Potential of decaying wood to restore root-available base cations in depleted forest soils

Walter C. Shortle, Kevin T. Smith, Jody Jellison, and Jonathan S. Schilling

Abstract: The depletion of root-available Ca in northern forest soils exposed to decades of increased acid deposition adversely affects forest health and productivity. Laboratory studies indicated the potential of wood-decay fungi to restore lost Ca. This study presents changes in concentration of Ca, Mg, and K in sapwood of red spruce (*Picea rubens* Sarg.), red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), and paper birch (*Betula papyrifera* Marshall) during the decay process at two experimental forests for 12 years and to compare concentrations of exchangeable Ca, Mg, and Al in decayed wood residues at 10 and 12 years with those in the forest floor. Significant loss of mass indicated by decreasing wood density occurred after 2–8 years in conifers and after only 2 years in hardwoods. A significant gain in wood K was observed at 2 years followed by a significant loss at 8 years. A negligible gain in Ca concentration occurred at 2 years and a substantial gain at 8 years. Observed changes in Mg concentration were variable. No significant difference in exchangeable Ca concentration was observed between decayed wood residue of spruce and maple and the forest floor. However, decayed wood residue had a much lower Al concentration and molar Al/Ca ratio, a condition characteristic of sites with high root-available Ca.

Résumé : La diminution du Ca disponible pour les racines dans les sols des forêts nordiques exposées à plusieurs décennies de dépôts acides accrus affecte la santé et la productivité de la forêt. Des études en laboratoire ont montré que les champignons de carie du bois avaient la capacité de restaurer le Ca perdu. Cette étude présente l'évolution de la concentration de Ca, Mg et K dans le bois d'aubier de l'épinette rouge (*Picea rubens* Sarg.), de l'érable rouge (*Acer rubrum* L.), de la pruche du Canada (*Tsuga canadensis* (L.) Carrière) et du bouleau à papier (*Betula papyrifera* Marshall) durant le processus de décomposition dans deux forêts expérimentales pendant 12 ans et compare les concentrations de Ca, Mg et Al échangeables dans les débris ligneux après 10 et 12 ans à celles qu'on retrouve dans la couverture morte. Une perte importante de masse, comme le révèle la diminution de la densité du bois, est survenue après 2 à 8 ans chez les conifères et après seulement deux ans chez les feuillus. Un gain important en K dans le bois a été observé après 2 ans suivi par une perte importante après 8 ans. Un gain négligeable dans la concentration de Ca est survenu après 2 ans suivi d'un gain substantiel après 8 ans. Les changements observés dans la concentration de Mg étaient variables. Aucune différence significative n'a été observée dans la concentration de Ca échangeable entre les débris ligneux cariés d'épinette, d'érable et la couverture morte. Cependant, les débris ligneux cariés avaient une concentration en Al et un rapport molaire Al/Ca beaucoup plus faibles, une situation caractéristique des stations où la disponibilité de Ca pour les racines est élevée.

[Traduit par la Rédaction]

Introduction

Calcium is the fifth most abundant element in the earth's crust. Other than N, Ca is considered the most important essential mineral for managing plant diseases (Rahman and Punja 2007). Calcium is also the fifth most abundant element in trees after H, C, O, and N (Shortle et al. 2008). Calcium is a structural link for wood components, regulates acidity, signals changes in various biological functions, and is needed to form protective layers in wood and bark (McLaughlin and Wimmer 1999). Therefore, living trees require a steady supply of Ca for wood formation and protection. This requirement for Ca is readily met for forests with calcareous soils with high base saturation but may become problematic for soils with a naturally low base saturation.

In the naturally acidic podzolic soils of humid northern forests in the northeastern United States, northern Europe, and the Siberian steppe, essential base cations are in short supply. The rooting zone for uptake of essential elements for these trees is primarily in the organic-enriched forest floor. Podzolization depletes dissolved organic matter and Ca from the rooting zone of naturally acidic forest soils (Ponomareva 1969). Depletion is accelerated by acid deposition resulting from regional emissions of S and N oxides (Shortle and Bondietti 1992). In the soil solution, the S and N oxides occur as strongly acidic anions. These anions tend to mobilize both

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essential base cations (e.g., Ca, Mg, and K) and potentially harmful Al. The mobilized ion pairs tend to leach out of the rooting zone of forest trees. The underlying mineral soil and parent material contain Al in an essentially inexhaustible supply. Mobilized Al may be directly toxic to the root system and at lower concentrations tends to displace essential Ca from ion-exchange sites in soil organic matter (Lawrence et al. 1995). Although small quantities of Al enter the roots and the tree transpiration stream, generally as organic chelates, Al is largely precipitated out of solution in the fine root cortex due to the decreased acidity relative to soil (Schröder et al. 1988). Consequently, Al concentrations in wood are generally very low. Declines in stem growth and increased mortality due to Ca depletion followed by Al mobilization have been documented in spruce (Shortle and Smith 1988; Shortle et al. 1997) and maple (Long et al. 2009).

