Nutrient Turnover by Fine Roots in Temperate Hardwood and Softwood Forest Ecosystems Varying in Calcium Availability

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Abstract : The effect of nutrient availability and forest type on the nutrient turnover of fine roots is important in terrestrial nutrient cycling, but it is poorly understood. I measured nutrient turnover of hardwoods and softwoods at three well studied sites in the northeastern US: Sleepers River, VT; Hubbard Brook, NH; Cone Pond, NH. Significant differences in nutrient turnover by fine roots were observed among sites, but not between forest types. The magnitude of differences for each element ranged from 3 times for P and N to 8 times for Ca and Mg between sites. Smaller differences of 0.2 to 0.8 times were observed between forest types. In hardwoods, the Sleepers River 'new' site had 23 kg ha^{-1} yr^{-1} Ca, 7 kg ha^{-1} yr^{-1} Mg, and 16 kg ha^{-1} yr^{-1} K turnover, owing to high root nutrient contents and turnover. Cone Pond had the highest turnover for Mn (0.8 kg ha^{-1} yr^{-1}) and Al (16 kg ha^{-1} yr^{-1}), owing to high nutrient contents. The Hubbard Brook hardwood site exhibited the lowest turnover of these elements. In softwoods, the variation in turnover of Ca, Mg, and K was lower than in hardwoods. The Hubbard Brook had the highest turnover for P (1.6 kg ha^{-1} yr^{-1}), N (31 kg ha^{-1} yr^{-1}), Mn (0.4 kg ha^{-1} yr^{-1}), Al (10 kg ha^{-1} yr^{-1}), Fe (6.4 kg ha^{-1} yr^{-1}), Zn (0.3 kg ha^{-1} yr^{-1}), Cu (34 g ha^{-1} yr^{-1}), and C (1.1 Mg ha^{-1} yr^{-1}). Root Ca turnover exponentially increased as soil percentage Ca saturation increased because of greater root nutrient contents and more rapid turnover at the higher Ca sites. These results imply that nutrient inputs by root turnover significantly increase as soil Ca availability improves in temperate forest ecosystems.

Key words : *fine root biomass, fine root nutrient concentrations, fine root production, fine root turnover, cone pond, hubbard brook, sleepers river*

Introduction

Fine roots play an important role in carbon and nutrient cycling in terrestrial ecosystems (Raich and Nadelhoffer, 1989; Eissenstat and Yanai, 1997; Pregitzer, 2002). Root turnover has been reported to be 26% of N uptake in a northern hardwood forest at Hubbard Brook in New Hampshire (Bormann *et al.*, 1977), 44-55% in oak stands in Wisconsin (Nadelhoffer *et al.*, 1985), 50% in an Engelmann spruce-fir stand at Loch Vale Watershed in Colorado (Arthur and Fahey, 1992), and 58% in a hardwood forest at Walker Branch Watershed in Tennessee (Johnson and Henderson, 1989). In nutrient budgets of these forest ecosystems, nutrient turnover by fine roots has been estimated by differences of other fluxes (Aber *et al.*, 1985; Nadelhoffer and Raich, 1992), but this budget approach is no more accurate than the least certain of the component fluxes.

The contrasting responses for fine root turnover by forest types and nutrient availability have limited the understanding of nutrient cycling in forest ecosystems (Aber *et al.*, 1985). Because root biomass, nutrient concentration, and turnover are notoriously difficult to measure, it would be useful to be able to predict these properties based on forest type and environmental factors. Knowing which of these factors are most important to measure when constructing a nutrient budget for a particular site would also be useful.

Hardwood forests differ from softwood forests in nutrient concentration and nutrient turnover by fine roots. Nitrogen turnover by fine roots in temperate hardwood forests has been reported to be more than twice that of softwood forests and P turnover has been reported to be four times higher in hardwood than softwood forests (Vogt *et al.*, 1986). Fine root longevity of softwood forests is generally greater than that of hardwood forests (Matamala *et al.*, 2003), but nutrient concentrations are lower (Gordon and Jackson, 2000). Therefore, nutrient turnover by fine roots is expected to be higher in hardwood than in softwood forests.

