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Complete List of Authors:	Fahey, Timothy; Cornell University, Natural Resources Heinz, Alexis; Cornell University, Natural Resources Battles, John; University of California Berkeley, Environmental Science Policy and Management Fisk, Melany; Miami University, Department of Biology Driscoll, Charles T.; Syracuse University Blum, Joel; University of Michigan Johnson, Chris; Syracuse University
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Fine Root Biomass Declined in Response to Restoration of Soil Calcium in a
Northern Hardwood Forest

AUTHORS: Timothy J. Fahey¹, Alexis K. Heinz¹, John J. Battles², Melany C. Fisk³,
Charles T. Driscoll⁴, Joel D. Blum⁵ and Chris E. Johnson⁴

AFFILIATION and ADDRESS:

¹ Department of Natural Resources, Cornell University, Fernow Hall, Ithaca, NY
14853 (tjf5@cornell.edu; akh24@cornell.edu)

² Department of Environmental Science, Policy and Management (E.S.P.M.),
University of California at Berkeley, Berkeley, CA, USA 94720--3114

³ Miami University, Department of Biology, Oxford, OH 45056
(fiskmc@miamioh.edu);

⁴ Department of Civil and Environmental Engineering, Syracuse University, Link
Hall, Syracuse, NY 13244 (ctdrisco@syr.edu, cejohns@syr.edu);

⁵ LSA Earth & Environmental Science, University of Michigan, 2534 CC Little, Ann
Arbor, MI 48109 (jdblum@umich.edu)

CORRESPONDING AUTHOR: Timothy J. Fahey¹ – tjf5@cornell.edu

Abstract

Forest health deteriorated in eastern North America as a result of depletion of available soil base cations by elevated inputs of acid deposition. We experimentally restored available calcium to soils of a forested watershed at Hubbard Brook, New Hampshire and measured the response of fine root biomass fourteen years after treatment. In this northern hardwood forest fine root (< 1 mm diameter) biomass declined significantly in response to the Ca addition treatment relative to pretreatment and reference forest conditions. The decline was greatest in the mid- and high-elevation hardwood zones of the watershed, where soils are thinnest and have the lowest base saturation and exchangeable Ca pools. Restoration of soil Ca appears to have reduced the allocation of C to root systems, coincident with observed increases in aboveground biomass and productivity. Therefore, we suggest that relatively higher tree C allocation to roots in the past contributed to the depressed aboveground productivity observed in northern hardwood forest ecosystems impacted by acid deposition.

Keywords: acidification, allocation, leaf area index, mycorrhizae, production

40 Introduction

41 Soils and surface waters in industrialized regions have been acidified as a
42 result of high atmospheric deposition of strong acids derived primarily from the
43 burning of fossil fuels (Likens et al. 1996; Schindler 1988). The negative effects of
44 acid deposition on forest growth and health have been suggested by both field
45 surveys (Schulze 1989) and controlled experiments (Eagar and Adams 1992).
46 However, forests are exposed to many stresses and isolating the mechanisms by
47 which acid deposition contributes to forest decline has been challenging (Manion
48 1991). Acid deposition can deplete available pools of soil base cations, especially
49 calcium and magnesium, leading to disruption of physiological processes in
50 sensitive tree species (DeHayes et al. 1999). Although air quality regulations in
51 North America and Europe have reduced acid deposition since the late 20th
52 century, severe depletion of base cations has caused persistent effects on
53 sensitive forests (Long et al. 2009; Battles et al. 2014) and soil base cation pools
54 continue to decline (Warby et al. 2009). Moreover, high acid deposition
55 continues to acidify soils in rapidly industrializing regions, like eastern Asia
56 (Dentener et al. 2006, Yang et al. 2015), with likely consequences for forest
57 ecosystems. Hence, a better understanding of forest responses to soil base cation

58 depletion is essential to characterize and quantify the effects of and recovery
59 from elevated acid deposition.