As trees die and woody parts are shed or broken, wood is added to the forest floor. Root-available Ca may be replenished at Ca-depleted sites by the action of wood-decay fungi. These fungi utilize the solar energy stored in cellulose and lignin (the two most abundant organic substances in nature) to enrich the decaying residue with Ca from external sources. An analogous process occurs with bark residue, which was not investigated in this report. Microcosm tests demonstrated movement of Ca into decaying wood of conifers (Ostrofsky et al. 1997; Connolly et al. 1999) and hardwoods (Clinton et al. 2009). Fungi that decompose wood are often large, long-lived organisms that produce extensive mycelial networks, including cords and rhizomorphs, which move essential elements for many metres through the forest floor in and out of decaying wood (Boddy and Watkinson 1995; Connolly and Jellison 1997; Lindahl et al. 2001). The presence of the common wood-decaying cord-forming fungus *Hypholoma lateritium* (Schaeff.) P. Kumm. 1871 in contiguous mineral soil, forest floor, and decaying logs suggests that the translocation of elements may be vertical through the soil profile as well as horizontal through the forest floor (Thompson et al. 2012). Although commonly regarded as microorganisms, the dominant wood-decay fungi in forest ecosystems are anything but "micro".

Previous research using a budgeting approach questioned the impact of coarse woody material on forest cation nutrition due to it comprising a small portion of the total ecosystem pool for essential cations (Arthur et al. 1993; Laiho and Prescott 2004). In our alternative conceptual approach, the physiological availability and flow of essential cations and their potential antagonists could have a role not identified by total pools in an element budget. The objective of this research was to follow the dynamics of essential base cation concentration during the first 10–12 years of the wood-decay process for several conifer and broad-leaved species at two northern forest locations. A smaller analysis was also conducted for wood after 19–24 years of decay, which could also be considered as part of the formation process of the organic forest floor.

Materials and methods

This report was developed from long-term field studies established in New Hampshire at the Bartlett Experimental Forest (BEF) in 1995 and in Maine at the Penobscot Experimental Forest (PEF) in 1996 and 1997 to determine the dynamics of Ca, Mg, and K in wood undergoing the wood-decay process. Wood samples in progressive stages of decay from these studies have been archived and are available for further study of biological processes of decay.

The tree species selected for study were red spruce (*Picea rubens* Sarg.) and red maple (*Acer rubrum* L.) at PEF and BEF and eastern hemlock (*Tsuga canadensis* (L.) Carrière) and paper birch (*Betula papyrifera* Marshall) at PEF. For each combination of location and species, 20 trees in a dominant or codominant position and 15–45 cm diameter at 1.3 m above ground were selected and felled. Time-zero reference disks, 5 cm thick, were cut from all felled stems at 3 and 7 m above the stumps. Small soil pits were dug next to the intervening 4 m bolt and samples of forest floor were collected. The position of each decaying stem section was mapped for future reference. Decaying wood of the 4 m bolt was taken at 2 year intervals (0–12 years) by first removing a 10 cm thick "cleaning" disk from the exposed lower end followed by removing a 5 cm thick sample disk for chemical analysis.

Wood sample disks (5 cm thick) were placed in labeled paper bags, air-dried at room temperature, and oven-dried at 90 °C for 48 h. Rectangular prism blocks were split from the sapwood (2.5–5.0 cm inward from the vascular cambium) of dried sample disks from a position 90° around the stem from the point of soil contact. Sapwood was selected for chemical analysis to reduce sources of variation in within- and between-species comparisons. For samples collected through 8 years of ground contact, the volume of each block was calculated from the mean of four measurements of each dimension (longitudinal, radial, and tangential) and weighed (±1 mg). Density ($g \cdot cm^{-3}$) was calculated as the mass to volume ratio. Blocks were chiseled into small pieces and ground in a Wiley mill (Thomas Scientific, Swedesboro, New Jersey) to pass a 1 mm mesh. After 10 or more years of ground contact, the sample bolts had lost sufficient structural integrity to make impractical the collection and measurement of sample blocks. Friable samples were split and scooped from sample disks and milled as described for the chiseled blocks. One gram portions of milled wood powder were ashed for 6 h at 550 °C, cooled, dissolved in 3 mL of 6 $mol \cdot L^{-1}$ HCl, and brought to a volume of 50 mL with deionized water. Concentrations of Ca, Mg, and K in ash solutions, analytical standards, and blanks were measured by inductively coupled plasma – optical emission spectroscopy (ICP-OES model 750; Thermo Jarrell Ash Corp., Franklin, Massachusetts).

Element concentrations determined by inductively coupled plasma – optical emission spectroscopy were converted from parts per million to $mmol \cdot kg^{-1}$ by dividing parts per million by the relative atomic mass. For each set of wood samples taken at 2 year intervals the mean concentration per unit mass and 95% confidence intervals of replicate samples were determined to present the temporal pattern of changing base cation concentrations. To compare wood samples on a constant volume basis ($mol \cdot m^{-3}$), the mass-based concentrations ($mmol \cdot kg^{-1}$) were multiplied by the wood density ($g \cdot cm^{-3}$). Significant differences between concentrations per unit volume at the incipient (2 year) and advanced (8 year) stage of decay and the initial concentration at time zero were indicated by the paired t test ($P < 0.05$). When fragmentation

Table 1. Mean density and range of decaying red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), red maple (*Acer rubrum*), and paper birch (*Betula papyrifera*) wood (standard deviation in parentheses, n = 18–20) at Bartlett Experimental Forest (BEF) in New Hampshire and Penobscot Experimental Forest (PEF) in Maine.

