# Concentrations of Ca and Mg in early stages of sapwood decay in red spruce, eastern hemlock, red maple, and paper birch

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**Abstract:** The decay of coarse woody debris is a key component in the formation of forest soil and in the biogeochemical cycles of Ca and Mg. We tracked changes in density and concentration of Ca and Mg in sapwood of red maple (*Acer rubrum* L.), red spruce (*Picea rubens* Sarg.), paper birch (*Betula papyrifera* Marsh.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) in Maine and New Hampshire. We repeatedly sampled 10 logs of each combination of tree species and location at the time of felling and at 2-year intervals for 6 years (birch and hemlock) or 8 years (spruce and maple). We found that density loss was essentially linear for the time period investigated, with birch and maple sapwood decaying at faster rates than spruce and hemlock. Repeated-measures analysis and regression modeling of log-transformed concentrations indicated a significant accumulation of Ca for sapwood of all tree species at both locations (30%–90% increase after 6–8 years of ground contact). Regression estimates of Mg concentration in spruce and maple declined about 20% during the 8 years of ground contact. There was no significant trend for Mg concentration in birch and hemlock. Variation in decay rates and trends in Ca and Mg concentration may be due to differences in sapwood quality, the community of wood decay fungi and associated organisms, or to abiotic conditions.

**Résumé :** La décomposition des débris ligneux grossiers est une composante clé de la formation des sols forestiers et des cycles biogéochimiques de Ca et Mg. Nous avons suivi les changements dans la densité du bois et la concentration de Ca et Mg dans le bois d'aubier de l'érable rouge (*Acer rubrum* L.), de l'épinette rouge (*Picea rubens* Sarg.), du bouleau à papier (*Betula papyrifera* Marsh.) et de la pruche du Canada (*Tsuga canadensis* (L.) Carr.) dans le Maine et le New Hampshire. Nous avons échantillonné à plusieurs reprises 10 billes de chaque combinaison d'espèces d'arbres et d'endroits au moment de l'abattage et à intervalle de 2 ans pendant 6 (bouleau et pruche) ou 8 ans (épinette et érable). Nous avons trouvé que la perte de densité était essentiellement linéaire pendant la durée de l'étude et que le bois d'aubier du bouleau et de l'érable se décomposait plus rapidement que celui de l'épinette et de la pruche. L'analyse des mesures répétées et la modélisation à l'aide de la régression du logarithme des concentrations ont montré qu'il y avait une accumulation importante de Ca dans le bois d'aubier de toutes les espèces d'arbres au deux endroits (augmentation de 30 % – 90 % après 6–8 ans de contact avec le sol). Les estimations de la concentration de Mg chez l'épinette et l'érable, obtenues par régression, ont diminué d'environ 20 % durant les huit années de contact avec le sol. Chez le bouleau et la pruche, la concentration de Mg n'a montré aucune tendance significative. La variation du taux de décomposition et les tendances dans la concentration de Ca et Mg pourraient être dues à des différences dans la qualité du bois d'aubier, la communauté des champignons de carie et des organismes associés ou à des facteurs abiotiques.

[Traduit par la Rédaction]

## Introduction

Coarse woody debris (CWD) on the forest floor is important as a specialized habitat for diverse plant and animal species (Carpenter et al. 1988) and as a component of biogeochemical cycles of carbon (Heath et al. 2003) and essential mineral elements (Carlyle et al. 1998). The degree of importance of CWD as a source of mineral elements to replenish forest soils remains controversial (Holub et al. 2001; Laiho and Prescott 2004). Dissolved organic carbon leached from CWD has been described as causing increased soil acidity and decreased base saturation in soil (Lindroos et al. 2003; Spears and Lajtha 2004), whereas laboratory and field studies have suggested that decaying wood accumulates base cations (Krankina et al. 1999; Ostrofsky et al. 1997). The cycling of Ca and Mg within the forest floor has received particular attention because of the potential impact of harvesting practices upon Ca and Mg pools possible ef-

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fects on Ca and Mg cycles from harvesting practices (Yanai et al. 2000; Sollins et al. 1987) and stand age structure (Hamburg et al. 2003). Biogeochemical cycles of Ca and Mg have been identified as being vulnerable to changes in atmospheric chemistry including acidic deposition and the mobilization of base cations (Driscoll et al. 2001). This mobilization can displace Ca with Al at ion-exchange sites in the rooting zone of forest trees (Lawrence et al. 1995). The addition of Ca to depleted forest soils improved tree health and growth, although the mechanism remains unclear (Juice et al. 2006). Differential sensitivity of forest soils to Ca depletion from changes in the chemical environment and forestry practices is being assessed (Huntington 2005).

