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NUTRIENT CONCENTRATIONS IN FINE ROOTS

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Abstract. Fine roots are an important source and sink for nutrients in terrestrial biogeochemistry. We examined the following hypotheses for fine root nutrients by analyzing data from 56 published studies: (1) that there is a general, inverse relationship of fine root nutrient concentrations with root diameter, and (2) that retranslocation of nutrients out of fine roots is minimal. We analyzed nutrient concentrations of roots ≤5 mm in diameter as a function of root diameter and root status (live, dead, and undifferentiated), including a comparison for coniferous and broad-leaved trees. For fine roots <2 mm in diameter, average C:N and C:N:P ratios were 43:1 and 522:12:1, significantly narrower than for 2–5 mm roots (79:1 and 920:12:1). Live roots <2 mm in diameter contained significantly more N, P, and Mg and less C than did roots 2–5 mm in diameter, but no significant differences were observed for K or Ca. Mean N and P concentrations were 11.0 and 0.9 g/kg, respectively, for live roots <2 mm diameter, compared to 6.5 and 0.6 g/kg in roots 2–5 mm in diameter. Mean N concentrations in live and dead fine roots were identical and may imply little retranslocation of root N with senescence, but conflicting evidence from Ca:N ratios highlights the need for further research. These results have practical implications for various ecological methods and for the representation of roots in biogeochemical models.

Key words: C:N:P ratios; calcium; carbon; coniferous vs. broadleaf trees; fine roots; magnesium; nitrogen; nutrient concentrations and retranslocation; phosphorus; potassium.

INTRODUCTION

Fine roots are an important source and sink for nutrients in terrestrial ecosystems. Plants depend on fine roots (<2 mm in diameter) for water and mineral uptake. Across a range of ecosystems, net primary production can be greater belowground than above (e.g., Caldwell 1987), and nutrient concentrations in fine roots may be higher than those in foliage (e.g., Meier et al. 1985) and their life-spans considerably shorter (Vogt et al. 1983). Nutrient release from decomposing roots is a pathway of significant nutrient flux in terrestrial ecosystems (Joslin and Henderson 1987, Fahey et al. 1988). In forests, for example, the amount of carbon and nutrients returned to the soil from fine root turnover may equal or exceed that from leaf litter (Joslin and Henderson 1987, Raich and Nadelhoffer 1989). Minimal retranslocation of nutrients from roots upon senescence may also contribute to the importance of fine roots in nutrient cycling (Aerts 1990, Nambiar and Fife 1991).

Given the relatively short life-spans of fine roots, understanding the relationship between fine root diameter and nutrient contents, and the extent to which nutrients are retranslocated prior to turnover, is important for estimating nutrient cycling in terrestrial ecosystems. In this paper we compile data from the literature to test the generality of an observed inverse relationship between nutrient concentrations and root diameter. We also apply our findings to the important, though unresolved, issue of nutrient retranslocation from fine roots. We consider six essential elements—carbon, nitrogen, phosphorous, potassium, calcium, and magnesium—selecting these elements because of their importance to a range of plant physiological activities and because sufficient data exist for their analysis. We use the term *nutrient* to encompass all six elements, even though carbon is not commonly considered a plant nutrient.

METHODS

To study patterns of nutrient concentrations in fine roots, we examined published accounts for roots ≤5 mm in diameter, building on the database of Jackson

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et al. (1996, 1997). The synthesized studies included data from a range of ecosystems and biomes, including grass, shrub, and tree functional types from temperate, tropical, boreal, and tundra systems. The preponderance of data came from experiments with temperate and coniferous trees. Study sites were a mixture of natural and manipulated ecosystems, including old growth, secondary growth, old fields, and plantations. Data from fertilized systems were excluded, as were results from pot or greenhouse experiments and studies with seedlings. Criteria for inclusion were that each study provide information on root status (i.e., live, dead, or undifferentiated) and that if a range of root sizes were reported (e.g., 1–3 mm, 3–5 mm) the reported range did not exceed 2.5 mm. For information on the 56 studies used for the database and the spreadsheet used in the calculations see the Appendix.