60 At the Hubbard Brook Experimental Forest (HBEF) in the northeastern
61 United States, long-term monitoring of forests, soils and surface waters has
62 provided a quantitative basis for evaluating ecosystem responses to acid
63 deposition; in particular, the magnitude of available soil calcium (Ca) depletion
64 during the 20th century has been estimated (Likens et al. 1998). On this basis, a
65 long-term experiment was initiated to replace the lost Ca through an
66 experimental addition of a Ca silicate mineral, wollastonite, to an 11.8 ha
67 watershed (WS1). By returning the soil base status of the experimental
68 watershed to conditions that existed prior to the “acid rain era,” we hoped to
69 demonstrate the effects of anthropogenic Ca depletion on ecosystem health and
70 productivity. As detailed in previous reports from this study, the gradual
71 replacement of lost Ca resulted in increased soil and surface water pH and
72 decreases in solution aluminum (Cho et al. 2010, Nezat et al. 2010, Johnson et al.
73 2014, Shao et al. 2015); improved health of acid-sensitive tree species, including
74 red spruce (Hawley et al. 2006) and sugar maple (Juice et al. 2006); and an overall
75 increase in forest biomass and aboveground productivity, relative to untreated,
76 reference watersheds (Battles et al. 2014). Moreover, in complementary, plot-

level studies at the HBEF the mechanism of Ca effects on sugar maple health and growth have been demonstrated (Huggett et al. 2007; Halman et al. 2013, 2014).

Two key features of forest recovery resulting from amelioration of soil Ca depletion on WS1 were observed: 1) promotion of wound closure and damage recovery following a severe ice storm that coincided with the experimental Ca additions (Huggett et al. 2007, Battles et al. 2014) and 2) increased aboveground growth associated with improved canopy health, including wood growth and leaf production (Juice et al. 2006, Battles et al. 2014). The latter effects raise the question of the mechanisms whereby low Ca supply in soils depleted by acid deposition might constrain leaf and wood production. One possible mechanism is an increase in carbon allocation to root systems seeking access to limited soil nutrients (Haynes and Gower 1995). The objective of the present study was to quantify fine root biomass in treated and untreated reference forests. We hypothesized that historical soil Ca depletion increased fine root biomass as well as the fine root: leaf biomass ratio. Thus, we predicted that these values would be greater in the untreated, reference forest than in the Ca-treated forest. If true, this may help explain the observed increase in aboveground production on the treated watershed (Battles et al. 2014). We expected differences in root biomass to be greatest in the mid- and high-elevation hardwood zones of the watersheds,

where the soils have been most severely depleted of base cations (Johnson et al. 2000), and where the aboveground growth response to treatment was most pronounced (Battles et al. 2014) . Finally, we expected the depth distribution of fine roots to extend deeper in the soils of the reference than the treated forest as the trees explored deeper soil layers for the limited supply of Ca.

Methods

Site Description. The HBEF is located in north-central New Hampshire, USA (43° 56' N, 71° 45' W), and has been the site of numerous forest research studies. Detailed description of the site is available elsewhere (Likens 2013). Briefly, the climate is humid-continental with short, cool summers and long, cold winters. Soils are predominantly well-drained Spodosols (Haplorthods) and Inceptisols (Dystrochrepts) of sandy-loam texture formed from glacial till. Overstory vegetation is dominated by northern hardwood trees: sugar maple, American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt. The HBEF is mostly second-growth forest developed following logging in the late 19th and early 20th century. Some areas were also affected by the 1938 hurricane and subsequent salvage logging, and by an intense ice storm in 1998 (Rhoads et al. 2002). While the ice storm caused considerable structural damage to the forest,

114 most of the damage was restricted to the mid- to-upper elevations of the
115 watersheds and by 2001, leaf area had recovered in affected areas (Green et al.
116 2014; Battles et al. 2014). The Ca amendment was conducted in experimental
117 watershed 1 (WS1, 11.8 ha in size, 488 to 747 m in elevation) on the south-facing
118 slope of the HBEF. A complete inventory of trees in each of three elevation zones
119 in the northern hardwood forest was conducted in 2001 (Table 1) and repeated in
120 2011. The nearby forest to the west of WS6 served as a reference for
121 measurement of root biomass and leaf area index (LAI), and a complete tree
122 inventory also was conducted on adjacent untreated reference WS6 in 2002 and
123 2012.