All wood exists along a continuum from the differentiation of secondary xylem to humus formation. Most studies on the dynamic chemistry of Ca and Mg in CWD have taken a chronosequence approach with little direct knowledge of the duration of wood decay or the initial chemistry of the wood. To reconstruct a decay chronology, decay classes based on physical appearance in the field (Triska and Cromack 1980; Sollins et al. 1987) have been used as an independent variable in previous studies of decaying wood. Alternative approaches, such as decomposition vector analysis, have refined the chronosequence approach (Harmon et al. 2000). The limitations of those approaches might be overcome by examining the decay process in individual pieces of wood over a long period of decay (Harmon 1992; Palviainen et al. 2004; Schowalter et al. 1998). Although such a design requires patience, such long-term decay studies with repeated measurements would enhance our understanding of nutrient dynamics in decaying wood. The objective of this research was to determine the changes in Ca and Mg concentrations during the first 6–8 years of sapwood decay in logs of several northeastern tree species in ground contact at forest locations in New Hampshire and Maine.

## Methods

The concentrations of Ca and Mg were determined in sapwood at the time of felling and at subsequent 2 year intervals in logs at the Bartlett Experimental Forest (BEF) in Bartlett, New Hampshire (44°4′N, 71°17′W, 250–310 m a.s.l.) and the Penobscot Experimental Forest (PEF) in Bradley, Maine, USA (44°50′N, 68°36–38′W, 40–60 m a.s.l.). In Bartlett, the summer (June–August) mean high and low temperatures are about 25 °C and 10 °C, respectively, with a total summer precipitation of about 34 cm. In winter, the mean high and low temperatures are about 0 °C and –13 °C with a total winter precipitation of about 30 cm. In Bradley, the summer mean high and low temperatures are about 26 °C and 12 °C, respectively, with a total summer precipitation of about 27 cm. The winter mean high and low temperatures are about –1 °C and –11 °C, respectively, with a total winter precipitation of about 24 cm.

Concentrations in sapwood of red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.) were measured during 8 years of ground contact at BEF and PEF. Concentrations in sapwood of paper birch (*Betula papyrifera* Marsh.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) were measured during 6 years of ground contact at PEF. At the time of tree felling, there were no indications of fungal infection of sapwood. At the time of final sampling, the sapwood was physically intact with bark mostly intact, corresponding to decay class I or II in the sense of Triska and Cromack (1980) and Sollins et al. (1987).

Twenty trees from each combination of species and location were selected to yield logs for analyses. Sample trees were dominant or codominant in canopy position and 15–45 cm diameter at breast height. Sample trees were felled in 1995 (red maple and red spruce at BEF), 1996 (red maple and red spruce at PEF), and 1997 (paper birch and eastern hemlock at PEF). Trees were felled close to the ground and bucked to yield a butt log and a second log (3 m and 4 m in length, respectively). Immediately after felling, two initial reference sample disks (5 cm thick) were sawn and collected to test the effects of stem height on initial concentration of Ca and Mg. The first initial reference disk was sawn from the top end of the butt log, corresponding to a height of 3 m in the intact tree. The second initial disk was sawn from the top end of the second log, corresponding to a height of 7 m in the intact tree and 4 m above the first disk. When present, the boundary between sapwood and heartwood or between sapwood and a central column of wound-initiated discoloration was marked on the disk face.

To test the effects of duration of ground contact on the concentration of Ca and Mg, samples were compared with the first initial reference disk. Two years after felling, a "cleaning disk" (10 cm in thickness) was sawn from the bottom of the second log and discarded. A sample disk (5 cm in thickness) was then sawn from the newly exposed bottom of the second log, marked, and retained. In the intact tree, this sample disk would have been about 10–15 cm from the initial disk sawn at the time of felling. Subsequent biennial collections used the same pattern of removal and discarding a cleaning disk immediately followed by the removal and retention of a sample disk from progressively higher positions along the second log. All sample disks were collected ≤60 cm from the first initial reference sample collected at the 3 m position aboveground. Sample disks were oven-dried at 95 °C for 48 h.

Rectangular prism blocks of sapwood were split from the sample disks for further analysis. Sample blocks contained sapwood located 90° along the stem circumference from the area of direct contact with the ground. Blocks were measured for density and concentration of Ca and Mg. 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 ratio of mass to volume. The effect of duration of ground contact on sapwood density for each combination of species and location was analyzed by linear regression. The annual proportional loss of wood density was described for each set of regression estimates using the following model:

$$[1] \quad D_t = D_0 e^{-kt}$$

where $D_t$ is the percentage of the initial density remaining at time $t$ (expressed in years), $D_0$ is the initial wood density, and $k$ is the decay rate constant (Naessert 1999; Yatskov et al. 2003). For computation, eq. 1 was rearranged, i.e.:

