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THE ROLE OF FINE ROOTS IN THE ORGANIC MATTER AND NITROGEN BUDGETS OF TWO FORESTED ECOSYSTEMS[1]

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Abstract. Standing crop, rates of production, mortality, decomposition, and nitrogen dynamics of two size classes of fine roots (0–0.5 mm and 0.5–3.0 mm diameter) were estimated for 1 yr in a 53-yr-old red pine (*Pinus resinosa* Ait.) plantation and in an adjacent 80-yr-old mixed hardwood stand in north-central Massachusetts. Dry matter of live fine roots was higher in the hardwoods (mean = 6.1 Mg/ha; annual range 3.6–8.6 Mg/ha) than in the plantation (mean = 5.1 Mg/ha; annual range 2.5–7.8 Mg/ha). Dead root mass was similar in the hardwoods (mean = 4.4 Mg/ha) and the plantation (mean = 4.0 Mg/ha). Nitrogen standing crop of live roots in the hardwoods was higher than in the plantation (mean = 65 kg/ha and 42 kg/ha, respectively).

Net fine root production was estimated from changes in standing crop. Production estimates ranged from 4.1 to 11.4 $Mg \cdot ha^{-1} \cdot yr^{-1}$ in the hardwoods and from 3.2 to 10.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$ in the plantation, depending on the assumptions made in the calculations. Concurrent estimates of total nitrogen requirement for this production ranged from 73 to 184 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the hardwoods and from 44 to 122 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the plantation. Decomposition, measured as mass loss from buried cloth bags, was ≈20% in 0.4-mm mesh bags and as high as 47% in 3-mm mesh bags after 1 yr. Integrating production and nitrogen requirements with estimates of decomposition rates and nitrogen mineralization for these ecosystems suggests that the lower estimates of production are more accurate.

Key words: decomposition; fine roots; Massachusetts; mixed hardwoods; nitrogen budget; Pinus resinosa; *production; soil organic matter.*

INTRODUCTION

Fine roots represent a large and dynamic portion of the below-ground biomass and nutrient capital and a significant part of net primary production in temperate forests (Harris et al. 1977, Santantonio et al. 1977, Persson 1978). According to existing models, fine root mortality transfers significant amounts of organic matter and nutrients into the soil and is important in forest nutrient cycles (Shugart et al. 1977, Aber et al. 1978). However, studies of organic matter and nitrogen dynamics in forest ecosystems have concentrated mainly on aboveground production (Bray and Gorham 1964, Whittaker et al. 1974, Bormann et al. 1977) and decomposition (Ovington 1962, Gosz et al. 1973, Aber and Melillo 1980). The role of fine roots in net primary production and nitrogen budgets of forests is poorly understood. The purposes of this paper are: (1) to compare fine root production, mortality, and decomposition in a red pine (*Pinus resinosa* Ait.) plantation and an adjacent mixed hardwood stand on the same soil type in north-central Massachusetts; (2) to estimate the importance of fine roots in maintaining stocks of soil organic matter and nitrogen; and (3) to evaluate different methods of calculating fine root production from sequential samples of live and dead dry matter.

METHODS

Study site

This ongoing study is being conducted at the Harvard Forest, Petersham, Massachusetts, USA. Two adjacent 1.3-ha stands with well-documented histories were chosen: a 53-yr-old red pine plantation, and an 80-yr-old mixed hardwood stand. Both were situated on Entic Haplorthods (Spodosol) of the Gloucester series. The soil was of glacial origin and was very stony (Lyford 1963, 1964). Low and poorly drained areas were excluded from the study site. The plantation had deeper forest floor and A2 horizons. Forest floors were both mors and the O2 horizon had a July 1978 ash-free mass of 33.5 Mg/ha in the hardwoods and 41.5 Mg/ha in the plantation. Mean July 1978 forest floor depths were 6.3 (±0.1) cm in the hardwoods and 8.0 (±0.1) cm in the plantation.

The area of the hardwood stand was cleared for pasture in the late 1700's and abandoned in the mid-

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1800's. Old-field succession led to a white pine (*Pinus strobus* L.) stand which was harvested around 1900 (Raup 1966). The present stand regenerated naturally following the harvest of white pine. Multiple-stemmed red maples (*Acer rubrum* L.) were removed in 1936 and the stand has been virtually undisturbed since. The current vegetation was dominated by red oak (*Quercus rubra* L., 70% of total basal area) and red maple with lesser amounts of yellow birch (*Betula alleghaniensis* Britton), beech (*Fagus grandifolia* Ehrh.), and white pine. The understory was sparse and consisted largely of red maple. Leaf litter fall was 4.4 $Mg \cdot ha^{-1} \cdot yr^{-1}$.

The plantation was established in 1925 following harvest of mixed hardwoods which had developed on an old field also abandoned in the mid-1800's. Hardwood weeding was carried out several times during the 1st 5 yr. The stand was pruned in 1948 and has been undisturbed since. Red pine accounted for 89% of the basal area in the plantation, with the remainder composed of white spruce (*Picea glauca* [Moench] Voss), red maple, and red oak. No significant understory was present. Leaf litter fall was 5.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$.