124 **Experimental Ca amendment.** In October 1999 (soon after leaf fall), 40.8 Mg of
125 powdered and pelletized wollastonite (CaSiO_3) was evenly distributed by
126 helicopter to WS1 (Peters et al. 2004). The wollastonite application resulted in a
127 Ca addition of approximately $1,028 \text{ kg Ca ha}^{-1}$. This delivery rate was chosen to
128 roughly double soil base saturation to estimated pre-industrial values (Peters et
129 al. 2004), and consequently to increase soil pH and decrease Ca to aluminum (Al)
130 ratios in soil solutions. By summer 2000 the treatment had significantly
131 increased pH in the Oie horizon (Cho et al. 2010), and the pH differences have
132 persisted (Table 2; Johnson et al. 2014). The wollastonite addition also

significantly increased the exchangeable Ca and decreased exchangeable Al in soils across the elevation gradient in WS1. With time since the addition, the impacts of the treatment (e.g., increasing pH and exchangeable and solution Ca, decreasing exchangeable and solution Al) were detected through the soil profile (Cho et al. 2012, Johnson et al. 2014).

Field sampling and laboratory processing. Prior to Ca treatment three large sampling plots (0.5 to 1 ha rectangular plots) were established across the elevation gradient in WS1 and in nearby forest west of WS6, the biogeochemical reference watershed for the HBEF. The plots in each forest were located in the northern hardwood forest zone at low (488-565 m), mid (565-660 m) and high (660-770 m) elevation. In each plot a network of twelve sampling locations was chosen randomly and at each location a litterfall trap (0.1 m^2) was positioned about 1.5 m above the ground. Leaf litterfall was collected from each trap beginning in 1992 for reference plots and in 1998 for WS1. Hardwood leaf litter was sorted by species for each litter trap each year, providing the amount of leaves per 0.1 m^2 . Area per leaf of each species was measured on both reference and treated sites in four years in order to convert leaf number to leaf area index (LAI, $\text{m}^2 \cdot \text{m}^{-2}$) for the northern hardwood forest. Because an ice storm greatly reduced leaf litterfall in parts of both treatment and reference watersheds

152 between 1999-2000 (Rhoads et al. 2002), we used litterfall values for 2001 to
153 represent pretreatment conditions.

154 In August 1998 (prior to treatment) soil cores were collected adjacent to
155 each of the 36 litterfall traps in WS1 and in the reference forest plots. A split PVC
156 corer of 5 cm diameter was hammered into the soil to a depth of 20 cm as
157 measured from the top of the mineral soil. Locations occupied by boulders and
158 root crowns were avoided. Soil cores were divided in the field into four layers:
159 forest floor organic horizon plus 0-5 cm mineral soil and 5-10, 10-15, and 15-20
160 cm mineral soil. Fine roots in this forest are highly concentrated in shallow soil
161 layers, with 80-90% of <1mm roots in forest floor plus 0-20 cm mineral soil (Fahey
162 et al. 1988, Yanai et al. 2006). The same field procedure was repeated in August
163 2013 fourteen years after treatment with cores again paired with litterfall traps.
164 Soil samples were returned to the laboratory and stored frozen until processed
165 for root biomass. Roots were hand sorted from soil cores into two diameter
166 classes (< 1 mm, 1-2 mm); live roots were distinguished by visual criteria and
167 retained for dry weight determination. Roots were dried to constant mass at 70
168 °C and weighed to ± 0.001 g. The root biomass data were computed on a grams
169 per m² basis (forest floor plus 0-20 cm mineral soil depth) after taking into
170 account the estimated area of each sampling plot that was occupied by boulders

and root crowns and hence was not sampled by root coring. A line intercept method was applied to determine this fraction (Fahey et al. 2005).

