

Root turnover and productivity of coniferous forests

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Summary Fine roots and mycorrhizae have recently been shown to produce a major portion of the organic matter entering decomposition. Roots and mycorrhizae constitute 63 to 70% of total net primary production in Douglas-fir and Pacific silver fir stands. The importance of roots in primary production makes the method of root extraction from the soil important. Wet-sieving with small mesh screens is more effective than hand-sorting for fine roots and mycorrhizae. Screen size, the efficiency of recovery, the physiological status of the roots and conversion factors to derive biomass from the numbers of root tips should be stated. Published data is enhanced if the phenological status of the stand, its age, tree density, and soil texture are quoted.

Given the large fluxes in fine root and mycorrhiza populations, single biomass estimates are not useful in studies of ecosystem structure and function. A better understanding needs accurate methods to distinguish live and dead roots, data on the production and turnover of large roots, and data on the transfer of nutrients accompanying the large input of roots to decomposition.

Introduction

The role of roots and mycorrhizae in the primary production and mineral nutrition of coniferous forests is attracting increased attention. The exclusion of mycorrhizae, until recently, reflects the problems in separating them from soil and studying them *in situ*. Data on the belowground ecosystem is needed to extrapolate to field conditions information on ion uptake and translocation, and respiration.

This review examines the contribution of roots (mycorrhizal and non-mycorrhizal) to the productivity of coniferous forests, provides information on the efficiency of two methods for estimating root biomass, and compares three methods of calculating root turnover.

Root classification

Several different systems have been employed to classify roots. One common system divides roots on the basis of the order they arise from a primary root, *e.g.*, first order lateral producing a second order lateral, *etc*⁴⁴. Roots providing structural support for the tree may be termed long lateral roots (or any of 20 or more other names) while the roots sometimes suggested as functioning in the absorption of water and nutrients may be called short roots and are very often mycorrhizal⁴⁴. Among the conifers, short roots are found throughout genera in the Pinaceae but not in the Cupressaceae⁴⁴. Lateral roots may be classified into

large and fine roots on the basis of diameter. There is no established convention defining the diameter size range of fine roots, although many biomass studies use 5 mm or 2 mm as the upper limit in diameter⁴³. Some researchers further subdivide fine roots into a number of size classes: 2–5 mm in diam, less than 2 mm in diam, less than 1 mm in diam, *etc.*

Mycorrhizae should be treated as a separate class of roots because they result from a mutualistic symbiotic association between a host and a fungus and have a profound effect on fleshiness, amount and type of branching, rate of elongation, root hair formation, and suberization. Beyond the morphological and anatomical differences, mycorrhizae play a major role in the mineral nutrition of trees and may confer disease or drought resistance⁴⁵. The association between host and fungus in mycorrhizae is so integrated that complete separation of the host and fungus is virtually impossible. In ectomycorrhizae, the most common type in the Pinaceae, short roots are covered with a mantle of hyphae of variable thickness from which hyphae extend out into the soil and intercellularly into the primary cortex to form a Hartig net. An individual hypha may extend more than 2 m from a mycorrhiza and form more than 120 lateral branches; 200 to over 2000 individual hyphae have been counted emerging from a single mycorrhiza⁴⁵. From the standpoint of function, mycorrhizae are extensions of the plant root system greatly extending the region of nutrient absorption beyond the 1–2 mm zone generally ascribed to roots³⁸.

Endomycorrhizae are found in the Cupressaceae and Taxodiaceae, and have relatively few external hyphae and root hairs near the apex of infected roots⁴⁵. Estimates of endomycorrhizal biomass in coniferous forests have not been reported, although there are values for fine root biomass (diam < 2 mm) for *Cryptomeria* (Taxodiaceae) and *Chamacyparis* (Cupressaceae)²².

Structure of root systems

The form and development of each root system is unique. Initial development appears to be under genetic control, although modified by soil (bulk density, moisture, temperature, texture, *etc.*) and plant factors (*e.g.*, root competition, photosynthate availability, tree density)^{19,44}. On level terrain, Douglas-fir first order lateral roots extend more or less equidistantly around the tree but asymmetrically on steeply sloping ground²⁸. First order laterals in Douglas-fir may extend 2.5 m from the stem²⁸. In large leaf pine, lateral roots may spread 14.3 m²⁰, 25 m for pines in sandy soils¹⁹.