			Density, g·cm^{-3}				
Species	Location		0 years	2 years	4 years	6 years	8 years
Spruce	BEF	Mean	0.47 (0.06)	0.47 (0.05)	0.42 (0.04)	0.43 (0.06)	0.40 (0.08)
		Range	0.40–0.65	0.40–0.56	0.35–0.51	0.27–0.55	0.24–0.54
Spruce	PEF	Mean	0.42 (0.05)	0.42 (0.07)	0.38 (0.08)	0.39 (0.11)	0.34 (0.07)
		Range	0.37–0.55	0.31–0.61	0.25–0.50	0.17–0.60	0.20–0.46
Hemlock	PEF	Mean	0.43 (0.04)	0.38 (0.04)	0.39 (0.05)	0.35 (0.08)	0.33 (0.05)
		Range	0.35–0.49	0.33–0.45	0.27–0.47	0.20–0.52	0.21–0.41
Maple	BEF	Mean	0.59 (0.05)	0.55 (0.07)	0.45 (0.06)	0.41 (0.12)	0.39 (0.13)
		Range	0.51–0.72	0.37–0.64	0.32–0.59	0.24–0.59	0.17–0.62
Maple	PEF	Mean	0.53 (0.03)	0.45 (0.06)	0.35 (0.08)	0.26 (0.08)	0.18 (0.06)
		Range	0.48–0.61	0.32–0.59	0.24–0.54	0.15–0.44	0.08–0.31
Birch	PEF	Mean	0.59 (0.04)	0.44 (0.04)	0.33 (0.07)	0.33 (0.12)	0.37 (0.11)
		Range	0.52–0.68	0.37–0.52	0.24–0.48	0.11–0.52	0.22–0.62

Table 2. Percent change from initial red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), red maple (*Acer rubrum*), and paper birch (*Betula papyrifera*) sapwood element concentrations at Bartlett Experimental Forest (BEF) in New Hampshire and Penobscot Experimental Forest (PEF) in Maine (significant differences by paired t test, n = 18–20: $^{**}P < 0.01$; $^{*}P < 0.05$; ns, not significant).

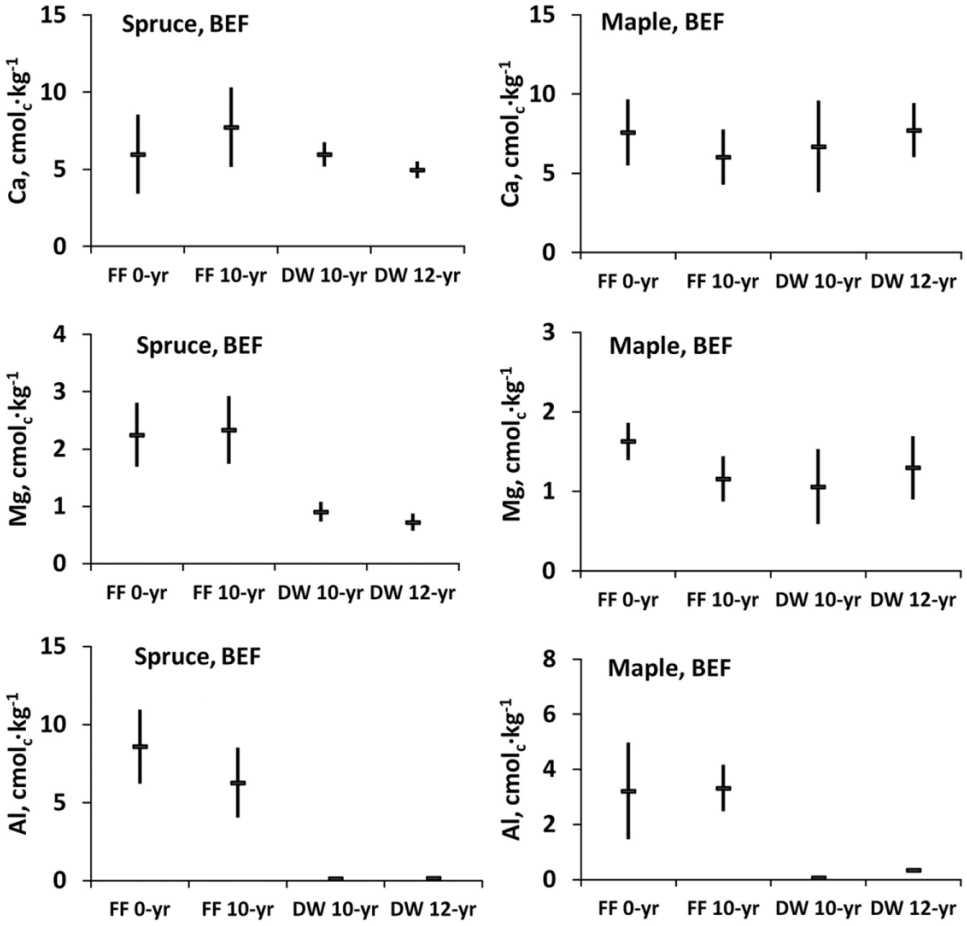
			After 2 years		After 8 years	
Element	Species	Location	Mass	Volume	Mass	Volume
K	Spruce	BEF	+44**	+44**	–35**	–46**
		PEF	+69**	+59**	–75**	–81**
	Hemlock	PEF	+119**	+92**	–8 ns	–27 ns
	Maple	BEF	+29**	+19*	–23 ns	–56**
		PEF	+26**	+6 ns	–64**	–87**
	Birch	PEF	+191**	+114**	–65**	–76**
Ca	Spruce	BEF	+15 ns	+14 ns	+129**	+90**
		PEF	+28 ns	+18 ns	+190**	+106**
	Hemlock	PEF	+14*	+2 ns	+94**	+48**
	Maple	BEF	+25**	+16**	+120**	+34**
		PEF	+3 ns	–13**	+528**	+107**
	Birch	PEF	+48**	+9 ns	+214**	+86**
Mg	Spruce	BEF	+23 ns	+24 ns	–7 ns	–23*
		PEF	+65**	+56**	+57**	+11 ns
	Hemlock	PEF	+29**	+14 ns	+31 ns	–3 ns
	Maple	BEF	–6 ns	–12*	–14 ns	–43**
		PEF	–19**	–32**	+240**	+15 ns
	Birch	PEF	+43**	+6 ns	+87**	+22 ns