Statistical Analysis. To evaluate the effects of the Ca-amendment on fine root biomass, we used a before-after-control-impact study design (Stewart-Oaten et al. 1986). This framework accounts for temporal changes that are unrelated to the treatment and thus any observed differences between watersheds can be attributed to the Ca- amendment. We emphasize the caveat that our experimental treatment is not replicated as a result of the high cost of the whole watershed treatment that was essential to element mass-balance calculations for the overall study (Johnson et al. 2014). Formally, the impact of the treatment can be quantified as the difference in the response between sites (WS1 and west of WS6 reference, see above) observed over time:

Equation 1
$$\text{Treatment Impact} = (\mu_{ca} - \mu_{cb}) - (\mu_{ta} - \mu_{tb})$$

where μ is the mean of the response variable; c represents the reference watershed; a the measurement period after treatments; b the period before treatments; and t the treated watershed. A key assumption with this approach is that in absence of the Ca-amendment, the differences between the sites would

be constant (Stewart-Oaten et al. 1986). The impact of the treatment on fine root biomass (<1mm; 1-2 mm) and the ratio of fine roots to leaf litter biomass was assessed with linear and linear mixed effects models (Pinheiro and Bates 2006).

The base model included both time (pre vs post) and treatment (no added Ca vs Ca-amendment) because in the simplest case the time:treatment interaction term serves as the test of the statistical significance of the treatment effect (Smith 2002). We also considered elevation class (low, medium, high elevation sites) as a potential co-variable given the documented patterns in forest composition (Bormann et al. 1970), soil chemistry (Cho et al. 2010) and productivity (Fahey et al. 2005) with elevation (Table 1). Since we sampled fine roots and measured leaf litterfall from the same locations both pre- and post-treatment, we included models with a random effects term to account for any differences among location. Before fitting the linear models for <1mm and 1-2 mm roots, we log-transformed the root biomass to maintain a normal distribution of the residual errors. To select which models were best supported by the data, we calculated the differences in the Akaike Information Criterion (AIC, Burnham and Anderson 2002). We used Akaike weights and evidence ratios to interpret the results.

Finally, we evaluated the slope of the bivariate fit of the log of fine root biomass versus soil depth to determine whether significant changes occurred in the depth distribution of fine roots in response to the treatment. Again, pre- and post-treatment estimates were available to support this analysis.

Results

Fine root biomass (< 1mm and 1-2 mm) was measured in 1998 (pre-treatment) and 2013 (14-yr post-treatment) in both the reference and the treated watershed (Table 3). In general, fine root biomass was lower in 2013 than in 1998 in WS1 (Fig. 1). The best fitting model for the effect of Ca-amendment on <1mm fine root biomass included elevation without a random effects term (Table 4). The support for this model was 37 times greater than the next best model. Fine root biomass was greatly reduced in the treated watershed compared to the reference watershed ($p < 0.001$, Time:Treatment term in ANOVA; Table 4). The response of fine root biomass also varied significantly with elevation, with the greatest response at higher elevation zones (Fig. 1).

Fine root cores were paired with leaf litterfall collectors in the hardwood forest, and we calculated the mass ratio of <1mm fine root biomass to leaf litterfall biomass for each location (Fig. 2). In general, whereas the fine root:leaf

227 biomass ratio declined between 2001 and 2013 in the treated watershed, it was
228 either constant or increased in the reference forest (Fig. 2). The statistical results
229 (Table 5) were similar to those for fine root biomass. Whereas the top two models
230 (with and without elevation effects) were indistinguishable, in both cases the
231 treatment effect was highly significant ($p < 0.0014$; Table 5); however, for the fine
232 root:leaf biomass ratio, differences with elevation were less pronounced than for
233 fine root biomass.