Rooting density (root diam > 2 mm) may reach 19 roots/0.25m² in Douglas-fir stands because of the spreading nature of the rooting systems, the extensive production of higher order laterals, and the intermingling of roots from different trees²⁸. Roots extend considerably beyond the width of the crown although rooting density decreases with distance from the stem^{19,33}. Spatial variation in fine root (diam < 2 mm) density has been reported independent of the proximity

of stems^{31,33,43}, although in a young Scots pine stand the largest amount of fine roots was 0.5 to 1.0 m from the stem³³. Other studies indicate fine root biomass decreases with distance from the stem^{11,39}.

Numerous studies have shown that most roots are found in the upper 50 cm of soil, and most root activity and mycorrhizae in the top 20 cm depending on soil aeration and fertility^{9,19}. Roots have been found at depths of 6 m in sandy soils¹⁹ and ectomycorrhizae at depths of 1 to 3 m⁹. Localized concentration of roots may occur in decaying roots, channels formed by decaying roots, decaying logs, and thick litter layers^{15,28}. Localized concentrations in more than one soil horizon may also occur due to fossil soil horizons¹⁹ or obstructions such as fragipan, bed rock, or cobbles and boulders²⁴. Completion of the vertical expansion of the structural root system has been reported to require 30 years in a number of species, but may require 70 years in Scots pine¹⁹.

The problems inherent in the excavation of root systems have favored indirect methods for estimating root biomass. One commonly used method for large roots (diam > 10 mm) is based on an allometric equation that relates root biomass to an easily measured tree parameter, *e.g.*, diameter at breast height^{19,43}. The applicability of such equations is probably restricted to similar conditions. Fine roots are usually lost during excavation of the trees used to develop the model. Soil cores have been utilized extensively to sample fine roots and circumvent the problems caused by excavation methods⁴. The usefulness of the coring method may be reduced if small diameter cores are used in soils with low rooting densities unless replication is increased.

Estimates of fine root and mycorrhiza biomass resulting from soil-coring methods are difficult to compare given the number of different methods employed to separate roots from cores. The main methods involve hand sorting, dry sieving, wet sieving, plus various permutations of these methods combined with magnification, and air or water separation of organic matter^{10,12,23,27,33,43}. A number of procedural and reporting problems hinder comparisons of the results of these different methods. Root tip numbers have been reported without an associated biomass conversion factor. Differences exist in the depth of soil sampled, phenological status of the stand (often not stated), stand age, tree density (often not stated), size and functional classification of roots, and uncertainty about the efficiency of different sampling methods. Consider the efficiency of different methods for recovering mycorrhizae. Many ectomycorrhizae range in size from 0.5 to 3.0 mm long and from 0.15 to 0.6 mm in diam⁹. Consequently, researchers using screens with openings larger than 0.5 mm may not recover all of the mycorrhizae, a common problem^{15,29,30,46}. Some researchers have deliberately discarded mycorrhizae before weighing fine roots^{31,41}, and other have been ambiguous about the method used³⁴ or fail to state mesh size¹³. An additional problem arises when only 'active' mycorrhiza biomass is reported without the proportion of total mycorrhiza biomass this fraction represents being stated^{15,16,46} or total mycorrhiza biomass alone presented^{9,10}.

Table 1. Increase in estimated root biomass after soil samples previously hand-sorted at 7x magnification were wet sieved. Cores extracted 23 May 1982 in a 35 year-old *Pinus strobus* stand near Ann Arbor, MI

Method	Core	Kg roots per ha (% total)	
		2-5 mm dia.	< 2 mm. dia. ^b
Hand-sort	1	5,986 (100)	7,378 (69)
	2	2,389 (97)	5,970 (60)
Wet sieve ^a	1	0 (0)	3,351 (31)
	2	74 (3)	4,053 (40)