Fine root classification

For this study the fine root system was defined as nonwoody roots <3 mm in diameter and their associated root tips. This classification was based on readily observable morphological features including those described by Lyford (1975). Essentially all roots >3 mm diameter have secondary xylem thickening, well developed phellem, are relatively inflexible, and are perennial. Another natural division occurs at about 0.5 mm in diameter. Roots smaller than this include all nonwoody root tips, virtually all of which were mycorrhizal, and nearly all unsuberized roots. These size classes have been used in some (Moir and Bachelard 1969, Strand 1970, Safford 1974), but not all (Edwards and Harris 1977, Santantonio et al. 1977) fine root studies.

Distinctions between living and dead roots were made on the basis of appearance and ease of disintegration (cf. Ares 1976, Valiela et al. 1976). Living roots were resilient, translucent, and white to tan; dead roots fragmented easily, were dull, and gray to black. These visual and manual criteria yielded reproducible results when selected samples were remixed and sorted a second time and provided a practical approach to classifying roots on the scale required by this study.

Field methods

Choice of a fine root sampling method was based on comparison of samples collected in June 1978 using a 19 mm diameter corer, a 50 mm diameter corer and a 0.01-m^2 template. All these sampling devices produced similar results, but the 19-mm cores could be more readily processed. Thirty samples were collected with the 19-mm corer in July 1978 to provide a more extensive test of variance and distribution of the sample populations and to estimate required sample size.

Fine root dry matter in the O1 and O2 and top 15 cm of mineral soil was estimated from nine 19 mm diameter core samples in each stand. Sampling points were located at randomly selected coordinates within a permanently marked grid. The plantation had been planted by hand; spacing was irregular and rows were not straight, resulting in a nearly random bole distribution. Samples were collected monthly beginning July 1978, except for February and March 1979, when the soil was frozen to beneath sampling depth. Stones, large roots, and boles which occupied the entire forest floor and upper 15 cm of soil were encountered at 9% of the sample points over the course of the study in both stands, and all standing crop estimates in these horizons were decreased by 9%.

Fine roots were separated from soil and organic matter using dissecting microscopes and microdissecting forceps. Fine roots were sorted into live and dead fractions by size class as described above. This method required an average of 15 h of sorting per core; faster methods such as sieving or flotation were much less accurate.

Below 15 cm in the mineral soil, dry matter of fine roots was esimated from 50 mm diameter core samples located randomly in each stand. Cores were excavated to the depth of the rooting zone (0.6–1.2 m) with particular care taken to avoid deflection of the corer by stones and to include fine roots growing along stone surfaces. Four cores were collected in each stand in July, October, and December 1978 and May 1979. Fine roots were separated from soil by sieving and flotation and the residue was carefully checked for root fragments.

Phenology of fine root extension was observed as growth into root-free soil columns. Thirty 50 mm diameter columns were established at random locations in each stand in July 1978 and five were collected in each stand bimonthly. Root-free columns were prepared by removing a 50 mm diameter core to a minimum depth of 15 cm into the mineral soil and refilling with sieved soil (6-mm mesh). Forest floor and mineral soil were sieved separately and packed into the core hole at approximately the same depth and compaction as the surrounding soil. Fine roots growing into the cores were collected and separated using the procedures described in the previous paragraph.

Decomposition rate was estimated using standard mesh bag techniques (Bocock 1964, Gosz et al. 1973). Three mesh sizes (0.1, 0.4, and 3.0 mm) and two soil positions (forest floor and top 10 cm of mineral soil) were used. The 0.1- and 0.4-mm mesh bags excluded meso- and macrofauna; 3.0-mm mesh allowed entry by mites, springtails, and other mesofauna found in the soil (Johnston 1936). The largest mesh size was only used for 0.5–3.0 mm diameter roots because smaller roots could not be contained.

Fine roots to be placed in bags were collected in July 1978 on the study site, gently rinsed, sorted into previously described size classes, and air dried at room temperature to constant mass (≈24 h). Bags contained 200 to 500 mg of live fine roots and were placed in the soil within 72 h of the root collection. The small mass of the sample was necessary to avoid matting of the roots within the bags. Fine roots from the forest floor and mineral soil were kept separate and incubated in the horizon of their origin. Five 0.4-mm mesh bags representing each of two size classes and two soil horizons were collected monthly in both stands (total of 40 bags monthly). Five bags each of 0.1- and 3.0-mm mesh were collected for each root size, soil depth, and stand in July 1979.

Chemical methods

All samples were dried to constant mass at 70°C. Subsamples were analyzed for moisture (dried for 48 h at 105°), ash (combustion for 12 h at 450°) and total nitrogen (N) (modified Kjeldahl procedure) (Miller and Miller 1948, Technicon Industrial Systems 1974). Because of the small amount of roots in each sample, samples from the same stand, root size, horizon, and collection date were composited for chemical analyses. Results are given in terms of ash-free dry mass unless stated otherwise.