234 We evaluated possible shifts in the depth distribution of fine roots between
235 years and watersheds by comparing the slope of bivariate linear models of log
236 (fine root biomass) vs. soil depth. High scatter was observed, and the high-
237 elevation hardwood zone was the only elevation stratum in which a consistent
238 response was evident (Fig. 3). In the reference watershed the slope was nearly
239 identical between years, whereas in the treated watershed the slope showed a
240 weak trend ($p = 0.14$) to be greater in 2013 than 1998, suggesting that fine roots
241 may have been distributed deeper prior to the treatment in WS1.

242 In contrast to the clear effects of treatment on the biomass of < 1 mm fine
243 roots, no significant effects ($P = 0.302$) were observed for treatment effects on
244 the biomass of 1-2 mm roots. Although 1-2 mm root biomass seemed to decline

in the high-elevation zone of WS1, it did not decline in the low and mid-elevations (Table 3). These larger roots comprised about one-third as much biomass as the < 1mm roots and showed relatively higher spatial variation within sites (Table 3).

Discussion

We replaced the Ca lost as a result of elevated leaching associated with acid deposition in the 20th century in the form of a rapidly-weathering silicate mineral in an experimental watershed (WS1) at the HBEF with the aim of returning soil base status to levels comparable to pre-20th century conditions (Peters et al. 2004, Johnson et al. 2014). Improved forest health (Juice et al. 2006, Hawley et al. 2006) and increased aboveground biomass and productivity (Battles et al. 2014) were observed on the treated watershed relative to reference sites (Table 6). Our observations in this study support the hypothesis that the aboveground productivity response on WS1 resulted in part from decreased tree allocation to roots: both fine root biomass (Fig. 1) and the fine root:leaf litterfall mass ratio (Fig. 2) declined significantly 14 years after Ca addition. Looking back in time, this result suggests that soil base cation depletion due to acidification probably caused decreased aboveground productivity on these naturally-acidic soils in part by stimulating an increase in belowground allocation to support greater fine root

263 biomass. Root biomass in forests can fluctuate significantly among years
264 (Makkonen and Helmisaari 2001), and some uncertainty is acknowledged because
265 our measurements were confined to only one post-treatment year. We also
266 emphasize that our large-scale treatment was not replicated in space, and the
267 results should be applied to broader regions with due caution.

268 Although biomass of small woody roots (1-2 mm) also tended to decline, at
269 least in the high elevation zone of the treated watershed (Table 3), the response
270 was less consistent, perhaps reflecting in part the much longer lifespan of these
271 high-order roots (Fahey et al. 2012) and a consequently delayed response. This
272 result also implies a likely response in root branching morphology with more low-
273 order (< 1mm; order 1-3) roots per unit high-order (1-2 mm; order 4-5) roots in
274 the treated forest.

275 Previous studies of Ca availability and liming effects on root biomass and
276 production in forests indicate variable responses. In tropical forests fine root
277 biomass typically is inversely related to soil Ca availability (Gower 1987, Cavelier
278 1992). Long-term liming of boreal conifer forests has often resulted in reduced
279 fine root biomass and production (Helmisaari and Hallbacken 1999, Saarsalmi and
280 Malkonen 2001), including apparently adverse effects on ectomycorrhizal root

tips (Lehto 1994). In contrast to the present study, liming can elicit tree growth reduction in *Picea abies*, accompanying reduced root biomass and production on some sites, possibly because of impaired N nutrition associated with reduced fine root and mycorrhizal growth (Lehto and Malkonen 1994). On WS1, Ca addition initially tightened the N cycle but did not significantly affect foliar N of the dominant trees (Groffman et al. 2006); higher soil N availability at HBEF than the Scandinavian boreal sites may contribute to these contrasting results. Notably, arbuscular mycorrhizal colonization of sugar maple can be stimulated by Ca addition (Coughlan et al. 2000, Juice et al. 2006).