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Environmental factors also affect nutrient turnover in roots. Studies of the effect of acid deposition on forests have focused on aboveground responses (McLaughlin et al., 1993; DeHayes et al., 1999; Tomlinson, 2003). But the loss of base cations from soil induced by acid rain could be expected to affect the nutrient concentrations of fine roots and the rate of fine root turnover. In a sessile oak stand, lime and gypsum fertilizations increased fine root biomass and decreased fine root turnover owing to lower fine root mortality and higher longevity (Bakker, 1999). In Norway spruce (*Picea abies* [L.] Karst.), acid irrigation decreased Ca and Mg concentrations in fine roots, but liming increased root nutrient concentrations of Ca and Mg and reduced concentrations of Mn and Al (Hahn and Marschner, 1998).

The purpose of this study was to measure nutrient turnover by fine roots as a function of forest type and nutrient availability. I selected three sites that differed in base cation status and Ca availability, and measured fine root biomass, chemistry, and turnover in hardwood and softwood stands at each site. I expected nutrient turnover by fine roots to be greatest at the high-Ca site and greater in hardwood than softwood stands because root turnover is higher at the high-Ca site than the low-Ca site and in hardwood than softwood stands.

Materials and Methods

1. Site description

I studied three sites in the northeastern US. These sites were selected to define a calcium gradient: Sleepers River, VT (SR) (highest stream Ca export); Hubbard Brook, NH (HB) (intermediate stream Ca export); and Cone Pond, NH (CP) (lowest stream Ca export) (Table 1). In each of these sites, both softwood and hardwood stands were studied. The SR site had a wide variation in soils, and it was expected that differences within this site would be similar to those across the gradient of sites would be found. Three hardwood stands were studied at SR. One stand, SRp, was on more acidic soil. The stand that was on Ca rich soil, SRr, seemed after initial investigation to be not representative of the site, and a new stand also in Ca rich soil, SRn, was added.

Dominant species are sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt), and white ash (*Fraxinus americana* Ehrh.) at SR, are white birch (*B. papyrifera* Marsh.), red spruce, and balsam fir at HB, and are red spruce, balsam fir, eastern hemlock, American beech, yellow birch, and sugar maple. More detailed description of study sites was reported in a separate paper (Park, 2006).

2. Precipitation inputs and streamwater outputs

Precipitation chemistry was similar across the four sites; pH was 4.3-4.4, and the sum of base cations ranged from 1.8 to 3.2 kg ha^{-1} yr^{-1} (Table 2). In contrast, streamwater chemistry varied dramatically across the sites. The lowest stream pH was 4.4 at CP; at the other extreme, SR had a mean pH of 7.6. These end values

Table 1. Topography and climate characteristics for study sites. The air temperatures shown are the coldest and warmest average months. The air temperature at CP is assumed to be the same as at HB. The precipitation at CP, HB, and SR is the average from 1991 to 1994. For HF, the precipitation is the average from 1985 to 1998.

Site	Location	Latitude	Longitude	Elevation (m)	Watershed area (ha)	Slope (°)	Mean aspect	Air Temperature (°C)	Precipitation (cm yr^{-1})
CP	NH	43°54′	71°36′	481-649	33	24	SE	-9 ~ 19	121
HB	NH	43°56′	71°45′	549-792	13	16	SE	-9 ~ 19	137
SR	VT	44°29′	72°10′	519-686	41	13	SE	-8 ~ 20	125

Table 2. Wet precipitation inputs and streamwater outputs at study sites. The values of precipitation inputs and streamwater outputs were the average of water years October 1991-September 1994 (Hornbeck et al., 1997). N is sum of NH_4^+-N and NO_3^--N. na = not available.