Selected samples (see Results) were analyzed for total lignin using an acetyl bromide digestion and spectrophotometric determination (Johnson et al. 1961). Bulk samples, collected periodically in each stand and separated by size class and soil horizon, were analyzed for total nonstructural carbohydrate (TNC) using a takadiastase digestion followed by a titrametric determination of reducing power (Smith 1969).

Statistical and computational methods

Individual fine root dry matter estimates for a given stand and sampling date were not normally distributed but were skewed upwards as indicated by 30 standing crop cores collected in each stand in July 1978. Tests for equal variance (Snedecor and Cochran 1967) among all monthly samples also indicated heteroscedasticity. A square-root transformation (Bartlett 1947) produced normal distributions and equal variances, allowing the use of normal parametric statistics. A least significant difference (LSD) test (Snedecor and Cochran 1967) with a 5% rejection level was used to detect significant difference between means of monthly standing crop samples. It is worth noting that the conclusions derived below would not be altered if the LSD test were applied to untransformed data. Litter bag data met the assumptions of equal variance and normal distribution and were analyzed accordingly.

Nitrogen, lignin, and TNC contents in kilograms per hectare were calculated by multiplying the untransformed mean standing crop estimate by the concentration of the corresponding composite sample.

DEAD \ LIVE	Increase	Decrease
Increase	P = ΔL + ΔD M = ΔD C = 0	P = ΔL + ΔD or 0 M = ΔD or (-ΔL) C = (-ΔL) - ΔD or 0
Decrease	P = ΔL M = ΔL C = (-ΔD)	P = 0 M = (-ΔL) C = (-ΔL) + (-ΔD)

FIG. 1. Decision matrix illustrating one method for estimating fine root production, mortality, and decomposition. The appropriate quadrant is selected according to the direction of change in live (L) and dead (D) standing crop during the interval between two sampling times. Production (P), mortality (M), and decomposition (C) for the sampling interval are calculated using the equations in the chosen quadrant. Where two equations are indicated, the one yielding the smaller result is used. Annual estimates are calculated by summing the estimates from all sampling intervals within the year.

Two methods were used to estimate production. The first method assumes a single annual pulse of fine root production. With this method, production was calculated as the sum of differences between annual maximum and minimum dry matter standing crops for each size class and soil depth (cf. Edwards and Harris 1977). The second method assumes rapid fine root turnover, and that even monthly sampling may miss some fine root dynamics. With this method, all changes in both live and dead standing crop between sampling dates, whether or not significantly different, were included in calculating production, mortality, and decomposition (cf. Santantonio 1980). The procedure can be explained using the decision matrix in Fig. 1. A quadrant was chosen according to the direction of change in live and dead fine root standing crop during the interval between two sampling dates. Production, mortality, and decomposition during each sampling interval were calculated using the equations within the chosen quadrant. Where a choice of two equations is given, the equation yielding the lower estimate was used. Annual estimates were the sums over all sampling intervals within the year. Nitrogen requirements associated with fine root production were calculated using the same procedures applied to the mass of N contained in the fine roots.

RESULTS

Annual mean fine root dry matter and nitrogen content differed between stands, as did distribution by depth (Table 1). The greater amount of live fine root dry matter and nitrogen in the hardwoods was largely due to different amounts in the forest floors. Annual mean dead root dry matter was similar in the two stands, but in the hardwoods a greater proportion of

TABLE 1. Annual mean dry matter and nitrogen content of live and dead fine roots <3.0 mm in diameter in a mixed hardwood stand and a red pine plantation. Samples were taken to maximum depth of rooting zone (0.6–1.2 m). *n* = number of sampling dates between August 1978 and August 1979. Standard errors given in parentheses.

		Hardwoods		Plantation	
Depth (cm)	*n*	Live	Dead	Live	Dead
		Dry matter (Mg/ha)			
Forest floor	10	2.5 (0.2)	2.4 (0.2)	1.1 (0.1)	1.6 (0.2)
0–15	10	1.7 (0.1)	1.1 (0.1)	1.5 (0.2)	1.3 (0.1)
15–30	4	0.9 (0.09)	0.5 (0.14)	1.0 (0.21)	0.5 (0.17)
30–45	4	0.8 (0.1)	0.3 (0.07)	0.9 (0.18)	0.3 (0.09)
>45	4	0.2 (0.08)	0.1 (0.07)	0.6 (0.24)	0.3 (0.10)
Total		6.1	4.4	5.1	4.0
		Nitrogen (kg/ha)			
Forest floor	10	35 (4.4)	35 (3.0)	13 (1.5)	23 (1.6)
0–15	10	15 (1.1)	14 (1.5)	14 (1.1)	7 (1.1)
15–30	4	7 (1.1)	4 (0.5)	7 (0.8)	3 (0.4)
30–45	4	5 (0.3)	2 (0.3)	5 (1.5)	2 (0.4)
>45	4	3 (1.0)	0.6 (0.2)	3 (0.9)	2 (0.5)
Total		65	56	42	38

the total was found in the forest floor. Amount of fine root dry matter and nitrogen declined below 15 cm in the mineral soil, as has been noted elsewhere (Scully 1942, Gaiser and Campbell 1951, Meyer and Gottsche 1971, Kochenderfer 1973).