Although Ca is an important plant macronutrient, it has not traditionally been regarded as a growth-limiting nutrient in forests; rather, Ca is thought to exert its role in tree nutrition primarily by buffering soil pH and thereby suppressing toxic metal effects (Rengel and Zhang 2003). However, recent studies have implicated Ca deficiency in reduced tree growth and health through effects on photosynthesis, carbohydrate metabolism and cold tolerance (McLaughlin and Wimmer 1999, Schaberg et al. 2006, Halman et al. 2008, 2013). Also, previous reports from the WS1 Ca treatment have indicated that forest recovery from ice storm damage was promoted by improved Ca supply on WS1 (Battles et al. 2014), supporting complementary observations from HBEF of

300 improved wound repair in sugar maple on Ca-amended plots (Huggett et al.
301 2007).

302 Restoration of soil Ca on WS1 resulted in significant increases in foliar and
303 fine root Ca concentrations in all the dominant tree species relative to untreated
304 reference sites (Green et al. 2013; T. Fahey, unpublished data), suggesting that
305 historical soil Ca depletion has impaired tree Ca acquisition on the experimental
306 watersheds at the HBEF. A significant increase in leaf area index (LAI) in the
307 hardwood forest zones was observed on WS1 (Green et al. 2013, Battles et al.
308 2014), and perhaps reduced Ca availability constrained leaf development on the
309 Ca-depleted reference sites. The increase in LAI coincided with higher
310 aboveground production during year 6 to 11 after treatments, which was
311 attributed to significantly greater leaf and wood production (Battles et al. 2014).

312 The present study indicates that this aboveground growth response was
313 accompanied by significantly lower fine root biomass, suggesting that reduced C
314 allocation belowground may have contributed to the increased tree growth.
315 However, fine root biomass is an incomplete indicator of belowground C
316 allocation because differences in fine root turnover and metabolism and
317 rhizosphere C flux also could contribute to variations in allocation. Park et al.

(2008) observed that fine root turnover increased with soil Ca availability across a gradient of New England forests. If restoration of Ca on WS1 resulted in increased root turnover, this would tend to counteract the proposed reduction in C allocation. Notably, the Ca gradient studied by Park et al. (2008) encompassed over a 20-fold range of soil Ca availability as compared with the roughly 2-fold increase associated with the present experiment (Table 2; Johnson et al. 2014). Nevertheless, further studies of root growth and turnover in the WS1 experiment are needed to confirm the mechanism of aboveground growth response suggested by our data.

Reduced allocation of C to roots is likely to result in long-term effects on soil C pools. Johnson et al. (2014) reported significant decreases in the pools of organic matter and C in the Oa horizon on WS1 starting seven years post-treatment. By 2010, the C pool in the Oa horizon had declined by 1130 g m^{-2} . This value is large compared to the decrease in fine root biomass observed in this study ($\sim 100\text{-}150 \text{ g m}^{-2}$; Fig. 1); however, together with increased litter decay (Lovett et al. 2016), lower belowground C allocation over several years could contribute to the observed decrease in soil C after the Ca treatment.

335 The greatest response of fine root biomass to soil Ca additions was
336 observed in the mid- and upper-elevation hardwood forest zones on WS1 (Fig. 1).
337 This result matches observations of increased tree biomass, growth and LAI,
338 which were also most pronounced at higher elevations, especially for sugar maple
339 (Table 6). Soils in the high-elevation hardwood zones on the experimental
340 watersheds at the HBEF are thinner and more base-poor than in the lower
341 elevations (Johnson et al. 2000), and soils and soil solutions also exhibited a
342 greater relative response to the Ca addition in this zone (Cho et al. 2010, 2012,
343 Johnson et al. 2014). Recent observations also indicate that nitrate
344 concentrations in soil solutions and streamwater draining the high elevations of
345 WS1 have increased markedly from near detection limits before 2010, reaching
346 over 1.5 mgN L⁻¹ in winter 2013 (C. Driscoll, personal communication). Although
347 the exact mechanism remains unknown, it seems likely that increased nitrate
348 leaching is linked with observed decrease in fine root biomass and forest floor C.