$$[2] \quad k = \frac{\log_e D_0 - \log_e D_t}{t}$$

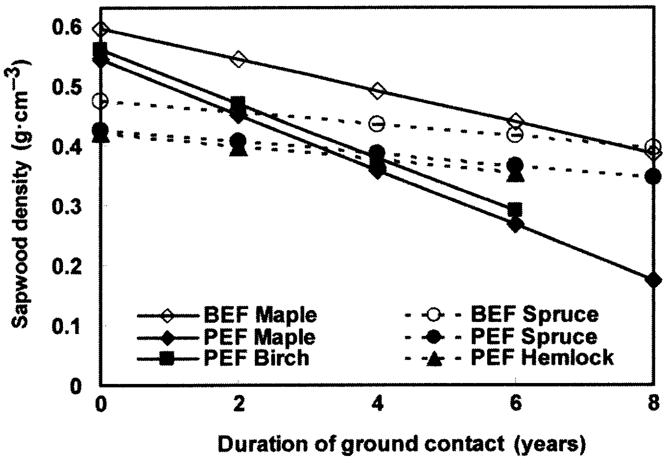
After density measurement, blocks were ground in a Wiley mill (Thomas Scientific, Swedesboro, N.J.) to pass a 1 mm mesh. One-gram portions of milled wood powder were precisely weighed and ashed for 6 h at 550 °C. After cooling, ash was dissolved in 3 mL of 6 $mol \cdot L^{-1}$ HCl and brought to a final volume of 50 mL with deionized water. Concentration of Ca and Mg in ash solutions, analytical standards, and blanks were measured by inductively coupled plasma optical emission spectrometry (ICP-OES model 750, Thermo Jarrell Ash Corp., Franklin, Mass.).

Expression of the dynamics of mineral element concentration in decaying wood is complicated by the progressive loss of mass through leaching of wood components and respiration by wood decay fungi. This problem has been addressed by volumetric sampling (Sollins et al. 1987) or through an adjustment based on differences in wood density associated with wood decay classes (Holub et al. 2001). In this experiment, ICP-OES analytical data were converted from parts per million (ppm) to $mmol \cdot kg^{-1}$ by dividing ppm by the atomic mass. Concentrations were compared on a constant-volume basis ($mol \cdot m^{-3}$) obtained as the product of the mass-based concentration ($mmol \cdot kg^{-1}$) multiplied by the wood density ($g \cdot cm^{-3}$). Statistical tests were applied to log-transformed concentrations of Ca and Mg ($\log_e$ Ca and $\log_e$ Mg, respectively) to reduce the potential effects of heterogeneity of variance and non-normality of distribution.

To test the effect of stem position on the initial concentration of Ca and Mg, element concentrations in the initial reference samples taken at 3 m and 7 m aboveground were compared using a paired $t$ test ($P < 0.05$). When found to be significantly different, the rate of change ($mol \cdot m^{-3} \cdot m^{-1}$) between the 3 m and 7 m positions was calculated, assuming a constant rate of change between the two positions.

Repeated-measures ANOVA (Moser et al. 1990) was used to identify significant sources of variation in Ca and Mg concentration in sapwood. For red spruce and red maple, the two-way treatment factors were location (BEF and PEF) and tree species and their interaction, and the repeated measure was duration of ground contact (0, 2, 4, 6, and 8 years). For paper birch and eastern hemlock, the one-way treatment factor was tree species, and the repeated measure was duration of ground contact (0, 2, 4, and 6 years). The 0 year values were obtained from samples collected at 3 m aboveground. Significance of the treatment factors and their interaction was tested at $P < 0.05$. Significance of the repeated-measures factor and the interaction of duration of ground contact with treatment factors was tested with the Greenhouse–Geisser adjusted probability value to account for the lack of sphericity (independence of variance) in the repeated measures. Significant sources of variation identified by repeated-measures ANOVA were further investigated by linear regression analysis. All statistical analyses were performed with SYSTAT software (version 10.2).

**Fig. 1.** Effect of duration of ground contact on sapwood density in logs of red spruce, red maple, paper birch, and eastern hemlock at the Bartlett Experimental Forest (BEF) and the Penobscot Experimental Forest (PEF). Trends are regression models described in Table 1.




## Results

Sapwood density decreased with increasing duration of ground contact (Fig. 1). After 8 years of ground contact, sapwood of red maple lost about 68% of initial density at PEF and about 35% at BEF. Red spruce lost about 18% of sapwood density over the same time period at the two locations. After 6 years of ground contact, sapwood of paper birch lost about 48%, and eastern hemlock lost about 16% of their initial density.

The broad-leaved species (red maple and paper birch) showed a stronger linear relationship than the conifer species (red spruce and eastern hemlock; Table 1). The substitution of negative exponential models for linear models did not improve the strength of the regression relationship (data not shown). Regression estimates of initial sapwood density at the time of felling ($y$ intercept, $b_0$) for red spruce were significantly higher at BEF than at PEF as indicated by the lack of overlap in the confidence intervals of $b_0$ (Table 1). However, initial wood densities of red maple were statistically similar for the two locations. Regression estimates for the rate of sapwood decay as indicated by the slope of the regression line ($b_1$) and the decay constant ($k$) calculated from the regression line also varied by location with the density of red maple sapwood decreasing more rapidly at PEF than BEF. Density loss of red spruce sapwood occurred at the same rates at BEF and PEF. The density of red spruce and eastern hemlock was lower at the time of felling but declined less rapidly during ground contact than that of red maple and paper birch (Table 1).

