine concentration in Douglas fir roots (1 to 1·5 cm in diameter) was high in winter and decreased to a low level in October before starting to accumulate again, suggesting it may function in nitrogen storage (Van Den Driessche and Webber, 1977). In fruit trees nitrogen is translocated from roots and old shoots to new shoots during spring but accumulates in roots during autumn and winter (Taylor, 1957). Given the large annual throughput of mycorrhiza biomass, withdrawal of nutrients in limited supply before shedding of structural carbohydrates would not be unexpected.

The concentration of nutrients in Douglas fir mycorrhizae falls within the range reported for fine roots (Table 4) and with the exception of phosphorus is considerably higher than that in 5 to 500 mm broad Douglas fir roots (Santantonio, Hermann and Overton, 1977). The lower concentrations in the mixed as opposed to the tuberculate mycorrhizae may result from leaching of nutrients during washing or withdrawal from the predominately dead mycorrhizae in the mixed sample. Further analyses of mycorrhizae collected during different phenological periods and of active and dead mycorrhizae should be done, given the small number of reported values.

Investigators have ignored mycorrhizae and, for the most part, root mortality in nutrient cycling studies. Consequently, budgets detailing the distribution of nutrients in the vegetation, forest floor, and mineral soil are often presented which underestimate the importance of belowground processes in nutrient cycling. Nitrogen budgets for coniferous forests (Table 5), for instance, show that the forest floor contains 2 to 20 times more nitrogen than roots. Budgets expanded to include nitrogen content of litterfall have led to the conclusions that litterfall is the most important nitrogen cycling mechanism and that 'exchange of nutrients within the rhizoplane may be designated as a minor cycle within the biological cycle . . .' (Heilman and Gessel, 1963).

In contrast, the few studies incorporating root mortality data have shown that throughput of roots is the most important cycling mechanism for nitrogen. Most of the nitrogen (87%) in an oak–hickory forest studied by Henderson and Harris (1975) is incorporated in the mineral soil with the remaining nitrogen contained in the vegetation (8%) and forest floor (5%). Roots contain 21% of the nitrogen in trees, within the range reported for conifers (Table 5). Throughput of fine roots ($\leqslant$ 5 mm) releases twice as much nitrogen as is contained in litterfall and 1·4 times more than is released during litter decomposition. Similarly, most of the nitrogen (74%) in a loblolly pine (*Pinus taeda* L.) plantation (Wells and Jorgensen, 1975) is contained in the mineral soil with smaller amounts present in the vegetation (13%) and forest

Table 5. *Distribution of nitrogen within different coniferous forests*

Location	Species*	Age (years)	Density (trees ha^{-1})	Nitrogen content (kg ha^{-1}) Foliage	Branches	Bole	Shrubs	Total aerial	Roots	Total tree†	Total forest floor	Total soil	Source‡
Washington	Psme	36	2223	104	62	131	7	297	32	329	175	2809	1
British Columbia	Psme	20	16000	101	37	47	0	185	ND	ND	276	3379	2
Washington	Psme	30 to 52	650 to 1600	ND§	ND	ND	1 to 59	112 to 455	48 to 100	174 to 504	184 to 657	1824 to 3551	3
Oregon	Psme	50	1626	171	125	126	0	422	41	463	85	6618	4
Ontario	Piba	30	2431	56	49	49	6	153	12	165	328	3729	8
Minnesota	Piba	46	1580	65	76	118	16	259	ND	ND	689	2312	5
Minnesota	Pigl	46	2187	153	127	102	1	382	ND	ND	752	2542	5
Minnesota	Pire	46	1780	131	60	155	26	346	ND	ND	538	2750	5
North Carolina	Pita	16	2200	82	60	115	0	257	64	321	300	1753	7
Scotland	Pisy	33	5155	89	79	106	1	274	81	355	1622	ND	6

* Psme, *Pseudotsuga menziesii*; Piba, *Pinus banksiana* Lamb.; Pigl, *Picea glauca*; Pisy, *Pinus sylvestris*; Pire, *Pinus resinosa*; Pita, *Pinus taeda*.

† Does not include mycorrhizae.

‡ 1, Dice, 1970; 2, Webber, 1977; 3, Heilman & Gessel, 1963; 4, Fogel, unpublished; 5, Alban, Perala & Schlaegel, 1978; 6, Ovington & Madgwick, 1959; 7, Wells & Jorgensen, 1975; 8, Foster & Morrison, 1976.

§ ND, no data.

floor (13 %). Roots contain 19 % of the nitrogen in these trees. Nitrogen released in fine root (≤ 10 mm) throughput amounts to 84 % of that contained in litterfall but is twice as large as the amount released during litter decomposition.

Table 6. *Annual nitrogen budget for a 50 year-old Douglas fir stand at Dinner Creek, Oregon (Fogel and Hunt, unpublished). Return, retention, and uptake during 1976 to 1977 in kg ha⁻¹ per year (% total)*

Component	Retention*	Release and Return†	Uptake‡
Foliage	171 (2)	14 (6)	34
Branches	125 (2)	<1	3
Bole	126 (2)	<1	9
Total Aerial	422 (6)	14 (6)	46
Roots	41 (1)	<1	2
Mycorrhizae	156 (2)	95 (43)	105
Total Tree	619 (8)	109 (49)	153
Forest Floor	85 (1)	17 (8)	17
Fungi	184 (3)	74 (33)	57
Soil§	6618 (88)	23 (10)	−23
Total Stand	7506 (100)	223 (100)	—

* Retention = standing crop × nitrogen concentration.
† Release and return = throughput × nitrogen concentration.
‡ Uptake = retention in 1977 to 1978 minus retention in 1976 to 1977.
§ Sampled to a depth of 1 m.

Preliminary data from a study by Fogel and Hunt in a 50 year old western Oregon Douglas fir stand (Table 6) indicate that almost all of the nitrogen (88 %) is incorporated in the mineral soil with the remainder apportioned between the vegetation (8 %) and forest floor (1 %). Non-mycorrhizal roots contain 7 % and mycorrhizae 25 % of the nitrogen present in the trees. Of the nitrogen released through transfers (e.g. litterfall and decomposition), mycorrhizae contribute 43 % to total release, followed by fungi (33 %), mineral soil (10 %), forest floor (8 %), and litterfall (6 %). Natural additions of nitrogen to Douglas fir stands in the Pacific Northwest are small. Rainfall adds about 1 kg N ha^{-1} per year, nitrogen fixation by free-living organisms can add between 0·1 and 0·2 kg N ha^{-1} per year to the existing capital (Miller, Lavender and Grier, 1976). Obviously, mycorrhiza and root dynamics are areas which need considerable additional research to fully evaluate their importance in nutrient cycling.

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