To promote comparability across studies, we adopted additional conventions for analyzing the data. The maximum soil depth sampled in all studies was 1 m, but the vast majority of experiments looked at roots from a single layer ≤30 cm deep; in the few cases where multiple depths were sampled we averaged across depths for a particular study. If data from multiple sites were reported, the data were pooled unless the sites differed in a meaningful way such as soil type, species composition, or climatic variables. Values from stands of different ages were also averaged. To prevent a single study from disproportionately influencing results, no study contributed more than four values to a given analysis.

For the comparisons of nutrient concentrations as a function of root diameter, we used the midpoint of the reported size range as the diameter of the roots for that particular datapoint (e.g., the midpoint from a study that examined roots 0–2 mm in diameter was 1 mm; as noted above, ranges larger than 2.5 mm were not used in the diameter comparisons). The nutrient concentration data are presented in a continuous fashion for all studies as a function of root diameter. We also tested mean nutrient concentrations categorically, comparing data from roots <2 mm in diameter against concentrations in roots 2–5 mm. For some tests the data were broken down into four categories: live, dead, undifferentiated (where authors did not distinguish between live and dead), and total (all data pooled). Separately, we calculated mean nutrient concentrations of dead roots <2 mm in diameter for N, P, K, and Mg (those nutrients with sufficient information) and compared concentrations against live roots in the same diameter class. Finally, we compared root nutrient concentrations for coniferous and broad-leaved trees; live, dead, and undifferentiated data were included in this analysis.

Size effects on root nutrient concentrations were tested with a two-sample Student's *t* test, which assumed unequal variances (Sokal and Rohlf 1981). A conservative Bonferroni adjustment can be made (15 total comparisons, 0.05/15 = 0.003, or instead the more commonly used sequential Bonferroni approach can be applied; see Rice 1989, Saville 1990). We compared: (1) live roots <2 and 2–5 mm in diameter, (2) live and dead roots <2 mm in diameter, and (3) total roots <2 and 2–5 mm in diameter. With the same statistical method we tested the size–nutrient relationship between coniferous and broad-leaved species for roots <2 mm in diameter. The curves shown in all figures were drawn using a least-squares approach and are the best fit based on r^2 values among linear, logarithmic, and exponential functions.

Results and Discussion

There was a significant inverse relationship between root diameter and nutrient concentration for three of the nutrients examined, N, P, and Mg, with no significant differences found for Ca or K (Fig. 1). For the categorical comparison of roots <2 mm and 2–5 mm in diameter, mean nutrient concentrations in live roots were significantly higher in roots <2 mm diameter than in those 2–5 mm in diameter for N, P, and Mg (65–70% higher for N and P; $P \leq 0.005$ in each case) and did not differ for Ca and K ($P \geq 0.25$; Table 1). As expected, roots <2 mm in diameter generally contained higher nutrient concentrations and significantly less C than contained in larger roots ($P < 0.001$), though the data for testing root C concentrations were scarce. The analysis of total roots yielded similar conclusions (Table 1). Comparison of live and dead roots <2 mm in diameter showed no evidence of retranslocation of fine root N (the mean concentration was, if anything, slightly higher in dead roots: 11.1 and 11.5 g/kg in live and dead roots, respectively; $P = 0.41$) (Table 1, Fig. 1). Average P and K concentrations were significantly lower in dead roots <2 mm in diameter compared to live roots (~30% lower; $P < 0.05$; Table 1). Mg concentrations on average were 25% lower in dead roots, but the comparison was not statistically significant (Table 1).