For both live and dead fine root dry matter, seasonal trends were similar in the two stands (Fig. 2). Live root mass declined during the winter from an autumn maximum, while dead mass increased. Most classes of live roots appeared to have a single annual maximum per year. The majority of month-to-month changes were not significant, but all live fine root classes above 15 cm depth in both stands showed significant ($P < .05$) differences between annual maxima and minima.

Root growth into root-free soil columns was also seasonal, occurring only in April and May when most of the significant increases in live fine root dry matter were observed. In addition, large numbers of new fine roots were observed in the early spring. Very few new roots, easily identified by their whitish color, translucence, and lack of suberin, were evident during the remainder of the year. This seasonal pattern of root growth was similar to the observations of Morrow (1950) in a sugar maple (*Acer saccharum* Marsh.) stand and Harvey et al. (1978) in a Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco)–larch (*Larix occidentalis* Nutt.) stand.

Percent N in fine roots also showed seasonal patterns, increasing during the spring and autumn and decreasing during the winter. Fluctuations were small and generally not significant. Seasonal changes in N content (kilograms per hectare) of fine roots were largely due to changes in dry matter standing crops rather than changes in percent N. The mass of nitrogen in live fine roots generally began increasing in spring and began decreasing during late autumn–early winter (Fig. 3). Mass of N in live and dead fine roots frequently diverged, notably during winter.

The percentage of live fine root dry matter as total nonstructural carbohydrate (TNC) was higher in the plantation than the hardwoods (Table 2). The ranges measured here were similar to starch concentrations obtained for oak fine roots by Woods et al. (1959),

TABLE 2. Percent total nonstructural carbohydrates (TNC) in fine roots collected from the forest floor of a mixed hardwood stand and a red pine plantation. Size classes are very fine (VF = <.05 mm diameter) and fine (F = 0.5–3.0 mm diameter).

	Percent TNC (ash-free dry mass)			
	Hardwoods		Plantation	
Date	VF	F	VF	F
July 1978	7	8	9	15
October 1978	. . .	15	15	15
August 1979	7	7	10	14
October 1979	9	15	12	14
December 1979	7	6	6	11

TABLE 3. Percentage of original dry matter of 0.5–3.0 mm diameter roots remaining after a 12-mo field incubation in mesh bags. Effects of two mesh sizes and burial at two soil depths were observed in both a mixed hardwood stand and a red pine plantation for the period August 1978–August 1979.

	Percent dry matter remaining (±SE)			
Mesh size	Hardwoods		Plantation	
(mm)	Forest floor	0–15 cm	Forest floor	0–15 cm
0.4	76.3 (3.2)	84.6 (2.4)	81.3 (1.2)	77.4 (1.8)
3.0	73.5 (6.8)	75.4 (4.3)	59.2 (2.3)	52.2 (2.9)

TABLE 4. Initial concentration of nitrogen, lignin, and total nonstructural carbohydrate (TNC) in fine root material used in mesh bag decomposition study. All roots were collected in July 1978 in a mixed hardwood stand and a red pine plantation. Collection depths were forest floor (FF) and top 15 cm of mineral soil (MS). Size classes were very fine (VF = <0.5 mm diameter) and fine (F = 0.5–3.0 mm diameter).

			Initial %		
Burial stand	Depth	Size class	Nitrogen	Lignin	TNC
Hardwood	FF	VF	1.3	21.9	6.5
		F	0.8	23.3	8.4
	MS	VF	1.0	. . .	. . .
		F	0.6	23.0	6.3
Plantation	FF	VF	1.2	21.8	8.5
		F	0.8	21.6	14.5
	MS	VF	1.0	24.8	10.4
		F	0.7	21.7	13.1