^a method of Fogel and Hunt¹⁰

^b includes mycorrhizae

Is wet sieving more efficient than hand sorting for estimating root biomass? Cores were removed from the top 30 cm of soil in a white pine plantation. After the soil was screened (2 mm), roots were hand sorted at 7 × magnification then wet sieved¹⁰ to recover any roots missed during hand sorting. Results (Table 1) clearly indicate that hand sorting is adequate for roots 2 to 5 mm in diam, but that wet sieving produces a 30 to 40% increase in the biomass estimate for roots < 2 mm diam. Higher values of non-mycorrhizal fine roots (diam 0.4-3 mm) were also produced by wet sieving than by excavation in a radiata pine stand³¹. The effect of mesh size on recovery was also shown in tests where a third more roots were retained by a 0.53 mm screen than by a 0.91 screen³⁶. Clearly the method of root extraction from soil should be given careful consideration and the method selected carefully described in subsequent publication.

Reported root biomass estimates

The estimates available⁴³ indicate that root biomass generally comprises 15 to 25% of total tree biomass in coniferous forests^{2,14,40}, although individual estimates range from 9 to 44 percent. Root biomass estimates for conifer stands less than 200 years old range from 3 to 85 Mg/ha; an estimated 209 Mg/ha has been reported for an old growth Douglas-fir stand⁴³. Reported fine root biomass estimates⁴³ range from 1 to 12.6 Mg/ha with a mean of 5 Mg. It is unclear but highly likely that mycorrhizae have not been included in these estimates. Mycorrhiza account for an additional 8% of total tree biomass in young Douglas-fir stands¹⁰. Given the large input of fine roots and mycorrhizae to the decomposition process^{8,10,13}, it is crucial to determine mycorrhiza biomass. Unfortunately, the few published estimates available (Table 2) illustrate the difficulties in comparing different studies. The biomass of Douglas-fir (*Pseudotsuga menziesii*) mycorrhizae appears to be much larger than that of pine

Table 2. Estimates of mycorrhiza biomass in coniferous forests

Species and location	Stand age	Sample depth (cm)	Stems ha ⁻¹	Standing Crop (kg ha ⁻¹)	Physiological class	Separation method	Reference
<i>Abies amabilis</i> USA	23	25	110,500	2,000°	active	1 mm screen-wet	46
<i>Abies amabilis</i> USA	180	25	510	2,700°	active	1 mm screen-wet	46
<i>Picea glauca-Abies lasiocarpa</i> Canada	?	100	329	1,870	total	hand-sort	23
<i>Pinus radiata</i> Australia	42	15	296	1,433	total	0.5 mm screen-wet	27
<i>Pinus resinosa</i> USA	38	50		1,450-2,380**	total	1.5 mm screen-wet	5
<i>Pinus rigida-Quercus</i> spp. USA	?	21	?	4.5-9.9 × 10 ⁻³ *	active	1 mm screen-wet	6
<i>Pinus sylvestris</i> France	10	32.5	26,875	989	active?	2 mm screen	29
<i>Pinus sylvestris</i> Sweden	20	30	1,100	50-380	active	2 mm screen	32
<i>Pinus sylvestris-Fagus sylvatica</i> France	65	26	2,200	1,380	active?	2 mm screen	29
<i>Pseudotsuga menziesii</i> UK	36	107	774	13,700 ⁺	active	0.9 mm screen-wet	36
<i>Pseudotsuga menziesii</i> USA	50	100	1,626	9,762-25,032	total	0.5 mm screen-wet	10
<i>Pseudotsuga menziesii-Larix</i> USA	250	38	4,631	18,377 ⁺	active	2 mm sieve-hand	15

+ + assuming each tip weighs 19.7 × 10⁻⁵ g dwt, recalculated from data presented in reference

* assuming each tip weighs 12.5 × 10⁻⁵ g dwt.

+ mostly for roots 0.5 mm.