The average C:N ratio of live roots <2 mm in diameter was 43:1, and the C:N:P ratio was 522:12:1. For live roots 2–5 mm in diameter, the C:N and C:N:P ratios were broader, 79:1 and 920:12:1, respectively. Such stoichiometric ratios place useful constraints on ecosystems and their biogeochemistry (e.g., Reiners 1986, Elser et al. 1996). N:P ratios estimated here for fine roots (12:1) are similar to published estimates for leaves and shoots. A review of shoot nutrient concentrations in 696 Australian species across a broad array of habitats yielded an average N:P ratio of 12.5:1 (Foulds 1993). Not only were their nutrient ratios sim-

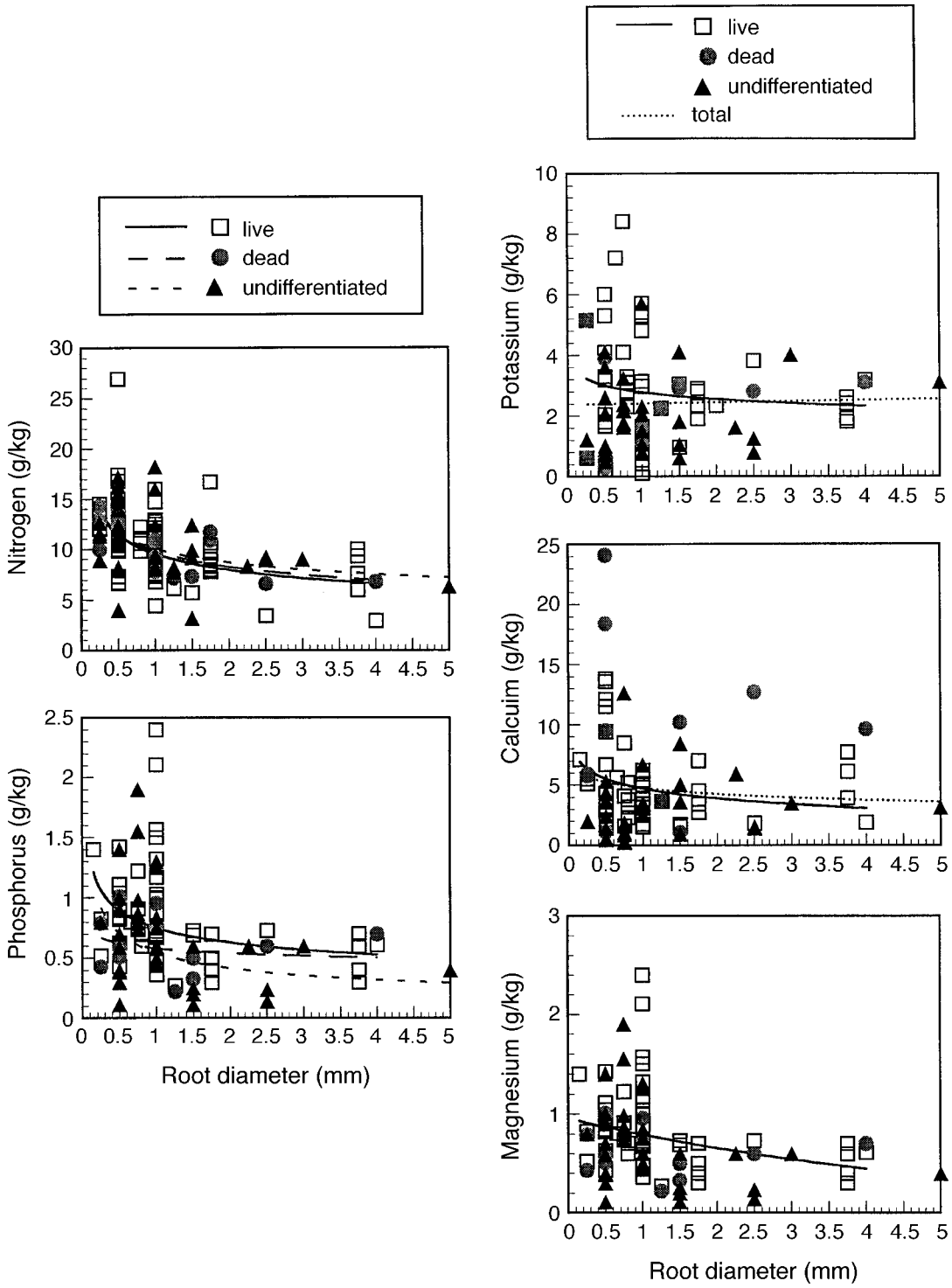

FIG. 1. Root nutrient concentrations (g/kg dry mass) as a function of root diameter (mm) for N (top left), P (bottom left), K (top right), Ca (middle right), and Mg (bottom right) for live, dead, or undifferentiated roots ≤5 mm. ''Total'' refers to the pooled data set (live, dead, and undifferentiated) for each of the three nutrients plotted on the right side of the figure. Best-fit curves determined by least-squares methods are depicted: for N, live ($r^2 = 0.26$, $P < 0.001$), dead ($r^2 = 0.54$, $P < 0.001$), undifferentiated ($r^2 = 0.16$, $P < 0.01$); for P, live ($r^2 = 0.13$, $P < 0.005$), undifferentiated ($r^2 = 0.11$, $P < 0.05$); and for Mg, live ($r^2 = 0.22$, $P < 0.001$). Other curves depicted show the best fit to the observed data but are not significant ($P > 0.05$).

TABLE 1. Nutrient concentration by dry mass for N, P, K, Ca, Mg, and C (mean, 1 SE, and *n*).

Nutrient	Root status	Roots < 2mm diameter: Nutrient concentration (g/kg) mean	1 SE	*n*	Roots 2–5mm diameter: Nutrient concentration (g/kg) mean	1 SE	*n*	*P*
N	live	11.1	0.02	54	6.5	0.12	6	0.005**
	dead	11.5	0.08	13				0.41
	total	11.4	0.04	96	7.2	0.07	12	<0.001***
P	live	0.92	0.007	41	0.56	0.007	6	<0.001***
	dead	0.64	0.019	11				0.008**
	total	0.82	0.005	80	0.50	0.006	12	<0.001***
K	live	2.8	0.03	40	2.6	0.03	6	0.36
	dead	1.7	0.05	11				0.048*