after 8 years did not allow for volume determination and density calculation, concentrations in decayed wood were compared with those in the forest floor at time zero and 10 years. Significant differences in concentrations of exchangeable K, Ca, Mg, and Al ($cmol_c \cdot kg^{-1}$) for the forest floor at 0 and 10 years and decayed wood at 10 and 12 years were indicated using the overlap rules for 95% confidence intervals (Cumming et al. 2007).

Forest floor samples were taken from small soil pits (dug down into the upper 15 cm of the underlying mineral soil) next to stem sections in ground contact at the time of felling (0 year) and 10 years after felling. Samples of the forest floor were placed in quart freezer bags and air-dried before sieving and analysis. The 0 and 10 year soil samples taken for spruce and maple at BEF and for maple and birch at PEF were analyzed using an suite of protocols approved by the US Environmental Protection Agency for forest soil analysis (including Ca, K, Mg, and Al) in the US Environmental Protection Agency certified Analytical Laboratory at the University of Maine, Orono. The same protocol was applied to 10 and 12 year decayed wood residues to compare element concentrations in the forest floor with those in decaying wood.

In addition to decayed spruce wood at PEF and BEF, decayed spruce wood with longer periods of ground contact in Maine was available from earlier studies (Connolly 1996). Decayed wood was taken from five decaying spruce logs at Howland, Maine (19 years), and at Kossuth, Maine (19 and 24 years), air-dried, oven-dried, and analyzed by the same

Fig. 1. Mean exchangeable Ca, Mg, and Al concentrations and 95% confidence intervals ($n = 20$) of the forest floor (FF) at the 0 and 10 year sampling interval and of decayed sapwood residue (DW) of red spruce (*Picea rubens*) and red maple (*Acer rubrum*) after 10 and 12 years in ground contact at Bartlett Experimental Forest, New Hampshire.



standard protocols for plant tissues and forest soils at the US Environmental Protection Agency certified Analytical Laboratory, University of Maine, Orono. Soil data from the same area as the decaying wood at Howland and Kossuth were available from 1993 (David and Lawrence 1996) and 2004. Soil analysis of the 2004 sampling was done by standard protocols at the US Geological Survey Laboratory, Troy, New York.

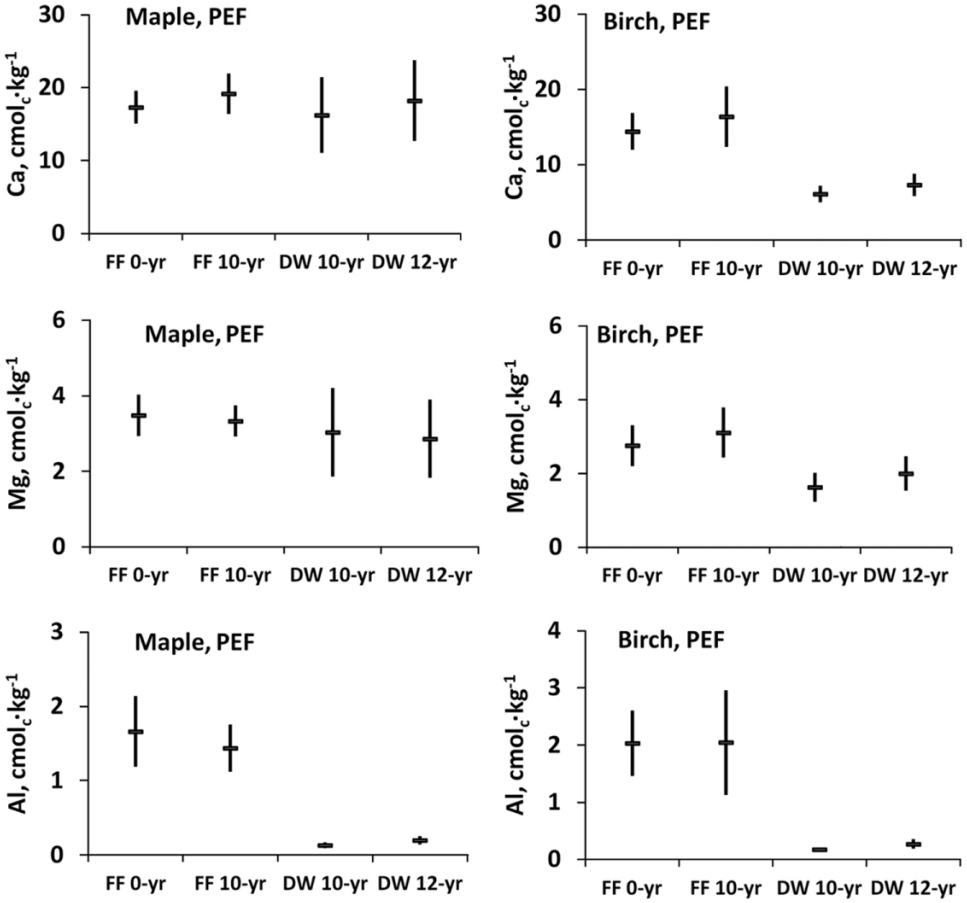
Ionically bound, exchangeable Ca of decayed wood at 19 years from Howland and Kossuth and sound wood at 0 years from the same sites was extracted by freeze–thawing using 30 mg of wood in 6 mL of 10 mmol·L^{-1} HCl (Minocha and Shortle 1993). Element concentration in the extract was determined by inductively coupled plasma – atomic emission spectroscopy (Varian Vista CCD, Palo Alto, California). The cation-binding capacity (cation-exchange capacity) for the same samples was determined by saturation with 10 mmol·L^{-1} $CaCl_2$ in acetate buffer, pH 5.5, at 121 °C for 20 min using 40 mg wood samples in 5 mL of $CaCl_2$ solution. After cooling to room temperature, the Ca-saturated wood was recovered on Whatman No. 541 filter paper in a Buchner funnel under suction and rinsed three times with 20 mL deionized water. The wood and filter paper were placed in aluminum pans and oven-dried overnight at 70 °C. The Ca concentration of the saturated wood was then determined by the same freeze–thaw procedure used for the unsaturated wood samples.