The concentrations of Ca and Mg were measured in logs at the time of felling and at subsequent 2-year intervals (Table 2). The Ca concentration data show a general, but not uniform, increase in concentration over time. Variation among logs also increases, with the coefficient of variation of the initial concentration of Ca in red maple at BEF was about 15% and about 38% after 8 years of ground contact. Visual inspection of the Mg concentration data also shows

**Table 1.** Regression models and decay constants for the effect of duration of ground contact on sapwood density at the Bartlett Experimental Forest (BEF) and Penobscot Experimental Forest (PEF).

| Location | Species | $N$ | Parameter | Coefficient | Lower CI[a] | Upper CI | Adjusted $R^2$ |
|---|---|---|---|---|---|---|---|
| BEF | Red spruce | 99 | $b_0$ | 0.475 | 0.454 | 0.496 | 0.16 |
| | | | $b_1$ | –0.010 | –0.014 | –0.005 | |
| | | | $k$ | 0.0215 | | | |
| | Red maple | 100 | $b_0$ | 0.590 | 0.556 | 0.623 | 0.37 |
| | | | $b_1$ | –0.026 | –0.033 | –0.020 | |
| | | | $k$ | 0.0457 | | | |
| PEF | Red spruce | 80 | $b_0$ | 0.426 | 0.398 | 0.453 | 0.11 |
| | | | $b_1$ | –0.010 | –0.016 | –0.005 | |
| | | | $k$ | 0.0240 | | | |
| | Red maple | 84 | $b_0$ | 0.543 | 0.519 | 0.567 | 0.80 |
| | | | $b_1$ | –0.046 | –0.050 | –0.041 | |
| | | | $k$ | 0.0928 | | | |
| | Paper birch | 72 | $b_0$ | 0.560 | 0.527 | 0.593 | 0.59 |
| | | | $b_1$ | –0.045 | –0.054 | –0.036 | |
| | | | $k$ | 0.0876 | | | |
| | Eastern hemlock | 75 | $b_0$ | 0.420 | 0.398 | 0.442 | 0.15 |
| | | | $b_1$ | –0.011 | –0.017 | –0.005 | |
| | | | $k$ | 0.0269 | | | |

**Note:** Regression models are in the form of $\hat{y} = b_0 + b_1x$, where $\hat{y}$ is the estimated density, $b_0$ is the $y$ intercept or initial wood density, and $b_1$ is the slope or rate of change in sapwood density. All regression models are significant at $P < 0.001$. Decay constants ($k$) are calculated from the regression models as the proportion of wood density lost per year. BEF, Bartlett Experimental Forest; PEF, Penobscot Experimental Forest.

[a]Confidence intervals ($P < 0.05$) of regression coefficients.