	total	2.6	0.06	79	2.6	0.03	12	0.45
Ca	live	5.0	0.06	40	4.2	0.09	6	0.25
	dead		insufficient data					
	total	4.8	0.05	73	4.8	0.10	12	0.50
Mg	live	1.6	0.02	36	0.6	0.00	6	<0.001***
	dead	1.2	0.03	7				0.18
	total	1.4	0.01	68	1.0	0.01	12	0.02*
C	live	480	0.78	13	515	0.1	2	<0.001***

Notes: The number of points for each calculation refers to individual values from published studies. Root status refers to the condition of root tissue on which nutrient analyses were performed. ''Total'' refers to the pooled data set (live, dead, and undifferentiated) for each nutrient. *P* values are for comparisons of <2 and 2–5 mm (live), live vs. dead (<2 mm), and all roots <2 vs. 2–5 mm (total).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ilar to ours, but absolute concentrations were similar as well. Average shoot concentrations were 10.0 g/kg N and 0.8 g/kg P in the Australian analysis compared to 11.0 g/kg N and 0.9 g/kg P for fine roots (Table 1). Due to the difficulty in harvesting roots, it would be very useful if nutrient concentrations in leaves or shoots could be used as a proxy for nutrient concentrations in roots. Whether this is the case remains uncertain, and differences in root tissue concentrations with different root diameters may complicate any potential relationships. There is some evidence that the very finest roots (e.g., <0.5 mm) may have higher nutrient concentrations than leaves, and that tissue N concentration may be a better indicator of root respiration than is root diameter (Pregitzer et al. 1997, 1998).

Nutrient concentrations in fine roots (<2 mm) of coniferous and broad-leaved trees differed significantly only for Mg (Fig. 2), with the mean Mg content of broad-leaved species higher than in conifers (1.5 and 1.1 g/kg, respectively; $n = 31$; $P < 0.01$; Fig. 2). There was a similar but nonsignificant trend for N (11.8 g/kg, $n = 50$, and 10.8 g/kg, $n = 36$, for broad-leaved and coniferous species; $P = 0.13$; Fig. 2). Neither P, K, nor Ca showed any significant differences (data not shown).