	pH	Ca^{2+}	Mg^{2+}	K^+	Al^{3+}	N	SO_4^{2-}
				kg ha^{-1} yr^{-1}			
Precipitation inputs							
CP	4.3	0.8	0.2	0.8	0.1	6.9	7.8
HB	4.3	1.0	0.3	0.6	0.2	7.6	9.3
SR	4.4	1.6	0.3	1.3	0.1	6.4	7.2
Streamwater outputs							
CP	4.4	3.6	1.0	0.8	4.3	0.2	13.4
HB	5.0	7.1	2.0	1.4	2.6	0.6	13.8
SR	7.6	139.3	6.7	7.9	0.1	1.4	17.1

represent the extremes of stream chemistry in the region (Hornbeck et al.; 1997). Base cations also differed dramatically; SR had 26 times greater export of Ca than CP. Consistent with its low pH, CP had the greatest export of Al.

2. Soil chemistry

At the CP and SR sites, county soil surveys and reconnaissance observations were used to locate one representative sampling pit per stand. Pedons were described using the protocols of the Soil Survey Division Staff (1993) and solum thickness was calculated as the distance from the top of the Oa or A horizon to the top of C horizon.

Soil samples for chemical analysis were collected by genetic horizon, air-dried, and screened to remove particles >2 mm. More detail description for soil collection and chemical analaysis is reported in a separate paper (Park, 2006).

3. Fine root collection and chemical analysis

Roots were sampled in June 2003 from hardwoods and softwoods. In each stand, soil cores were collected from five plots. The plots were chosen haphazardly with the condition that no obstructions (e.g., coarse fragments, large roots) to the depth of coring were encountered. I also avoided the tops and bottoms of recent tip-up mounds. More detail description for fine root collection and root sample processing are reported in a separate paper (Park, 2006).

After washing fine roots with tap water, live fine roots < 2 mm were sorted into three diameter classes delineated at 0.5 and 1.0 mm. Dead roots < 2 mm were distinguished from live roots by resilience, brittleness, and color of bark and xylem. Dead roots were not subdivided by diameter.

Before chemical analysis, roots were forcefully stirred in a plastic container with deionized water for 10 seconds to remove soil and organic particles from the surface of the roots. Nutrient losses during brief washings are not a significant source of error (Böhm, 1979). Washed samples were ground in a Wiley mill using a 1 mm screen.

A subsample was ground using a Wig-L-Bug and analyzed for C and N using a Carbon-Nitrogen elemental analyzer (Model NC2001). Another subsample (1 g) was ashed at 470°C, and then dissolved in 10 ml of 6N HCl. Concentrations of P, K, Ca, Mg, Al, Mn, Fe, Cu, and Zn in the acid solution were determined by inductively coupled plasma emission spectrometer (Perkin Elmer Optima 3300DV ICP-OES).

4. Nutrient turnover

Fine root (<1 mm diameter) dynamics were monitored using the minirhizotron method (Fahey et al., 1999), and root turnover coefficients were calculated as the ratio of the number of new roots observed during the course of the year to the average number of roots growing on the tubes across observation dates (Park, 2006). Nutrient turnover was calculated as the nutrient contents (<1 mm diameter) multiplied by root turnover coefficients.

5. Statistics

Analysis of variance procedures with Tukey's multiple comparison test were used to test the effect of site, root diameter, and forest type on root nutrient concentrations and contents. Regression analysis was used to explore the relationship between root chemistries and soil characteristics.