Results

Sapwood density decreased with high sample variability as wood decay progressed over the first 8 years of ground contact (Table 1). After 2 years, no significant decrease in density occurred in spruce, but significant decreases ($P < 0.05$, $n = 18$–20) averaging 6%–25% did occur in hemlock, maple, and birch. After 8 years, significant decreases in density ($P < 0.01$, $n = 18$–20) averaging 16%–22% occurred in spruce and hemlock and 33%–66% in maple and birch. Even after 8 years, some stem sections had a density equivalent to the initial sound wood, while other samples had decreased by more than 50% within 4–6 years. Decayed wood with a density below 0.1–0.2 g·cm^{-3} was readily fragmented and no longer allowed for accurate volume measurement. Although no floristic analysis was attempted, corticioid and stereaceous fungi were frequently found on the decaying logs as well as various gilled and poroid forms on both the wood and adjacent soil.

After 2 years in ground contact, K concentrations of decaying sapwood increased significantly per unit mass in all cases and per unit volume, except in maple at PEF (Table 2). The overall increase in K concentration after 2 years was 72% per unit mass and 48% per unit volume and both increases were highly significant ($P < 0.001$, $n = 116$–119). After 8 years, K concentration decreased significantly per

Fig. 2. Mean exchangeable Ca, Mg, and Al concentrations and 95% confidence intervals ($n = 20$) of the forest floor (FF) at the 0 and 10 year sampling interval and of decayed sapwood residue (DW) of red maple (*Acer rubrum*) and paper birch (*Betula papyrifera*) after 10 and 12 years in ground contact at Penobscot Experimental Forest, Maine.



unit mass relative to the initial concentration, except in hemlock and maple at BEF, and per unit volume in all cases except hemlock (Table 2). The overall decrease in K concentration after 8 years was 43% per unit mass and 63% per unit volume and both decreases were highly significant ($P < 0.001$).

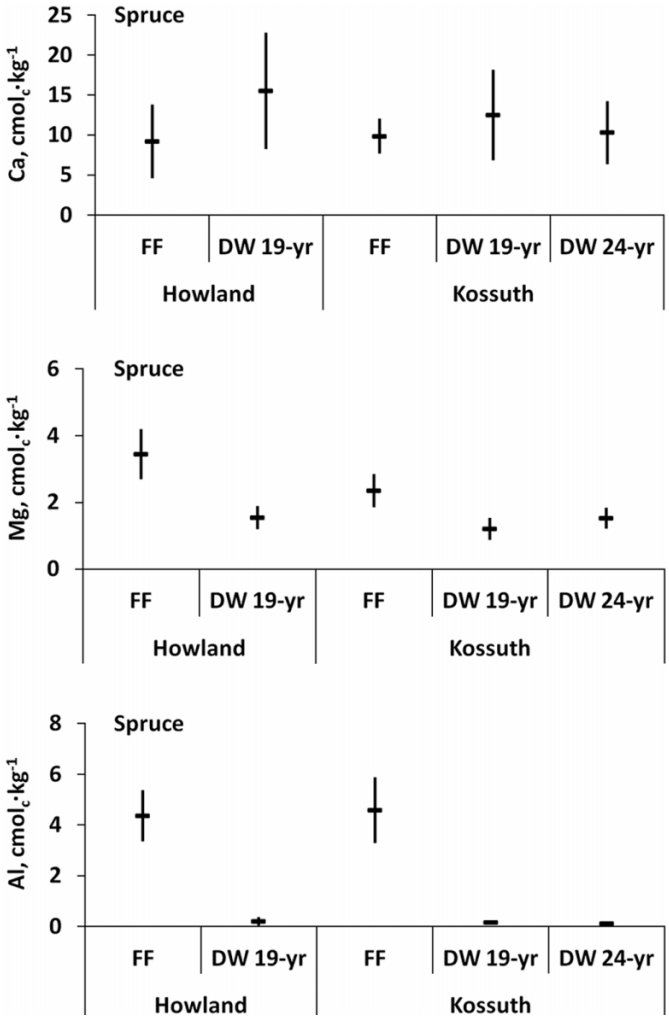
After 2 years in ground contact, Ca concentrations did not change significantly or had small increases per unit mass and generally no change per unit volume with a small decrease in maple at PEF (Table 2). The overall change in Ca concentration per unit mass after 2 years was an increase of 21% ($P < 0.001$, $n = 112$–114) and an increase of 8% ($P < 0.05$) per unit volume. After 8 years, Ca concentration increased significantly per unit mass and volume relative to the initial Ca concentration in all cases (Table 2). The overall increase in Ca concentration after 8 years was 209% per unit mass and 78% per unit volume and both the threefold increase per unit mass and nearly doubling per unit volume were highly significant ($P < 0.001$).