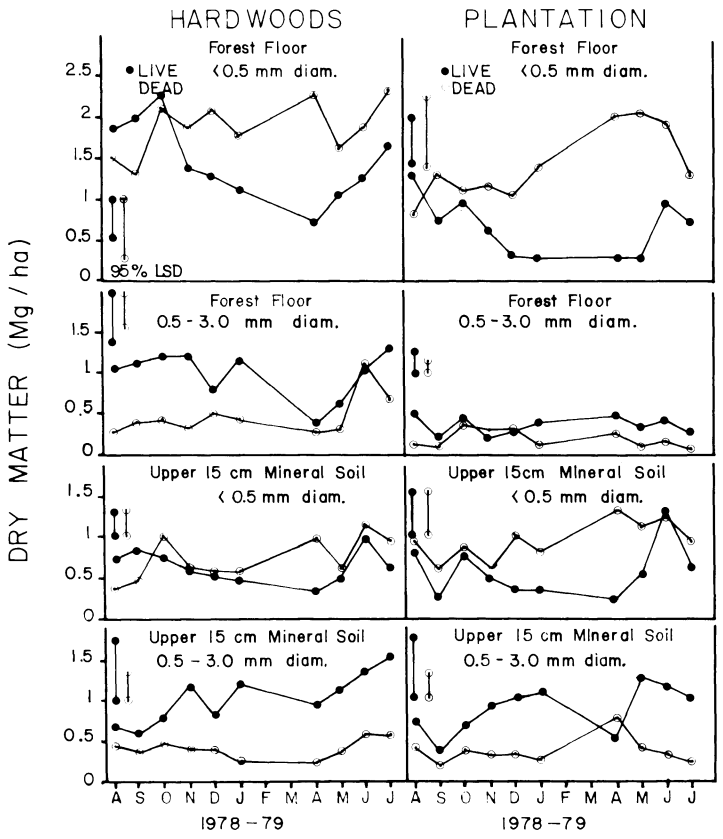

FIG. 2. Fine root dry matter standing crop (Mg/ha) from August 1978 to July 1979. Each point is the mean of nine samples. Samples were collected separately from the forest floor and upper 15 cm of mineral soil in a mixed hardwood stand and a red pine plantation. Least significant differences (LSD) at the 95% level were calculated separately for each class.

who reported a range of 6–8% in May and 17–18% in November.

Results of the 0.4-mm mesh bag decomposition study showed similar patterns for most root size, soil position and stand combinations (Fig. 4). Between 12% and 25% of the original mass disappeared during 1 yr.

Large-mesh (3.0-mm) bags showed more rapid disappearance than fine mesh (Table 3). The greater losses may have been due to spillage, different environmental conditions within bags of different mesh sizes or greater consumption of roots in coarse mesh bags. Disappearance from very fine mesh (0.1-mm) bags was not significantly different ($P < .05$) than from 0.4-mm mesh bags. Within each category of fine roots, mesh size had no significant effect on % N in fine root litter remaining after 1 yr.

Initial lignin, nitrogen, and TNC concentrations of fine root material placed in litter bags are given in Table 4. Work with hardwood leaves has shown that the rate and nitrogen dynamics of decay are predicted by the initial lignin and nitrogen content of the material (Aber and Melillo 1980, Melillo et al. 1982). None of these relationships holds for root decomposition. Rather, loss of mass from decomposing fine roots was most accurately predicted by the ratio of initial %TNC: initial % nitrogen ($r^2 = .89$, $n = 7$, $P < .005$) and was also well predicted by initial %TNC alone ($r^2 = .62$, $n = 7$, $P < .025$). No significant relationship with horizon, root size, or stand was detected. Most of the loss of mass from decomposing fine roots occurred during the first few months following burial (Fig. 4). The mobility of TNC and the correlation between TNC and decay rates suggest that much of the observed loss of mass was due to TNC loss. It appears that different biochemical constituents affect decomposition in fine roots and in leaves.

Estimates of fine root production differed substantially depending on the method of calculation employed (Table 5). Total annual fine root production for the period August 1978 through August 1979 was estimated at 5.4 Mg/ha in the hardwoods and 4.1 Mg/ha in the plantation, assuming a single annual cycle of root production. Assuming more rapid fluctuations of root growth and mortality and using the monthly calculation method, the corresponding estimates are 11.4 and 10.9 Mg/ha or 2.1 and 2.7 times greater. Annual N requirements associated with these production es-

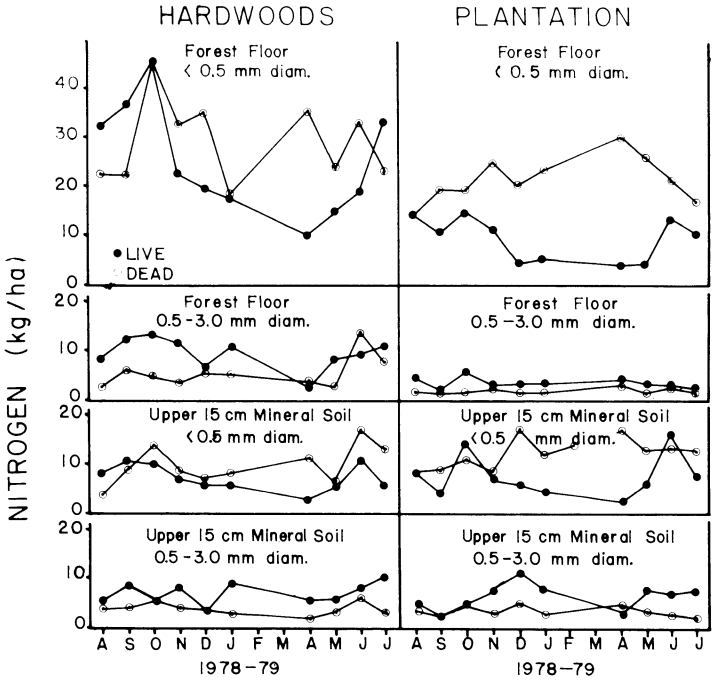

FIG. 3. Fine root nitrogen standing crop (kg/ha) from August 1978 to July 1979. Values were calculated by multiplying N concentration of composite samples of each size and depth class of fine roots by the corresponding mean dry matter of that class. Samples were collected separately from the forest floor and upper 15 cm of mineral soil in a mixed hardwood stand and a red pine plantation.

timates, assuming an annual cycle of fine root production, were 73 kg/ha in the hardwoods and 44 kg/ha in the plantation. Using the monthly calculation method the requirements were 184 and 122 kg/ha, respectively.