**Table 2.** Mean concentration of Ca and Mg in decaying logs at BEF and PEF.

| | | | | Duration of ground contact (years) | | | | |
|---|---|---|---|---|---|---|---|---|
| Element | Location | Tree species | Units | 0 | 2 | 4 | 6 | 8 |
| Ca | BEF | Red maple | $mol \cdot m^{-3}$ | 8.5 (0.3) | 9.4 (0.5) | 10.9 (1.6) | 12.3 (1.1) | 11.8 (1.0) |
| | | | $mmol \cdot kg^{-1}$ | 14.5 (0.4) | 16.1 (0.9) | 18.6 (2.6) | 21.2 (2.0) | 20.2 (1.8) |
| | | Red spruce | $mol \cdot m^{-3}$ | 9.0 (0.4) | 11.3 (1.4) | 11.3 (1.4) | 13.4 (1.8) | 17.7 (1.9) |
| | | | $mmol \cdot kg^{-1}$ | 19.2 (0.6) | 24.0 (2.8) | 24.0 (2.8) | 28.9 (4.0) | 37.2 (3.9) |
| | PEF | Red maple | $mol \cdot m^{-3}$ | 8.6 (0.3) | 7.6 (0.4) | 12.3 (0.9) | 14.3 (1.3) | 17.0 (2.2) |
| | | | $mmol \cdot kg^{-1}$ | 15.9 (0.6) | 14.2 (0.8) | 23.0 (1.8) | 26.8 (2.5) | 31.9 (4.2) |
| | | Red spruce | $mol \cdot m^{-3}$ | 7.5 (0.5) | 8.5 (1.0) | 12.2 (1.6) | 11.8 (1.3) | 15.2 (1.7) |
| | | | $mmol \cdot kg^{-1}$ | 17.6 (0.7) | 20.5 (2.8) | 29.6 (4.1) | 28.2 (3.2) | 36.7 (4.8) |
| | | Paper birch | $mol \cdot m^{-3}$ | 8.6 (0.3) | 9.2 (0.4) | 14.2 (1.8) | 18.3 (3.4) | |
| | | | $mmol \cdot kg^{-1}$ | 14.4 (0.4) | 15.6 (0.8) | 24.1 (3.0) | 31.6 (6.4) | |
| | | Eastern hemlock | $mol \cdot m^{-3}$ | 7.1 (0.2) | 7.3 (0.3) | 7.9 (0.4) | 10.0 (1.0) | |
| | | | $mmol \cdot kg^{-1}$ | 16.7 (0.6) | 17.1 (0.8) | 18.4 (0.8) | 23.3 (2.2) | |
| Mg | BEF | Red maple | $mol \cdot m^{-3}$ | 2.4 (0.1) | 2.1 (0.1) | 2.5 (0.3) | 2.1 (0.2) | 1.6 (0.2) |
| | | | $mmol \cdot kg^{-1}$ | 4.1 (0.1) | 3.6 (0.2) | 4.3 (0.5) | 3.6 (0.4) | 2.9 (0.4) |
| | | Red spruce | $mol \cdot m^{-3}$ | 1.5 (0.08) | 2.0 (0.2) | 1.8 (0.2) | 1.6 (0.2) | 1.3 (0.1) |
| | | | $mmol \cdot kg^{-1}$ | 3.2 (0.2) | 4.4 (0.4) | 3.7 (0.5) | 3.5 (0.4) | 2.8 (0.3) |
| | PEF | Red maple | $mol \cdot m^{-3}$ | 2.8 (0.1) | 1.8 (0.1) | 2.2 (0.2) | 2.5 (0.3) | 2.6 (0.4) |
| | | | $mmol \cdot kg^{-1}$ | 5.2 (0.2) | 3.6 (0.3) | 4.6 (0.5) | 6.2 (1.1) | 5.7 (1.0) |
| | | Red spruce | $mol \cdot m^{-3}$ | 1.7 (0.08) | 2.6 (0.3) | 2.0 (0.2) | 1.9 (0.2) | 1.9 (0.2) |
| | | | $mmol \cdot kg^{-1}$ | 4.0 (0.1) | 6.4 (0.7) | 4.9 (0.4) | 4.5 (0.5) | 4.6 (0.6) |
| | | Paper birch | $mol \cdot m^{-3}$ | 3.3 (0.1) | 3.4 (0.2) | 3.6 (0.4) | 3.9 (0.8) | |
| | | | $mmol \cdot kg^{-1}$ | 5.5 (0.2) | 5.8 (0.3) | 6.2 (0.6) | 6.9 (1.5) | |
| | | Eastern hemlock | $mol \cdot m^{-3}$ | 1.5 (0.09) | 1.7 (0.1) | 1.8 (0.1) | 1.8 (0.1) | |
| | | | $mmol \cdot kg^{-1}$ | 3.4 (0.2) | 4.0 (0.2) | 4.3 (0.2) | 4.2 (0.3) | |

**Note:** Samples were collected at about 3 m aboveground in the intact tree. Values are means expressed on a volume basis ($mol \cdot m^{-3}$) that corrects for the loss of wood density during decay with SEs given in parentheses. To facilitate comparison, mean values are also shown on a mass basis ($mmol \cdot kg^{-1}$), corrected for the loss of wood density (uncorrected $mmol \cdot kg^{-1}$ multiplied by the ratio of the density at the time of harvest and at the time of felling).

**Table 3.** Comparison of Ca and Mg concentrations in sapwood at 3 and 7 m aboveground.

| | | | | Mean concentration ($mol \cdot m^{-3}$) | | | |
|---|---|---|---|---|---|---|---|
| Element | Location | Species | *N* | 3 m | 7 m | $t_{calculated}$ | $P^a$ |
| Ca | BEF | Red maple | 19 | 8.45 | 8.11 | 1.6 | 0.12 |
| | | Red spruce | 20 | 9.04 | 8.13 | 2.4 | 0.01 |
| | PEF | Red maple | 20 | 8.57 | 9.30 | 2.8 | 0.01 |
| | | Red spruce | 19 | 7.50 | 7.45 | 0.16 | 0.87 |
| | | Eastern hemlock | 19 | 7.10 | 7.16 | 0.17 | 0.87 |
| Mg | BEF | Red maple | 19 | 2.39 | 2.60 | 1.9 | 0.08 |
| | | Red spruce | 20 | 1.52 | 1.47 | 1.1 | 0.29 |
| | PEF | Red maple | 20 | 2.78 | 3.27 | 6.3 | <0.001 |
| | | Red spruce | 19 | 1.70 | 1.82 | 1.0 | 0.33 |
| | | Eastern hemlock | 20 | 1.46 | 1.48 | 0.3 | 0.76 |

**Note:** Concentration differences at the two stem heights were tested using a paired *t* test of log-transformed values. Nontransformed mean values are shown to aid comparison.

[a]Probability values for a two-tailed test.