After 2 years in ground contact, Mg concentration per unit mass increased significantly in three cases, decreased significantly in one case, and did not change significantly in two cases with an overall increase per unit mass of 21% ($P < 0.001$, $n = 113$–114) but no significant change on a volume basis (Table 2). After 8 years, Mg concentration per unit mass increased significantly in three cases and did not change significantly in three cases relative to the initial Mg concentration with an overall increase of 76% (mostly attributed to a large increase in maple at PEF) ($P < 0.001$) per unit mass but no significant change on a volume basis.

After 10 and 12 years of decay in ground contact, when determination of molar concentrations of essential base cations could no longer be expressed on a volume basis, the concentration of exchangeable Ca and Mg of decaying wood was compared with the concentration in the forest floor (Figs. 1, 2, and 3). Exchangeable Ca concentrations of decayed wood of spruce and maple at 10 and 12 years and the forest floor at 0 and 10 years did not differ significantly as indicated by overlapping 95% confidence intervals (Figs. 1, 2, and 3), but decayed wood of birch had a significantly lower concentration as indicated by no overlap of confidence intervals (Fig. 2). Exchangeable Mg concentrations of decayed wood of maple and the forest floor did not differ significantly, but decayed wood of spruce and birch had a significantly lower concentration. Exchangeable Al concentrations of decayed wood was significantly and substantially less than in the forest floor. After 10–12 years of ground contact, Al/Ca ratios in decaying wood were generally between 0.01 and 0.03 in wood and between 0.6 and 2.6 in the adjoining forest floor.

Exchangeable Ca concentrations of decayed spruce wood after 19 years of decay in ground contact at Howland and Kossuth and after 24 years at Kossuth did not differ signifi-

Fig. 3. Mean exchangeable Ca, Mg, and Al concentrations and 95% confidence intervals (soil: $n = 10$, wood: $n = 5$) of the forest floor (FF) at Howland and Kossuth, Maine, in 2004 and of decayed sapwood residue (DW) of red spruce (*Picea rubens*) after 19 and 24 years of decay in ground contact.



cantly from those in the forest floor (Fig. 3) as in the case of 10 and 12 years of decay at BEF and PEF (Figs. 1 and 2). Exchangeable Mg and Al concentrations of decayed wood were significantly lower than those in the forest floor as at BEF and PEF.

After 19 years of ground contact, decayed wood residue of spruce at Howland and Kossuth had a significant five- to sixfold increase in exchangeable Ca and a fourfold increase in cation-binding capacity (Fig. 4). The concentrations for Ca in Fig. 4 are greater than in Fig. 3 due to differences in the method of base cation extraction. Freeze–thawing in 10 mmol·L^{-1} HCl (Fig. 4) mobilizes 20%–25% more Ca than 30 min exposure to 1 mol·L^{-1} NH_4Cl (Fig. 3) due to the greater activity of the dilute acid than of the neutral salt.

Decayed stem sections of all species were penetrated with fine absorbing roots and mycelial cords (Fig. 5). The same colonization by roots and mycelial cords was observed in decayed wood of all sizes, including shed branches and dead roots. Feeder roots of trees were abundant down through the forest floor and less so in the underlying mineral soil.

Discussion

In a preliminary report of decay over the first 6–8 years of this study (Smith et al. 2007), mean density loss was essentially linear for this time period with the sapwood of hardwoods maple and birch decaying faster than that of the conifers spruce and hemlock. However, there was considerable variability in the rate of decreasing mass per unit volume estimated as dry density (a conservative estimate of mass loss due to greater shrinkage of volume as decay progressed) (Table 1). A 50% loss of mass per unit volume took 6–8 years in conifers and 4–6 years in hardwoods in some logs, while others remained essentially sound over the same period (see range, Table 1). This variation was consistent with variation caused by multiple species of fungi in laboratory decay tests. Spruce wood decayed by nine different wood-decay fungi for 8 months had a range of mass loss of 2%–69% with an average of 28% ± 20% (Ostrofsky et al. 1997); southern beech wood decayed by 12 different wood-decay fungi for 4 months had a range of mass loss of 0%–90% with an average of 35% ± 22% (Clinton et al. 2009).