DISCUSSION

Estimates of fine root production obtained from sequential samples of standing crop can vary widely depending on the period of time between samples and the periodicity of fine root production-mortality cycles. Although much work emphasizes periodicity on at least an annual cycle (Morrow 1950, Edwards and Harris 1977, Harvey et al. 1978) the question of cycle length remains crucial to estimating fine root production.

Deciding which calculation method to use on the standing crop data depends largely on the time scale of fluctuations in fine root standing crop. If the fluctuations are large and short term, on the order of a month or less, using the difference between annual or seasonal maxima and minima is inappropriate, and production could be calculated only by considering monthly or shorter term changes. If fluctuations are seasonal or annual, then the maximum-minimum approach would yield more realistic results. Any method which considers all changes between sampling dates is subject to error in proportion to the number of intervals considered. Small, nonsignificant changes may be real or they may be sampling artifacts (Persson 1978).

Either phenological observation or the implications for overall production and nitrogen dynamics in the ecosystem can be used to decide which method yields the most accurate predictions. Observations on root growth phenology in the two stands studied indicate annual rather than continuous or monthly production. In both stands three lines of evidence support annual patterns: (1) observation of new root tips in soil pits only in the spring, (2) growth of roots into root-free soil cores only in April and May, and (3) increases in live root dry matter during the spring. Increases in the dry matter of 0.5–3.0 mm diameter roots would involve radial growth and may have occurred during autumn (Fig. 2), but the increases were not statistically significant.

Three variables may be used to judge the accuracy of each method in relation to total ecosystem dynamics: (1) relation to total production, (2) the amount of nitrogen required for fine root production, and (3) the contribution of root litter to total forest floor organic matter. The higher estimates of root production are difficult to reconcile with estimates of total ecosystem primary productivity. Whittaker (1975) estimates that net primary productivity of temperate forests ranges between 6 and 25 $Mg \cdot ha^{-1} \cdot yr^{-1}$ with a mean of 12.5 $Mg \cdot ha^{-1} \cdot yr^{-1}$. The higher root production values ap-

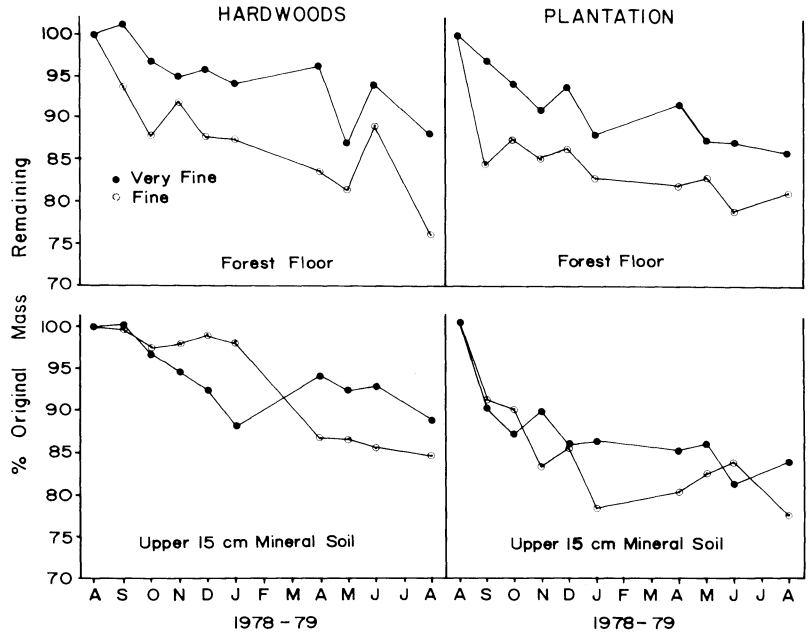

FIG. 4. Percent of original dry mass of fine roots remaining in 0.4-mm mesh litter bags. All bags were placed in the field in July 1978 and a specified number were retrieved at monthly intervals. Initial materials were collected separately from both the forest floor and upper 15 cm of mineral soil in a mixed hardwood stand and a red pine plantation. Fine roots were divided into very fine (<0.5 mm diameter) and fine (0.5–3.0 mm diameter) size classes. Bags were buried in the stand and depth corresponding to the origin of their contents. Values are means of five bags; standard errors are <5% of the means.

proach these estimates and would require nearly a doubling of total net production estimates.