° estimated from fig. 3 in reference cited

** root diam. 1 mm

Table 3. Comparison of fine root biomass in stands of different species composition near Ann Arbor, Michigan

Species	Site	Stand age	Kg roots per ha in top 30 cm of soil		
			< 2 mm dia. (% total)	mycorrhizae (% total)	total fine roots
<i>Pinus strobus</i>	Michigan ^a	35	11,750 (94) 15,815 (95)	736 (6) 900 (5)	12,486 16,715
<i>Quercus/Carya</i>	Michigan ^a	60	11,259 (88)	1,526 (12)	12,785
<i>Pseudotsuga menziesii</i>	Michigan ^a	30	1,661 (22) 2,760 (33)	5,978 (78) 5,491 (67)	7,639 8,251
	Oregon	50			
	maximum ^b		11,916 (49)	12,199 (51)	24,115
	minimum ^b		1,948 (29)	4,752 (71)	6,700

^a same soil type, cores extracted 23 May–8 June 1982

^b recalculated from Fogel and Hunt¹⁰

or spruce. The biomass of *Abies* mycorrhizae may be similar to Douglas-fir if the proportion of active to total mycorrhizae is the same (mean = 8%) as measured for Douglas-fir (Fogel unpubl). The resulting standing crops in the 23 and 180 year-old *Abies* stands (25.2 and 34.0 Mg/ha) compare very well to the 25.0 Mg/ha reported for Douglas-fir¹⁰. Mycorrhiza biomass was compared in stands of mixed hardwood (*Quercus* and *Carya* dominates), white pine, and Douglas-fir growing on the same sandy glacial kame. Cores were extracted and wet sieved as described earlier¹⁰. The results of this study (Table 3) indicate that among the Michigan stands the Douglas-fir plantation has the smallest fine root biomass, but has the largest biomass and proportion of mycorrhizae. The estimates for the Michigan Douglas-fir stand approximate the minimum standing crop reported for a similarly aged Douglas-fir stand in Oregon¹⁰.

Root production and turnover

Direct measurement of mycorrhiza and fine root production in established stands are extremely difficult *in situ*³⁹ and most studies have estimated production and turnover on the basis of changes in the biomass of various fractions over a given period. No significant seasonal differences in the biomass of large conifer roots have apparently been detected^{28, 32, 43}. Several researchers have reported that 30–86% of the fine roots turnover annually^{10, 32, 42}, similar to the values reported for deciduous trees⁹. The large turnover in fine roots and mycorrhizae represents a considerable 'cost' to trees and constitutes a rather large sink of carbon, from 63 to 77% of total net primary production in coniferous forests^{1, 14}. These results indicate that roots are more important than

leaf and branch litter in returning organic material to the soil, 4 to 5 times more material is returned by roots than by litter^{10,32}. Studies in which root turnover has been assumed to contribute half as much as litter to the soil should be reexamined^{32,47}.

The large turnover of mycorrhizae and fine roots results from grazing and/or senescence accompanied by decomposition. Estimates of total grazing do not exist although partial estimates indicate that soil fauna consume 0.3 to 10% of the estimated production of roots in temperate forests^{14,26}. Senescence of fine roots has been attributed to stresses imposed on the root system by drought, periodic high water tables, extreme soil temperatures, defoliation, parasitism, over-fertilization, and in some instances by internal hormonal control^{11,17,25,35,37,48}.

The high turnover of fine roots has been explained as an 'adaptive strategy'. Root sloughing, with subsequent microbial immobilization, could help retain nutrients in the upper soil horizons when the tree is under stress¹⁴. Reynolds³⁷ has calculated that during drought, roots consume energy reserves in one week equivalent to their own dry weight. This high 'cost' for maintenance respiration would make it 'advantageous' for a tree to maintain a small mass of roots during periods of stress. Withdrawal of essential nutrients just prior to root senescence, analogous to deciduous leaves, is an attractive hypothesis that deserves study. The rate of withdrawal, however, is important because this mechanism requires the tree to be stress tolerant thereby reducing its capacity for stress avoidance.

A second explanation is based on the assumption that most absorption of water and nutrients occurs immediately behind the root apex³⁷ and that localized regions of water and nutrient depletion occur in soil. If this were the case shedding roots in depleted zones would avoid the high costs of respiration allowing new roots to exploit untapped soil zones for water and nutrients^{7,37}. This explanation fails to take into account the role of mycorrhizal fungi in extending the absorption zone of roots beyond the 1–2 mm zone generally ascribed to roots³⁸.