Variation due to differences in wood-preserving substances, which causes widely different decay rates of heartwood among tree species, was eliminated by using sapwood. Variation due to environmental conditions could affect initial infection and colonization of decay fungi in sapwood. However, such effects would likely diminish under longer periods of ground contact and have a minor contribution to variation in decay rates once the wood-decay fungi and associated microorganisms have colonized the wood. For example, wide differences in initial moisture content had no effect on the rate of decay of spruce (conifer) and sweetgum (hardwood) sapwood under laboratory conditions (Peterson and Cowling 1973). Therefore, we suggest that most of the variation in mass loss may be due to variation in the species of decay fungi, as supported by the variety of fruiting bodies observed on the decaying stem sections during this study.

During the first 8 years in ground contact when decaying wood passed from the incipient stage (mass loss less than 15%) at 2 years to the advanced stage (mass loss up to 50% or more) at 8 years, concentrations of the essential base cations K, Ca, and Mg were compared using the initial sound state as a point of reference. After 8 years as the wood in an advanced stage of decay became fragmented, the reference point was changed from the initial sound wood to the forest floor into which the fragments of decayed wood were being incorporated. These comparisons of exchangeable Ca, Mg, and Al between the fragmenting decayed wood and the forest floor indicated the potential for enrichment within the first few decades after tree death and decay.

During the incipient stage of wood decay after 2 years in ground contact, K enrichment occurred relative to the initial concentration in sapwood (Table 2). After this initial gain, K concentration decreased to a net loss in the advanced stage of decay after 8 years (Table 2). During the initial stage of decay, wood becomes ionized and the concentration of K^+ increases rapidly causing a decrease in electrical resistance (Shortle 1982; Shortle and Smith 1987). After this initial increase, K was removed, presumably by the activity of cord-forming, wood-decaying fungi that have been shown to move K, a highly mobile, essential base cation, in and out of

Fig. 4. Mean exchangeable Ca concentration and mean cation-exchange capacity (CEC) with 95% confidence intervals (n = 5) of red spruce (*Picea rubens*) sapwood at felling (0 year) and after 19 years of decay in ground contact at Howland and Kossuth, Maine.

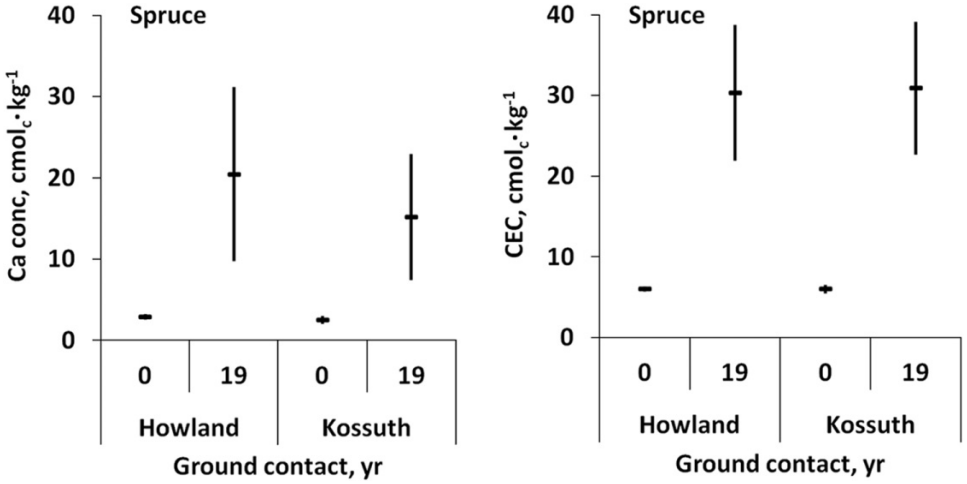


Fig. 5. Decayed red spruce (*Picea rubens*) stem section penetrated by fine roots, mycelium, and mycelia cords (inset) after 12 years in ground contact.

decaying wood along with other essential elements, N and P (Boddy and Watkinson 1995; Connolly and Jellison 1997; Lindahl et al. 2001).

Magnesium enrichment occurred along with K enrichment in three of six cases during the incipient phase of wood decay after 2 years in ground contact, but in the other three cases, Mg remained unchanged or was lost (Table 2). This pattern of gains and losses for Mg continued into the advanced stage of decay after 8 years and is expected as large cord-forming wood-decaying fungi move Mg in and out of decayed wood along with N, P, and K.

Calcium enrichment was negligible during incipient decay after 2 years but was substantial during advanced decay after 8 years in ground contact, averaging nearly a doubling of the initial concentration per unit volume (Table 2). After 8 years, wood in an advanced state of decay had become removed by animal activity. This was especially evident for birch at PEF where density appeared to remain constant after 4 years, while that of maple continued to decline (Table 1). Removal of decayed wood by wood-inhabiting arthropods and their predators left less-decayed wood available for sampling. The wood fragments or their digestion products then become in-

corporated into the forest floor. The presence and proximity of deposited wood have been demonstrated to affect invertebrate communities of the forest floor (Evans et al. 2003).