Plants rely on essential nutrients for a variety of functions. Some nutrients are major constituents of all organic material (e.g., C and N), while others serve more specific physiological and biochemical functions such as regulating enzymes (e.g., Ca and Mg) and as enzyme cofactors (e.g., K). Concentrations of C, a key structural element, increased as root diameter increased, but these results were based on a very small sample size ($n = 13$ for the smaller size class, $n = 2$ for the larger). In contrast, an inverse relationship between nutrient concentrations and root diameter was observed for N, P, and Mg. For K and Ca, there was a similar, but nonsignificant trend. It may be that no general relationships exist for K and Ca over the range of diameters examined here, but at least two other explanations are possible. The first is that our sample size may be insufficient to detect statistical differences (six entries in the 2–5 mm size category for Ca and K). A second explanation is that Ca and K may play a greater structural role than we assumed; for instance, Ca is a component of pectins in the cell wall.

As reported in individual studies (Aerts 1990, Nambiar and Fife 1991), we found no evidence for N retranslocation from fine roots, though our results suggest some retranslocation of P and K (30% or so on average). Mean N concentrations were essentially identical in live and dead roots (values were slightly higher in dead roots, 11.5 vs. 11.1 g/kg; ($P = 0.41$), which may reflect random variation or, instead, a trend towards increasing N concentrations, as frequently observed for leaf litter in the initial stages of decomposition (Barnes et al. 1998). To test further whether N retranslocation occurs, we examined Ca:N ratios in roots. Relative to

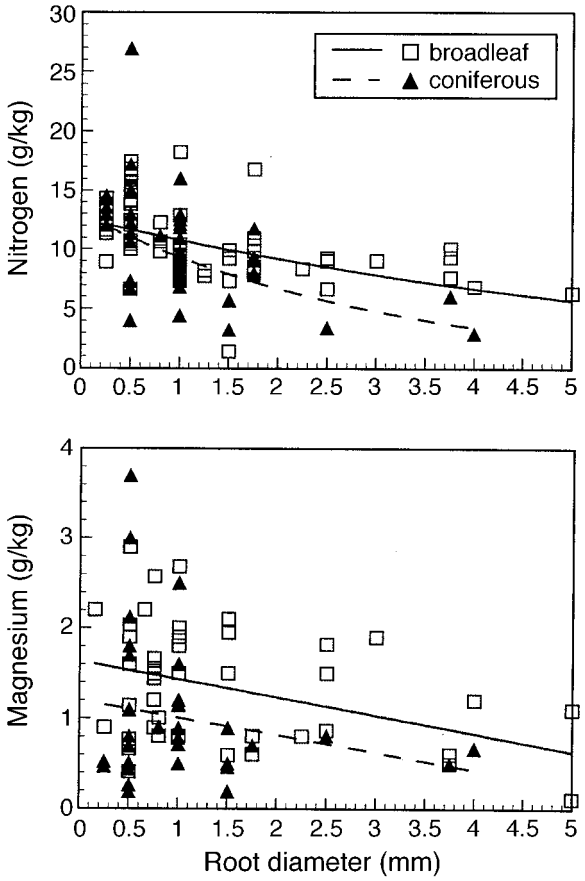

FIG. 2. Root nutrient concentrations (g/kg dry mass) as a function of root diameter (mm) for N (top) and Mg (bottom) for broad-leaved and coniferous roots ≤5 mm in diameter. Total data (for live, dead, and undifferentiated roots) were used. Nutrient concentrations in fine roots (<2 mm) of coniferous and broad-leaved trees differed significantly for Mg, with a higher mean Mg content in roots of broad-leaved species than in roots of coniferous species (1.5 g/kg compared with 1.1 g/kg, $n = 31$ for each; $P < 0.01$). There was a similar but nonsignificant trend for N (11.8 g/kg, $n = 50$, and 10.8 g/kg, $n = 36$, for broad-leaved and coniferous species, respectively; $P = 0.13$).