**Table 4.** Repeated-measures ANOVA of Ca and Mg concentration for decaying logs of red spruce and red maple.

| | | $\log_e$ Ca | | | $\log_e$ Mg | | |
|---|---|---|---|---|---|---|---|
| | df | *F* | *P* | G–G[a] | *F* | *P* | G–G[a] |
| **Between subjects variation** | | | | | | | |
| Location | 1 | 0.29 | 0.59 | | 8.9 | 0.004 | |
| Species | 1 | 0.03 | 0.86 | | 13.6 | <0.001 | |
| Location × species | 1 | 3.48 | 0.07 | | 0.1 | 0.71 | |
| Error | 61 | | | | | | |
| **Within subjects variation** | | | | | | | |
| Duration | 4 | 28.1 | <0.001 | <0.001 | 6.9 | <0.001 | <0.001 |
| Duration × location | 4 | 3.4 | 0.01 | 0.02 | 3.7 | 0.006 | 0.016 |
| Duration × species | 4 | 1.7 | 0.15 | 0.17 | 6.8 | <0.001 | <0.003 |
| Duration × location × species | 4 | 1.0 | 0.40 | 0.39 | 2.3 | 0.06 | 0.08 |
| Error | 292 | | | | | | |

**Note:** Separate repeated-measures ANOVA were conducted on log-transformed concentrations of Ca and Mg.

[a]Significance of repeated measures was tested with the Greenhouse–Geisser adjusted probability value.

increased variation following ground contact but without a consistent tred over time.

The effect of position along the bole on initial concentration of Ca and Mg was tested at the time of felling. The Ca concentration in red maple at PEF was significantly higher at a height of 7 m than at 3 m (Table 3), with a rate of increased concentration with increasing height along the bole of about 0.18 $mol \cdot m^{-3} \cdot m^{-1}$ (expressed in original units). In contrast, Ca concentration in red spruce at BEF was significantly lower at 7 m than at 3 m, corresponding to a rate of decrease of –0.25 $mol \cdot m^{-3} \cdot m^{-1}$ with increasing height from 3 m to 7 m up the bole. The concentration of Mg in red maple at PEF increased with increasing height along the bole at a rate of about 0.12 $mol \cdot m^{-3} \cdot m^{-1}$. These differences in initial concentration attributable to position along the intact stem were considered to have a trivial effect through the sampled length of the log (≤60 cm) and were not used to adjust subsequent analyses. Initial Ca concentrations at the two stem heights were not significantly different for red maple at BEF or red spruce and eastern hemlock at PEF. Initial Mg concentrations at the 3 m and 7 m positions were not significantly different for red spruce at either location, red maple at BEF, or eastern hemlock at PEF.

Repeated-measures ANOVA for decaying logs of red spruce and red maple showed that the log of the concentration of Ca ($\log_e$ Ca) during 8 years of ground contact was not related to the main treatment factors of location, tree species, or their interaction (Table 4). The $\log_e$ Ca concentration in spruce and maple sapwood was related to the repeated-measures factor of duration of ground contact and the interaction of duration × location. Regression analysis of the effect of duration on $\log_e$ Ca by location yielded linear models for the BEF and PEF locations (Table 5; Fig. 2A). Regression estimates after 8 years of ground contact indicated an increase in Ca of 49% and 87% (in the original units of $mol \cdot m^{-3}$) at BEF and PEF, respectively, for maple and spruce.

Repeated-measures ANOVA for decaying logs of paper birch and eastern hemlock showed that $\log_e$ Ca was significantly related to the main treatment factor of tree species, to the repeated-measures factor of duration of ground contact, and to the interaction of duration × species (Table 6). Re-

**Table 5.** Regression models of significant sources of variation for log-transformed concentrations of Ca and Mg in logs in ground contact.