The source of K added to wood early in the decay process and of Ca and Mg added thereafter is not known. However, bioweathering of mineral sources is known to occur by a wide variety of fungi (Hoffland et al. 2004; Finlay et al. 2009) and has been demonstrated for a fungus decaying spruce wood in a microcosm (Connolly et al. 1999). Atmospheric deposition is another potential source for enhanced element concentrations in decay fungi as demonstrated for N (Watkinson et al. 2006) and heavy metals (Gabriel et al. 1997). Bark to the outside and heartwood to the inside of sapwood were not considered sources of base cations for decaying sapwood because all three tissues increase in cation concentration in laboratory decay tests, although at different rates of cation increase and structural breakdown.

Wood-decay fungi produce fruiting bodies rich in N, P, and K on decaying logs with concentrations as much as 38, 115, and 136 times, respectively, greater than in the logs on which they are found (Harmon et al. 1994). No such large differences between fungal tissue and decaying logs were observed for Ca by Harmon et al. (1994). Unlike the macroelements N, P, K, and Mg needed for the growth and development of all fungi, Ca is a microelement for fungi with only trace amounts needed for growth (Griffin 1994). Consequently, wood-decay fungi do not take up and sequester large amounts of Ca, leaving Ca in the decayed wood residue to be incorporated into the forest floor. In contrast with the wood-decay fungi, forest trees require Ca as a dominant macronutrient, the requirement for which is only exceeded by N (Young et al. 1965).

The exchangeable Ca of decayed wood residue of spruce and maple after 10 and 12 years in ground contact was equivalent to that of the forest floor (Figs. 1 and 2) as was that of spruce after 19 and 24 years (Fig. 3). The lower concentration in birch after 10 and 12 years (Fig. 2) is attributed to the removal of some of the advanced decayed wood by animal activity. Exchangeable Mg of decayed wood was less than that of the forest floor in spruce but equivalent in maple. As in the earlier stages of decay, Mg has greater mobility than Ca in soils. Exchangeable Al is much lower in decayed wood than in the forest floor, which overlies the mineral soil from which Al can be mobilized by increased acidity (Lawrence et al. 1995, 2005).

Decayed spruce wood after 19 years of soil contact increased five- to sixfold in ionically bound Ca and fourfold in cation-binding capacity, indicating that the Ca was stored both in an exchangeable form and as salts with varying degrees of solubility (Fig. 4). The oxyanions of decayed wood that can bind divalent cations such as Ca^{2+} are most likely the carboxyls of oxidized side chains of lignin (Filley et al. 2000).

This ionically bound Ca becomes available for absorption by fine roots and mycorrhizae even before fragmentation incorporates the residue into the forest floor as seen by feeder roots and mycelial cords penetrating wood in an advanced stage of decay (Fig. 5). The mycelial cords observed may be from wood decay fungi moving essential elements in and out of the decaying wood or from mycorrhizal fungi bringing mineral nutrients accumulated in decaying wood to trees for their growth and development. The concentration of feeder roots and mycelial cords in spatially well-defined pieces of decaying wood argues for a greater role for tree nutrition than might be inferred from mean deposition rates of wood to the forest floor. Feeder roots and mycelial cords preferentially exploit spatially defined pieces of wood and are not uniformly distributed across the forest floor or within forest soil. This complicates accurate modeling or prediction of optimal wood deposition rates in managed forests but was the case in this research.

Laiho and Prescott (2004) reviewed two studies involving mean inputs of Ca from wood deposited per unit area of forest floor, finding that those inputs were not likely to be significant in the context of larger biogeochemical cycles. To the contrary, the results reported here suggest that dismissing the role of decaying wood from having a significant role in Ca cycling is premature, given the spatial heterogeneity in resource availability and acquisition. Some of the controversy about the importance of decaying boles and forest nutrition comes from the fact that the forest floor and coarse woody debris are seen as two different things rather than different stages of the same thing. Finding the mass of fine roots in the forest floor seven times greater than in decay class IV decayed wood and 10 times greater than in decay class III wood was taken as an indication of the low importance of boles in northern hardwood forests (Arthur et al. 1993). However, our study indicates that decayed wood after a decade in soil contact when analyzed by the same standard procedures as forest floor samples already has an equivalent concentration of Ca and in some cases Mg. The major difference between decayed wood and the forest floor was the degree of fragmentation into smaller bits to allow greater root penetration.

Evidence indicates that the death and decay of trees are a key part of stand development (Allen et al. 1997) and some level of disease, death, and decay is essential for healthy stand development (Shortle et al. 2000; Manion 2003). During the decades of stand development, roots die and decay, branches are shed and decay, and trees die and decay. This provides a steady supply of wood to fuel the weathering, transport, and storage of root-available elements needed to sustain tree growth.

This study indicated that decayed wood residues can in most cases be enriched in exchangeable Ca to a concentration equivalent to that in the associated forest floor in less than a decade and that the enrichment may persist for another decade or more. The decayed wood residue differs from the forest floor in that it has a very low molar Al/Ca ratio, a condition favoring Ca uptake by trees (Schröder et al. 1988; Cronan and Grigal 1995). As such, the action of wood-decay fungi on deadwood appears to be potentially important in recovery of tree health and productivity at sites where acid deposition has depleted Ca and mobilized Al. This recovery includes reduced Al/Ca ratios in the forest floor and associated soil, increased Ca uptake, and improved growth and resilience (Shortle et al. 1997).

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