Results

1. Root nutrient contents

Root nutrient contents varied with site and forest type (Figure 1). Consistent with soil Ca availability, Ca contents were the highest at the Ca-rich SR hardwood sites (SRr and SRn) in all size classes of roots. The "poor" SR site (SRp) was like the other sites (CP and HB) in
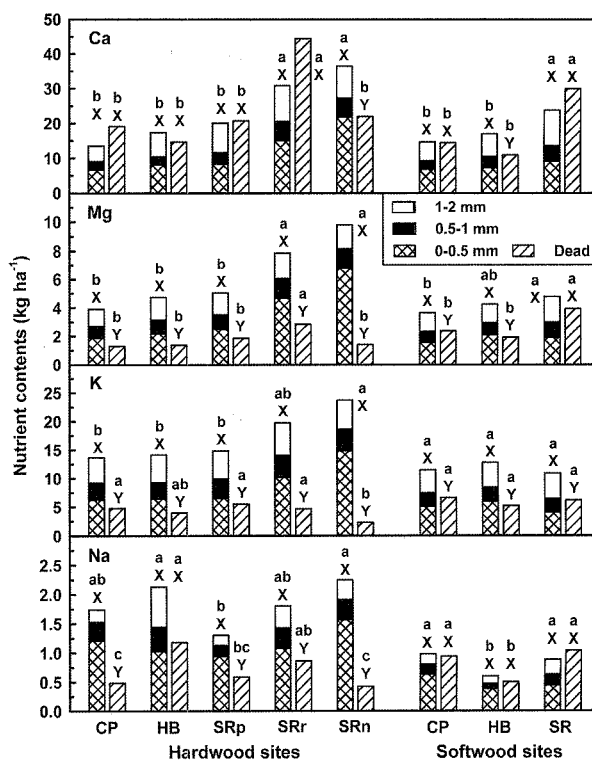

Figure 1. Fine root calcium, magnesium, potassium, and sodium contents in hardwoods and softwoods at CP, HB, and SR in June, 2003. Means sharing the same letter are not significantly different at α = 0.05. Lower case letters denote differences by site within vitality and forest type. Upper case letters denote differences between total live and dead roots within site and forest type.

the Ca contents of roots, confirming that the range of variation within the Sleepers River catchment is as large as the regional gradient I studied. Dead roots, like live roots, had high Ca contents at SRr; but SRn, because of low dead root biomass, did not have particularly high Ca contents in dead roots. Among the softwood sites, the highest Ca contents in both live and dead roots were also found at SR.

Magnesium and K contents of live roots in hardwood sites tended to be highest at SRr and SRn. Magnesium contents of dead roots were the highest at SRr for hardwoods and at SR for softwoods. However, unlike Ca contents, there was no significant effect of site on Mg or K contents of live roots of softwoods. Sodium contents were consistently lower at HB than other study sites in both the live and dead roots of softwoods, but there were no trends in hardwoods.

Phosphorus, N, Zn, and Cu contents of live roots did not differ significantly by site in hardwoods. In softwoods, P and Cu contents were highest at CP; but there were no differences in N and Zn contents (Figure 2 and 3). Dead roots of both hardwoods and softwoods had higher P, N, Zn, and Cu contents at CP or SRp, except for N contents of softwoods, which were not distinguish-

able by site.

As expected, Mn and Al contents were highest at CP and SRp in both live and dead roots of hardwoods. In softwoods, CP had the highest Mn and Al contents of live roots but was not statistically distinguishable from HB (Figure 2 and 3).

Most element contents were higher in live roots (<2 mm diameter) than dead roots (Figure 1-3). Magnesium, K, and Cu contents were significantly higher in live roots than dead roots in both hardwoods and softwoods with the exception of Mg and Cu in softwoods at SR, which can be attributed to the high dead root biomass in this site. Phosphorus, Na, N, and C contents were higher in live roots than dead roots in hardwoods, but there were no statistical differences in softwoods because of the difference of dead root biomass between hardwoods (51% of live roots) and softwoods (112% of live roots). In hardwoods, Mn contents were not different between live roots and dead roots except for low dead root contents at SRn, but Mn contents were higher in live roots than dead roots in softwoods.