N, Ca should be less mobile. Thus, if N retranslocation occurs, the Ca:N ratio of dead roots should be higher than that of live roots. By comparing live and dead root data separately across studies for roots <2 mm in diameter, we found that the Ca:N ratio of dead roots was 71% higher on average than that of live roots (0.77 and 0.45, respectively). Data averaged solely from those studies that reported N and Ca concentrations for both live and dead roots ($n = 6$ for each, all roots <2 mm) also showed a shift in the Ca:N ratio from 0.64 (live) to 0.98 (dead), a 53% increase. While these findings suggest that N retranslocation may occur, we are unable to discern from the Ca:N ratios whether the relative increase in Ca (i.e., the implied loss of N and tissue) takes place before or after senescence; such changes could occur before root senescence through retranslocation or after senescence through leaching or decomposition of dead roots.

The topic of nutrient retranslocation from fine roots has remained unresolved for more than a decade (Nambiar 1987). Resorption is a well-established strategy employed by plants to conserve nutrients. Nutrient translocation out of leaves before they are shed can exceed 50% of N and P pools in the leaves (e.g., Chapin and Kedrowski 1983, Killingbeck and Costigan 1988, Scott et al. 1992). Similar data for roots are lacking. Compared to leaves, roots present unique methodological challenges: discerning when a root dies is difficult, and roots lack the abscission zone of leaves. Roots may also be closely associated with other organisms, such as soil biota or symbionts, and differ in their degree of lignification. These and other factors will influence the nutrient content of roots even within the same plant, further complicating an assessment of retranslocation. Experiments are needed in which these variables can be more closely controlled to address the retranslocation question definitively (see Aerts 1990 for one approach).

Studies whose data we included in this paper represented a wide array of biomes, ecosystems, plant functional types, species, and soil types. In spite of the inherent variability, we were able to discern a significant negative relationship between root diameter and nutrient content for N, P, and Mg, the same trend for K and Ca, and a significant positive relationship for C. Despite these general relationships, there are many sources of variation in our analyses, and they may mask important temporal and spatial variation in root nutrient concentrations. The use of size ranges for reporting root nutrient data (i.e., not knowing precise diameters) adds one source of error to the relationships we observed. Local factors may also be important; for example we detected a trend toward decreasing N and P concentrations with depth (data not shown), a result found before in specific studies (e.g., Klinge 1975, Kimmins and Hawkes 1978, Pregitzer et al. 1998). There were also additional comparisons that we hoped to make (e.g., across plant functional types and biomes) where the data were insufficient to draw conclusions with confidence.

The analyses presented here are intended to spur the generation and testing of hypotheses on the role of roots in nutrient cycling. For example, much research has focused on nutrient losses accompanying annual litterfall (e.g., Killingbeck 1996). Further research is needed to determine if the patterns of nutrient retention seen in aboveground tissues also occur in roots. A related topic is the fate of nutrient losses from roots: are

nutrients released from decomposing roots preferentially reabsorbed by plants? What are the mycorrhizal contributions to root nutrient re-acquisition? Finally, root life-span is widely influenced by a host of factors, including seasonality, herbivory, carbohydrate allocation, and nutrient availability (Eissenstat and Yanai 1997). With respect to nutrient contents, there is evidence to support the hypothesis that fine root life-span decreases as N content increases (Hendricks et al. 1993), but more work is needed to address all of the above factors. The modeling of terrestrial nutrient fluxes should benefit from improved estimates of fine root turnover and nutrient contents. Our synthesis of root nutrient concentrations is one step in that process.

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APPENDIX

A list of the 56 studies used for the database and the spreadsheet used in the calculations, with results from each study, are available in ESA's Electronic Data Archive: *Ecological Archives* E081–002.