Nitrogen requirements for fine root production as estimated by the two methods (Table 5) approach estimates of total N mineralization and N uptake in temperate forests. Measured N mineralization rates in temperate forests range from 50 to 300 $kg \cdot ha^{-1} \cdot yr^{-1}$ with an average of 100 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Larcher 1975, Ellenberg 1977, Remacle 1977). Nitrogen demand by above-ground vegetation in temperate forests ecosystems generally falls in the same range of 50 to 150 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Melillo 1981). Thus, as for carbon, the availability of nitrogen for root production argues for the lower production rates. In fact, large amounts of nitrogen would have to be retranslocated from senescing fine roots to bring total above- and below-ground nitrogen requirements in line with measured availabilities, even using the lowest fine root production estimates. Retranslocation would allow some of the demand to be met from internal pools.

A final consideration in determining which production estimate is most reasonable is the load placed on the decomposition system by the eventual transfer of the production to dead root litter pools. Percentage of

TABLE 5. Fine root production and nitrogen requirement for August 1978–August 1979 using two contrasting assumptions of the periodicity of root growth (annual or less than monthly). Methods of calculation are described in the text. Size classes are very fine (VF = <0.5 mm diameter) and fine (F = 0.5–3.0 mm diameter). Estimates extend to maximum depth of rooting zone (0.6–1.2 m).

	Hardwoods				Plantation			
	Annual		Monthly		Annual		Monthly	
Depth	VF	F	VF	F	VF	F	VF	F
				Production ($Mg \cdot ha^{-1} \cdot yr^{-1}$)				
Forest floor	1.7	1.0	3.3	2.8	1.0	0.3	2.5	1.0
0–15 cm	0.7	1.0	1.9	2.1	1.0	0.9	3.4	2.3
15+ cm	0.2	0.8	0.6	0.7	0.2	0.7	0.5	1.2
Total	2.6	2.8	5.8	5.6	2.2	1.9	6.4	4.5
Grand total		5.4		11.4		4.1		10.9
				Nitrogen requirement ($kg \cdot ha^{-1} \cdot yr^{-1}$)				
Grand total		73.1		183.7		44.3		121.9

TABLE 6. Estimates of soil organic matter annually derived from fine roots in the entire rooting depth and the forest floor (O2) of a mixed hardwood stand and a red pine plantation. Calculations based on two contrasting assumptions of root production periodicity (annual vs. less than monthly) are compared. Calculations and assumptions are described in the text. Decomposition rates (k) required to maintain O2 mass in steady state are also calculated. Values in parentheses represent the assumption that all consumed dead roots eventually appear as soil organic matter. MOR = mortality, RSP = respiration, CNS = consumption, RT = root litter transfer, LT = leaf litter transfer, M = mass of O2 horizon. MOR − RSP − CNS = RT.

	Organic matter transfer rates							
	Entire rooting depth				Forest floor (O2)			
	MOR	RSP	CNS	RT	RT	LT	M	k
	($Mg \cdot ha^{-1} \cdot yr^{-1}$)				($Mg \cdot ha^{-1} \cdot yr^{-1}$)		(Mg/ha)	(yr^{-1})
Hardwoods								
Annual	5.4	1.1	0.4	3.9	1.9	2.4	33.5	0.13
Monthly	11.4	2.4	0.8	8.2	4.1	2.4	33.5	0.19
Plantation								
Annual	4.1	0.9	1.0	2.2	0.7 (1.0)	2.9	41.5	0.09 (0.09)
Monthly	10.9	2.4	2.7	5.8	1.9 (2.8)	2.9	41.5	0.12 (0.14)

original mass lost after 1 yr from fine roots in litter bags ranged from 12 to 25%. Similar losses have been reported for fine roots of Scots pine (*Pinus sylvestris* L.) of 25%/yr (Berg 1981) and for Douglas fir of 15%/yr (Fogel and Hunt 1979). The low percentage mass loss of fine roots in litter bags as compared to leaf litter is surprising in view of the relatively high N concentration in fine roots. In leaf litter, lignin concentration has been shown to influence decay rate strongly, causing leaf litter with high lignin concentrations to decay more slowly than would be expected on the basis of N content alone (Melillo et al. 1982). Although litter bags may have some effect on decomposition rate, there is no prior reason to believe that roots should decompose as fast as leaves. We feel that the low decomposition rate is due to unknown chemical and physical properties of the roots, exclusion of meso- and macrofauna from the bags, and separation of roots from intimate contact with soil.