Only Al contents were lower in live roots than dead roots in softwoods, but there were no differences in hardwoods except for high Al contents in live roots
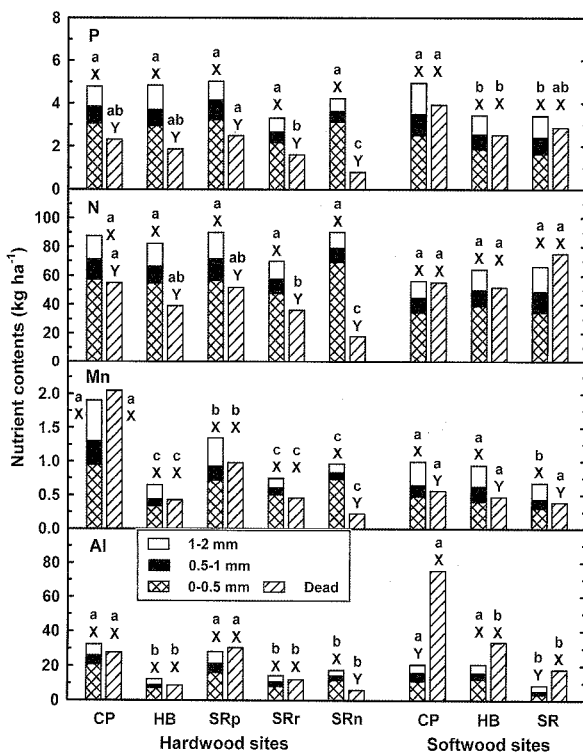

Figure 2. Fine root phosphorus, nitrogen, manganese, and aluminum contents in hardwoods and softwoods at CP, HB, and SR in June, 2003. Means sharing the same letter are not significantly different at α = 0.05. Lower case letters denote differences by site within vitality and forest type. Upper case letters denote differences between total live and dead roots within site and forest type.
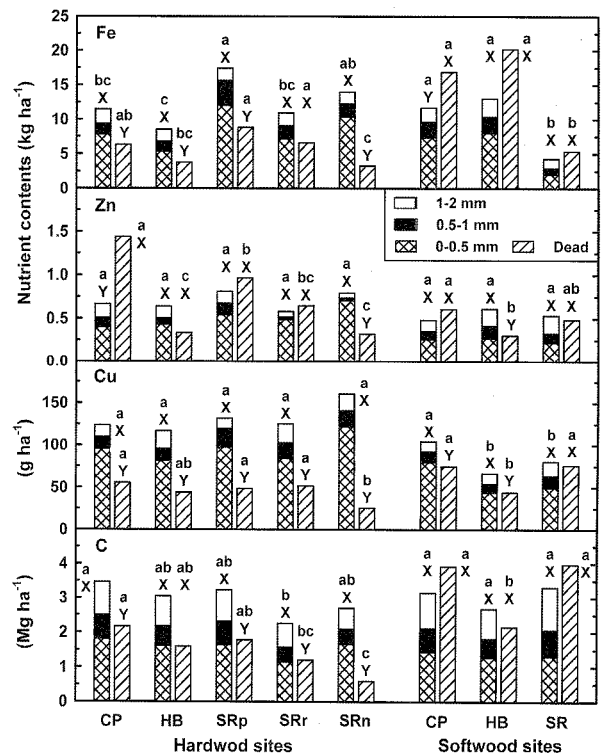

Figure 3. Fine root iron, zinc, cupper, and carbon contents in hardwoods and softwoods at CP, HB, and SR in June, 2003. Means sharing the same letter are not significantly different at α = 0.05. Lower case letters denote differences by site within vitality and forest type. Upper case letters denote differences between total live and dead roots within site and forest type.

owing to very low dead root biomass at SRn. In hard-woods, Fe contents were higher in live roots than dead roots but were lower in softwoods.

Calcium and Zn contents were lower in dead roots than live roots at SRn because of very low dead root biomass at this site (24% of live roots). Other sites didn't show any significant differences with the exception of low Ca and Zn in softwoods at HB.