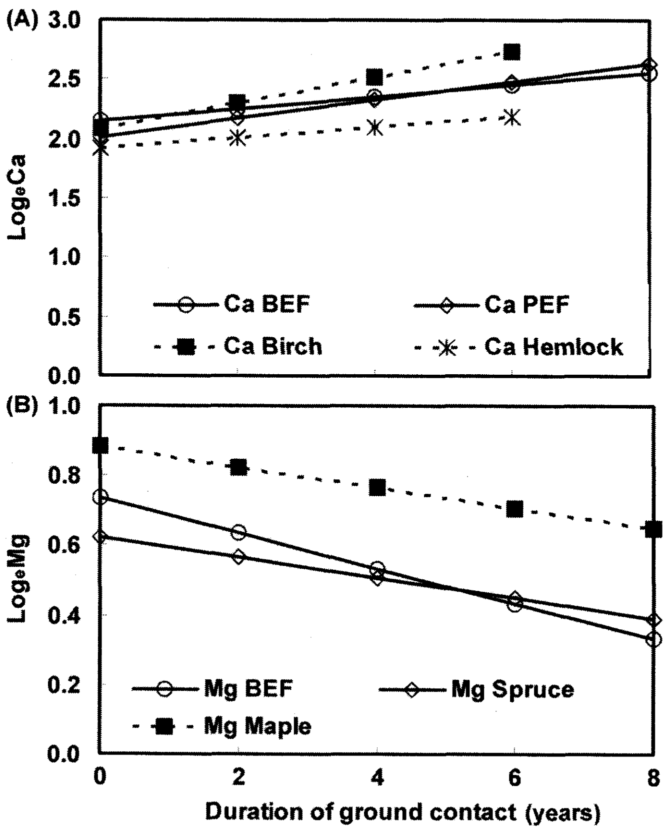
| Element | Location | Species | $N$ | Parameter | Coefficient | Lower CI[a] | Upper CI | $P^b$ | Adjusted $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| Ca | BEF | Maple, spruce | 200 | $b_0$ | 2.152 | 1.972 | 2.060 | <0.001 | 0.12 |
| | | | | $b_1$ | 0.050 | 0.031 | 0.069 | | |
| Ca | PEF | Maple, spruce | 190 | $b_0$ | 2.012 | 1.849 | 1.909 | <0.001 | 0.22 |
| | | | | $b_1$ | 0.078 | 0.057 | 0.993 | | |
| Ca | PEF | Birch | 80 | $b_0$ | 2.080 | 1.940 | 2.220 | <0.001 | 0.29 |
| | | | | $b_1$ | 0.108 | 0.070 | 0.145 | | |
| Ca | PEF | Hemlock | 80 | $b_0$ | 1.914 | 1.817 | 2.011 | 0.002 | 0.12 |
| | | | | $b_1$ | 0.039 | 0.014 | 0.064 | | |
| Mg | BEF | Maple, spruce | 194 | $b_0$ | 0.735 | 0.622 | 0.848 | <0.001 | 0.08 |
| | | | | $b_1$ | –0.060 | –0.096 | –0.023 | | |
| Mg | BEF, PEF | Maple | 195 | $b_0$ | 0.881 | 0.757 | 1.005 | 0.025 | 0.02 |
| | | | | $b_1$ | –0.029 | –0.054 | –0.004 | | |
| Mg | BEF, PEF | Spruce | 190 | $b_0$ | 0.624 | 0.517 | 0.732 | 0.009 | 0.03 |
| | | | | $b_1$ | 0.034 | –0.051 | –0.062 | | |

**Note:** Significant sources of variation (constant volume basis) identified by repeated-measures ANOVA (see Tables 4 and 6). Regression models are in the form of $\hat{y} = b_0 + b_1x$, where $\hat{y}$ is the estimated log-transformed concentration, $b_0$ is the $y$ intercept or initial concentration, $b_1$ is the slope or rate of change in concentration, and $x$ is the duration of ground contact.

[a]Lower and upper bounds of the 95% confidence interval of the estimated model parameter.

[b]Probability level for the significance of the complete regression equation.

**Fig. 2.** Significant trends from regression modeling of log-transformed (A) calcium and (B) magnesium concentrations (mol·m$^{-3}$) in sapwood during ground contact at BEF and PEF.




gression analysis of the effect of duration by species yielded linear models of the effect of duration on $\log_e$ Ca for birch and hemlock (Table 5; Fig. 2A). Regression estimates after 6 years of ground contact at PEF indicated an increase of 91% and 31% in hemlock and birch, respectively.

The main treatment factors of location and species were significant sources of variation in the concentration of Mg ($\log_e$ Mg) (Table 4). The $\log_e$ Mg for decaying sapwood in logs of red spruce and red maple was significantly related to the repeated-measures factor of duration of ground contact as well as the interactions of duration × location and duration × species (Table 4). Regression analysis yielded significant linear models of the effect of duration of ground contact on $\log_e$ Mg for sapwood at the BEF location (Table 5; Fig. 2B). Regression estimates after 8 years of ground contact show decreased Mg concentration of about 33% (in the original units) at BEF for maple and spruce. The $\log_e$ Mg in birch and hemlock was significantly related to tree species but not to duration of ground contact or the interaction of duration with species (Table 6).

## Discussion

Sapwood decreased in density with increased duration of ground contact for all four tree species tested. Comparisons of these rates of density loss with previously published values (e.g., Yatskov et al. 2003; Naessert 1999) is of questionable value because of the lack of differentiation in the earlier work between sapwood and heartwood. This is an important distinction in that the latter is generally more resistant to decay. Differences in decay rates and initial wood densities between the BEF and PEF locations may be due to climate differences with the interior montane BEF having slightly cooler temperatures and greater precipitation than the more coastal PEF. However, the potential differential effect of climate on decay rates is not compelling in this research.

The linear decrease in density we found over 6–8 years of ground contact may not remain linear over longer time periods. Previous research on *Betula* and other species in boreal Russia shows that decay rates may be comparatively slow during the first decade of ground contact, become rapid in the second decade and then moderately slow through the following six decades (Yatskov et al. 2003).