Production, mortality, and decomposition can be combined to estimate the contribution of fine roots to soil organic matter pools (Table 6). Using the hardwoods as an example, fine root production was estimated at 5.4 $Mg \cdot ha^{-1} \cdot yr^{-1}$, assuming an annual production cycle. Since this flux is large relative to the average standing crop (6.1 Mg/ha), we have assumed that mortality must approximate production. Mortality of 4.1 $Mg \cdot ha^{-1} \cdot yr^{-1}$, estimated by the difference between annual maximum and minimum standing crop of dead roots, is smaller but not significantly different from production. There are three pathways for dry matter to leave the dead root compartment: microbial respiration, consumption by meso- and macrofauna, and transfer to soil organic matter. The sum of these pathways must equal inputs if soil organic matter is in steady state. Respirational loss, from the fine mesh litter bag study, was approximately 20% in the 1st yr or 1.1 Mg/ha. Loss from the coarse mesh bags, assumed to be largely consumption, was an additional 7% or 0.4 Mg/ha, for a total of 1.5 Mg/ha. This left 3.9 Mg/ha to be transferred to the soil as secondary products and fragments, most of which would no longer be recognizable as fine roots. These would pass through a 2-mm sieve and would be classified as soil organic matter.

Values for the plantation can be obtained in the same way (Table 6). The larger proportion of root disappearance assumed to be due to consumption in this stand makes the fate of consumed material very important. Some ingested materials are respired by consumers and the remainder of the material is returned to the soil; the proportion of ingested organic matter which is respired is unknown. Table 6 also contains estimates for parameters derived from the monthly methods of calculating production.

We can now assess the acceptability of the production calculation methods in terms of their implications for forest floor mass. Root litter transfers to the forest floor are listed in Table 6 (49% of total root litter transfer in the hardwoods, 32% in the plantation, based on distributions of production within the soil profile). The plantation values have a second number in parentheses which represents the assumption that all consumed dead roots appear as forest floor organic matter. The realized value should fall between the two.

These values can be added to estimated transfer of organic matter to the O2 horizon from decomposing leaves (2.4 $Mg \cdot ha^{-1} \cdot yr^{-1}$ and 2.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$ for the hardwoods and plantation, respectively [J. M. Melillo and J. Aber, *personal observation*]). The sum of leaf and fine root litter input to the forest floor can be related to O2 mass to estimate the O2 decay rate required to maintain steady state. Calculations were performed using a first-order, steady-state model:

$$k = T/M$$

(cf. Jenny et al. 1949)

where k = rate of decomposition (yr^{-1})
T = annual transfer of organic matter from leaves and fine roots ($Mg \cdot ha^{-1} \cdot yr^{-1}$)
M = mass of O2 horizon (Mg/ha)

Estimated decomposition rates are given in Table 6.

Decomposition rates in the hardwoods, calculated using the above equation, are all greater than the available measured values for Northeastern hardwood forests (.096 yr^{-1}, Gosz et al. 1976, Melillo 1977; .056 yr^{-1}, Woodwell and Marples 1968). These are consistent with the lower fine root production estimates. In the plantation, the range of values is fairly small, as root litter transfer accounts for a relatively small proportion of the total input to the O2. No comparable measured data are available for red pine stands.

Estimates of the contribution of fine roots to soil organic matter could be further reduced by considering the effect of TNC. TNC in senescing fine roots could have several fates: root respiration, retranslocation into nonsenescent tissues, conversion into structural biomass, or leaching. Leached TNC could be used by other organisms and either respired or converted into structural biomass which could eventually enter the soil organic matter pool. Respiration and retranslocation would not result in the immediate transfer of organic matter to the soil. Loss of mass due to either of these pathways should not be included in estimates of fine root litter production. Potential fine root respiration rates (as CO_2 per unit dry mass per hour) of 0.1 to 0.5 mg $\cdot g^{-1} \cdot h^{-1}$ have been reported (Boyer et al. 1971, Edwards and Harris 1977). Even assuming lower rates in senescing fine roots, a considerable portion of TNC could be lost via respiration. Retranslocation of stored carbohydrates has been well studied in woody roots (Dumbroff and Elmore 1977, Wargo 1979), but not fine roots. Lambers (1979) suggests that respiration is the more likely fate of fine root nonstructural carbohydrates, at least in nonsenescing roots. TNC which is converted into structural biomass would be measured as such at a subsequent sampling date.

Respiration of TNC by the root prior to senescence may cause a decrease in root mass which should not be included in calculations of net fine root production or contributions to soil carbon pools. TNC may change by 9% or more of the total dry matter mass over the course of the year (Table 2). This percentage difference between maximum root TNC and minimum root TNC could be subtracted from production estimates.

Conclusion

Annual net production of fine roots in the two forest ecosystems was similar in magnitude and phenology. Production of fine roots (non TNC-corrected data) was slightly higher than leaf production in the hardwood stand (5.4 vs. 4.4 $Mg \cdot ha^{-1} \cdot yr^{-1}$) and was less than needle production in the plantation (4.1 vs. 5.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$). The difference between the stands was due largely to greater production of fine roots in the hardwood forest floor.

Large annual production coupled with relatively slow decomposition rates for fine roots indicates that a large portion of soil organic matter and nitrogen is derived from fine roots. Considering these estimates in relation to other ecosystem parameters suggests that recently applied methods of measuring and calculating root production in temperate forest ecosystems may yield significant overestimates. Calculations of production using annual maximum and minimum dry matter values yield the most acceptable estimates of net production for the two stands studied.

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