2. Root nutrient turnover

Patterns across sites in nutrient turnover in roots reflect patterns in biomass, nutrient concentration, and turnover rate (Figure 4-6). Fine root turnover rate (<1 mm in diameter) differed by a factor of two across stands, with three stands having low turnover rates (0.29 and 0.32 yr^{-1} for HB and SRp site in hardwoods and 0.28 yr^{-1} for CP site in softwoods) and five having high turnover rates (0.59, 0.62, and 0.83 yr^{-1} for CP, SRr, and SRn hardwood sites and 0.64 and 0.68 yr^{-1} for HB and SR softwood sites) (Park, 2006).

In hardwoods, SRn had the highest nutrient turnover in most nutrients except for Mn and Al, owing to high turnover coefficients and/or nutrient contents. After SRn, the order of Ca, Mg, and K turnover was SRr > CP > SRp > HB. The SRr sites had both high turnover and high nutrient contents; CP had high turnover but low nutrient contents. SRn had 23 kg ha^{-1} yr^{-1} Ca, 7 kg

ha^{-1} yr^{-1} Mg, and 16 kg ha^{-1} yr^{-1} K turnover, which was approximately six times higher than HB, which had the

Figure 5. Phosphorus, nitrogen, manganese, and aluminum turnover by fine roots (< 1 mm) in hardwoods and softwoods at CP, HB, and SR.

Figure 4. Calcium, magnesium, potassium, and sodium turnover by fine roots (< 1 mm) in hardwoods and softwoods at CP, HB, and SR.
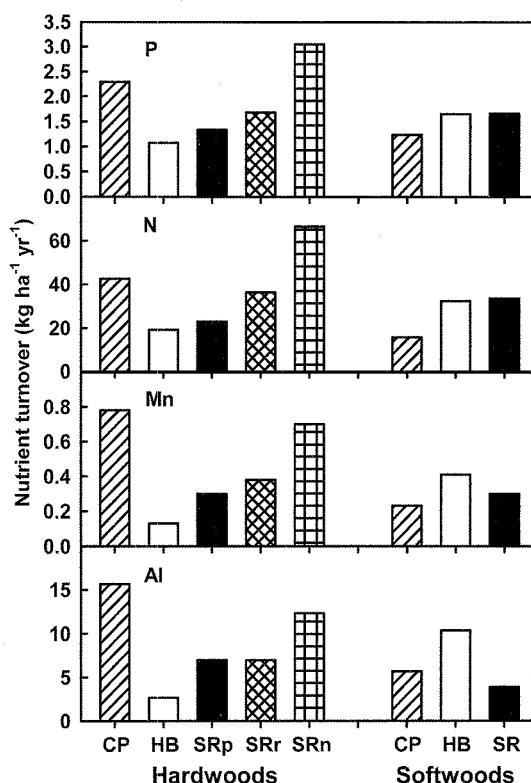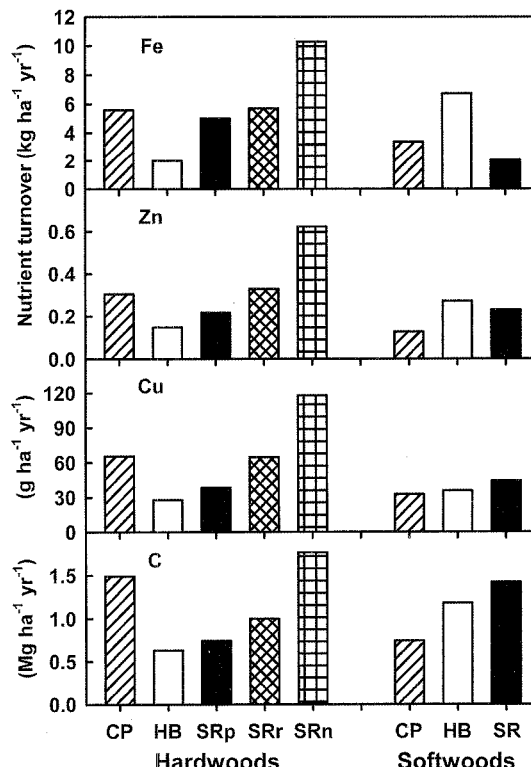