Given the importance of roots in primary production and the difficulties in estimating biomass, it is important to examine the different assumptions made in deriving production and turnover estimates. A direct comparison of the three methods employed was attempted by utilizing monthly estimates of mycorrhiza biomass and decaying roots (generally included in biomass by most researchers) for a Douglas-fir ecosystem (Fogel unpubl, Fogel and Hunt¹⁰). The first method assumes an acceptable method of separating live (active) from dead (inactive) roots does not exist. Root production (growth) is calculated by summing the differences between significantly different peaks and troughs in monthly or seasonal biomass estimates^{10,13}. Positive increments are used to estimate production and decrements the return to soil (throughput *fide* Fogel and Hunt¹⁰). Calculated production in the Douglas-fir ecosystem totals 15.3 Mg/ha and throughput 14.6 Mg/ha; mortality is not estimated by this approach.

Method 2 for estimating production and turnover assumes that differences in standing crops are real even if they are not significantly different statistically³². No attempt is made in this approach to reconcile simultaneous changes in live and dead standing crops. Production and mortality are estimated as the sum of all positive increments, minus a correction factor, in the standing crops of live and dead root fractions respectively. A minimum estimate of production by this method is 2.4 Mg/ha, mortality 37.0 kg/ha, and throughput 36.4 Mg/ha.

Method 3 is similar to method 2, but adds the assumption that production and mortality occur simultaneously. Production, mortality, and throughput estimates are obtained by balancing changes in the standing crop of each root fraction during each sampling interval⁴². For example, if live root standing crop decreases 10 kg/ha and dead root standing crop decreases 5 kg, production would be 0 kg, mortality would be 10 kg, and throughput would be 15 kg/ha. Estimated production in the Douglas-fir ecosystem is 2.4 Mg/ha, mortality 45.1 Mg/ha, and throughput 46.9 Mg/ha.

Methods 1 and 3 accurately estimate the measured total standing crop of mycorrhizae on the last sample date when throughput is subtracted from the sum of the initial standing crop, production, and mortality. Method 2 overestimates the final measured standing crop by 3 Mg. The production estimated by methods 2 and 3 is identical. Method 3 produces estimates 22% larger for mortality and 29% larger for throughput than method 2. Santantonio⁴² reported differences in the estimates of method 3 compared to method 2 of 30–60% in production, 50–70% in mortality, and 50–65% in throughput. Method 1 yields what are generally regarded as conservative estimates because steady state conditions are assumed and mortality is not taken into account. Throughput estimated by the latter method is lower than those estimated by methods 2 and 3, 40% and 31% respectively, but production is 530% larger than calculated by either of the other methods. The much larger production estimated by method 1 is due to the inclusion of mortality in the production estimate and perhaps an underestimation of the live biomass in methods 2 and 3. Method 3 produces estimates very similar to those of method 1 if only the maximum and minima preceding and following the maximum are used in the calculation rather than all 12 monthly standing crops. All three methods of estimating production and turnover indicate large fluxes in mycorrhiza production are matched by almost equally large fluxes in throughput.

Resolution of the question of which of the three methods yields the best estimate of production will depend on obtaining accurate estimates of the quantities of live and dead mycorrhizae. In practice, it has been very difficult to distinguish live and dead mycorrhizae or for that matter roots and the possibility for individual errors is great⁴. The problem of classifying the physiological status of ectomycorrhizae is compounded by their small size and the possibility of host tissues continuing to be active after death of the fungal symbiont. Common

criteria for characterizing live mycorrhizae include: turgidity, color, integrity of root apex, association with mycelia, hyphal strands, or rhizomorphs, and when sectioned, color of host tissues¹⁵. Generally no attempt is made to determine the proportion of live to dead mycorrhizae. Underestimates of live mycorrhiza biomass may result from partial separation from soil, errors in classifying the physiological status of individual mycorrhizae, and from improper handling. For example, exposure to dry air for only a few minutes is sufficient to make small roots shrivel and die²⁴.

Vital stains have been used by several investigators in an attempt to avoid subjective use of morphological criteria in distinguishing live and dead roots. The stains employed have included 2, 3, 5-triphenyltetrazolium chloride, 2,3,4-triphenyltetrazolium bromide, and congo red⁴.

Unfortunately, roots of various plant species react quite differently to staining. Thus, dye adsorption is apparently related to the physical properties of the roots as well as to root cation exchange capacity.

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