**Table 6.** Repeated-measures ANOVA of Ca and Mg concentration for decaying logs of paper birch and eastern hemlock.

| | $\log_e$ Ca | | | | $\log_e$ Mg | | |
|---|---|---|---|---|---|---|---|
| | df | *F* | *P* | G–G[a] | *F* | *P* | G–G[a] |
| **Between-subject variation** | | | | | | | |
| Species | 1 | 28.4 | <0.001 | | 62.1 | <0.001 | |
| Error | 38 | | | | | | |
| **Within-subject variation** | | | | | | | |
| Duration | 3 | 20.6 | <0.001 | <0.001 | 1.9 | 0.13 | 0.16 |
| Duration × species | 3 | 3.8 | 0.01 | 0.02 | 1.1 | 0.35 | 0.34 |
| Error | 108 | | | | | | |

**Note:** Separate repeated-measures ANOVA were conducted on log-transformed concentrations of Ca and Mg.

[a]Significance of repeated measures was tested with the Greenhouse–Geisser adjusted probability value.

Various nonlinear models have been applied to trends of mass and density loss during wood decay (Harmon et al. 2000; Lambert et al. 1980). The rates of density loss we observed were difficult to compare with the decomposition vectors of Harmon et al. (2000). In that earlier study, estimates were made for entire logs that contained both sapwood and wood altered in density and decay resistance through heartwood formation or responses to injury and infection. Also, the earlier decomposition vectors were constructed from observations made 3 years apart, with the initial observations made over a wide range of duration of ground contact (Harmon et al. 2000). Although the sapwood in this experiment had retained its volume and structural integrity, wood fragmentation in later stages of the wood decay process would complicate estimates of density and expressions of concentration on a constant volume basis.

Initial concentrations were consistent with a previous analysis of the effect of elevation on Ca and Mg concentration in sound wood (Arthur et al. 1999). During the decay process, Ca concentration significantly increased in the sapwood of red spruce, eastern hemlock, red maple, and paper birch. This increase was somewhat species-dependent, with sapwood of paper birch increasing in Ca concentration at a higher rate than eastern hemlock. In contrast, Mg concentration significantly decreased in the sapwood of spruce and maple and exhibited no significant trend in hemlock and birch.

Fungi may be responsible for the importation of Ca and Mg into the decaying sapwood. Wood decay fungi and their many associated microorganisms, plants, and animals directly or indirectly use the energy and essential elements stored in wood to support their own metabolism and to maintain a favorable environment. The wood decay fungi are especially well suited for the redistribution of mineral elements in forest soil and in the forest floor. Cellulose and other carbon polymers provide an energy source that although highly contested among natural communities of wood decay fungi and their associates, is not broadly available for acquisition by other potential competitors. Access to large amounts of potential energy in the form of wood is facilitated by a foraging growth habit. Mycelial growth also provides an extensive interface for element uptake, a distributive network for directed transport, and linkage across horizons within the soil profile.

Previous research has shown that wood decay fungi redistribute mineral elements in the forest floor (Boddy and Watkinson 1995) and that base cations can be both exported out of (Harmon et al. 1994) and into decaying wood (Ostrofsky et al. 1997). The potential for wood-decay fungi to influence Ca cycling in forests by biologically weathering soil parent material and transporting mobilized Ca vertically through soil has been demonstrated under glass (Connolly et al. 1999). Comparison of samples collected from the same logs over time likely reduced variation due to differences in initial sapwood density and wood chemistry among trees. These initial differences were especially likely to affect concentrations early in the decay process. The tracking of individual logs also avoided the problem of approximating the residence time of ground contact and the initial chemistry of CWD.

Rates of wood decay in fallen logs vary in response to initial wood quality (sapwood, heartwood, previous injury, and infection), temperature, precipitation, and availability of inoculum of wood decay fungi and associated organisms (Rayner and Boddy 1988; Boddy 2001). Soil characteristics, such as moisture retention, and the availability of essential elements, such as N, that are naturally present in low concentration in wood would likely affect decay rates. Tracking the loss of density in sapwood from specific logs provided a means to determine the effects of location and tree species during early stages of the decay process. Harmon (1992) suggested that differences among species in rates of sapwood decay were likely to be minor. Although that may be true over a sufficiently long period of ground contact, rates of density loss during the first 6–8 years of ground contact for red maple and paper birch sapwood were significantly greater than for red spruce and eastern hemlock. This may be due to greater incidences of white rot in broad-leaved trees and brown rot in coniferous trees. Brown rot tends to reduce wood density more slowly than white rot.

Surveys of CWD abundance and the relationship of other organisms to CWD benefit from the use of decay classes that are readily assigned in the forest. However, most biogeochemical interest is in the flow of elements into, out of, and within the forest. Meeting this interest requires linking chemical changes to a defined time course. The calibration of these coarse categories with duration of ground contact at particular locations should enhance the value of both methods to biogeochemical modeling. The research presented here shows that CWD is a sink for soil Ca during some portion of the wood decay process. This finding has potential implications on managing CWD as a dynamic element of the biogeochemistry of Ca, an element sensitive to depletion in acidified soils or overharvested forests. This research does not identify the source of the Ca accumulating in the decaying logs. The biogeochemical significance of the accumulation depends on whether the redistribution is from soil associated with the adjacent forest floor, from deeper in the soil profile, or from the atmospheric deposition of particulates.

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