Figure 6. Iron, zinc, cupper, and carbon turnover by fine roots (< 1 mm) in hardwoods and softwoods at CP, HB, and SR.
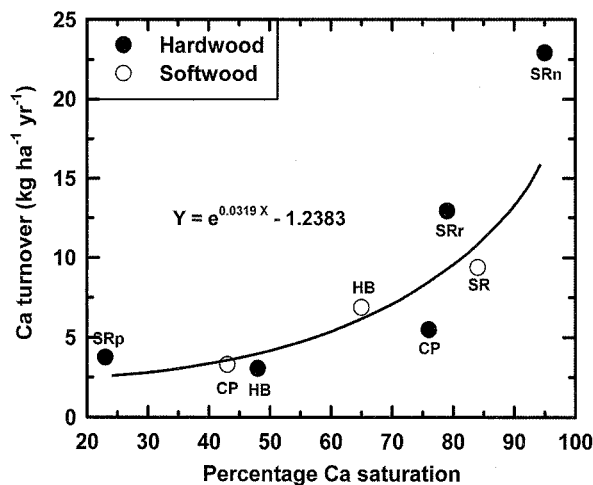
Figure 7. Calcium turnover along a Ca gradient in the top soil in both hardwoods and softwoods at CP, HB, and SR.

lowest nutrient turnover for these nutrients. CP had the highest turnover for Mn (0.8 kg ha^{-1} yr^{-1}) and Al (16 kg ha^{-1} yr^{-1}) because of high nutrient contents. The HB hardwood site had the lowest turnover of most elements because of low turnover coefficient or nutrient contents. Sodium, Fe, Zn, and Cu turnover were high at SRr and CP owing to high turnover coefficients.

In softwoods, the order of turnover for most nutrients was HB > SR > CP because of high turnover coefficients, but HB had similar Ca and Na turnover to SR. HB had 6.6 kg ha^{-1} yr^{-1} Ca, 1.8 kg ha^{-1} yr^{-1} Mg, and 5.3 kg ha^{-1} yr^{-1} K turnover. The difference of magnitude between high and low turnover for Ca, Mg, and K of softwoods was not as much as those of hardwoods. HB had the highest turnover in P (1.6 kg ha^{-1} yr^{-1}), N (31 kg ha^{-1} yr^{-1}), Mn (0.4 kg ha^{-1} yr^{-1}), Al (10 kg ha^{-1} yr^{-1}), Fe (6.4 kg ha^{-1} yr^{-1}), Zn (0.3 kg ha^{-1} yr^{-1}), Cu (34 g ha^{-1} yr^{-1}), and C (1.1 Mg ha^{-1} yr^{-1}). SR had the lowest turnover for Al and Fe because of low nutrient contents; and CP had the lowest turnover for N, Zn, and C because of low turnover coefficients, but there were no differences between CP and SR for P, Mn, and Cu turnover in softwoods.

Root Ca concentrations and contents exponentially increased as soil percentage Ca saturation increased at the top soil layer, but root Ca concentrations was marginally significant ($P = 0.056$). Root Ca turnover also showed exponential increase as soil percentage Ca saturation increased (Figure 7) because of high nutrient contents and nutrient turnover at the high Ca status.

Discussion

I found greater differences in nutrient turnover by fine roots among sites than between forest types. The magnitude of differences between sites for each element ranged from 3 times for P and N to 8 times for Ca and

Mg, but only from 20 to 80% between forest types (Figure 4-6). These results were not surprising because nutrient contents were not significantly different between forest types and root turnover was not consistent within forest type (Park, 2006).

Root turnover of Ca (Likens et al., 1998), K (Likens et al., 1994), and P (Yanai, 1992) recently estimated at Hubbard Brook Experimental Forest was 9, 10, and 14 times more than those estimated by Whittaker et al. (1979) and 3, 2, and 3 times more than ours. The reasons for relatively high nutrient turnover in the recent studies are that Whittaker et al. (1979) underestimated fine root turnover with only 20% of woody-root production.

Recent studies overestimated root turnover by 200% (Tierney and Fahey, 2002) because I used a TC about half of that observed for each site, assuming that a proportion of the fine roots has a longer lifespan than the interval of observation (Park, 2006). I should note the uncertainty in the magnitude of root turnover rates when I compare my nutrient turnover by fine root with other studies. However, my patterns are not sensitive to turnover coefficients among study sites because one factor was applied uniformly to all sites (Park, 2006).

Nitrogen and K turnover by fine roots at my low fertility sites are similar to those of Joslin and Henderson (1987), Van Praag et al. (1988), and Burke and Raynal (1994), but that of my high fertility sites are much higher than those reported in this sentence. Phosphorous and Mg turnover by fine roots are similar to those values reported above with exception of SRn. My values for Ca turnover at sites with high Ca availability are similar to those above, but the values in my low Ca availability sites are much smaller than those referenced above.

Nutrient turnover by fine roots has been reported to account for approximately 37% for P (Yanai, 1992), 53% for K (Likens et al., 1994), and 25% for Ca (Likens et al., 1998) in total nutrient uptake, but based on my estimation, it comprised only 11, 28, and 7% for P, K, and Ca, respectively. These proportions are much smaller than those of Vogt et al. (1983, 1987), Joslin and Henderson (1987), and Burke and Raynal (1994). These differences in estimates of fine root turnover indicate that the importance of root turnover to nutrient budgets differs between studies resulting from differences of the systems studied or the methods used.

One strength of my experimental design was a direct comparison of values between hardwood and softwood stands in adjacent locations, which have reasonably similar soil and climatic conditions. The magnitude of differences among sites in hardwoods was much higher than that of softwoods in all elements: 3 to 8 times for hardwoods and 1 to 3 times for softwoods. I found

greater nutrient turnover in hardwoods than softwoods at CP and SR. However, nutrient turnover at HB was much smaller in hardwoods (about 50% less) than softwoods because of low root turnover coefficient.

Variation in species composition within forest type could complicate the effect of site in this study. Johnson and Henderson (1989) found that watershed level exports did not represent the amount of available nutrients in the active rooting zone, even though Ca^{2+} and Mg^{2+} exports in watershed level were significantly different among sites (Table 2). Species-related differences in nutrient cycling were sufficient to produce significant differences in base-cation contents of the forest floor and mineral soil over short time intervals (Finzi et al., 1998; Fuginuma et al., 2005).

Nitrogen has been shown to be a limiting factor of forest productivity and nutrient turnover by fine roots (Aber et al., 1985; Cole and Rapp, 1981; Pastor et al., 1984; Johnson and Henderson, 1989), but my results show that Ca might be one of the controlling factors for nutrient turnover by fine roots (Figure 7). In my study, N in the soils was not measured, but there was no relationship between soil N and exchangeable Ca^{2+} concentrations in these sites (Ross et al., 2004).

Furthermore, Ca may become a more significant limiting factor for nutrient turnover as well as forest productivity in the northern United States because Ca accumulation in living trees has increased following forest harvesting (Johnson and Henderson, 1989; Arthur et al., 1999), atmospheric Ca deposition has decreased, and base cations leaching has continued due to acid deposition in these regions (Likens et al., 1996, 1998). The variation of nutrient turnover by fine roots across a Ca gradient should be concerned in the nutrient cycling study in forest ecosystems.

Acknowledgements

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