349 In the highest-elevation hardwood zone, we observed a weak trend in the
350 depth distribution of fine roots between pre-treatment and 14-yr post-treatment;
351 fine roots appeared to be distributed more deeply in the soil before treatment
352 (Fig. 3). In contrast, Schulze (1989) suggested that shallow rooting of declining
353 *Picea abies* on acidified soils might be attributed to higher soil base saturation in

surface horizons associated with recycling of base cations in plant litter. Moreover, Bullen and Bailey (2005) showed that during the 20th century acidification of soils in a New Hampshire conifer forest, root Ca acquisition moved progressively from deeper to shallower horizons. Notably, the Ca treatment on WS1 resulted in only marginally increased base saturation and Ca availability in mineral soil as of 2010 (Johnson et al. 2014); thus, possible increase in fine root deployment in surface soils in the high elevation hardwood zone may reflect relatively high Ca supply associated with leaf litter recycling (Fahey and Blum 2011) relative to deeper soil layers. Previous research at the HBEF (Blum et al. 2002) indicated that mycorrhizae contributed significantly to weathering of Ca from apatite in mineral soil of these base-poor watersheds, perhaps contributing to deeper rooting prior to the treatment.

The large-scale Ca addition to WS1 at the HBEF was explicitly designed to measure long-term responses of forest ecosystem dynamics to the amelioration of soil base cation depletion resulting from human activity in the 20th century. Our results suggest that one key effect of soil Ca depletion on naturally acid soils was increased fine root biomass in northern hardwood forests. Widespread observations of improved health and growth in northern hardwood forests in response to base cation additions (Wilmot et al. 1996, Moore et al. 2012, Long et

al. 2009) may be partly explained by responses in tree C allocation belowground. Further study of fine root dynamics in Ca-amended forest soils is needed to clarify the mechanisms of forest ecosystem responses to base cation depletion and its mitigation.

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563

Draft

Table 1. Forest composition and structure in Watershed 1 in 2001. All trees ≥ 2 cm included. Only areas of watershed defined as hardwood forest included. Standard error (se) is the sampling error for the 25 x 25m plots included in each elevation zone (Low = 488-565 m elevation; Mid = 565-660 m; High = 660-747 m).

	Low (n = 54)		Mid (n = 47)		High (n = 26)	
	mean	se	mean	se	mean	se
Density (# ha ⁻¹)	2,031	95	2,147	99	2,852	199
Basal area (m ² ha ⁻¹)	31.3	0.9	28.4	0.8	26.3	0.8
Aboveground biomass (Mg ha ⁻¹)	281.0	9.5	203.4	8.4	115.3	5.3
(% basal area)						
American beech	12		25		46	
Sugar maple	43		45		23	
Yellow birch	23		27		10	

571 Table 2. Soil pH (in water), base saturation and pools of exchangeable cations at three depths
 572 before (1998) and 11 years after (2010) wollastonite (Ca Si O_3) treatment of Watershed 1 at the
 573 Hubbard Brook Experimental Forest, New Hampshire. "Oie" refers to the combined Oi and Oe
 574 soil horizons. Adapted from Johnson et al. (2014).

575

Soil property	Depth	1998	2010
pH in water	Oie	3.88	4.71
	Oa	3.82	4.42
	0-10	3.96	4.16
Base saturation (percent)	Oie	49	83
	Oa	33	61
	0-10	12	19
Exchangeable Ca ($\text{kmol}_c \text{ ha}^{-1}$)	Oie	2.1	9.8
	Oa	4.4	4.8 ns
	0-10	3.2	3.7 ns
Exchangeable Al ($\text{kmol}_c \text{ ha}^{-1}$)	Oie	0.50	0.51 ns
	Oa	9.6	3.4
	0-10	30.5	22.2

576

577 ns – no statistically significant difference between 1998 and 2010.

Table 3. Fine root biomass (A. <1mm and B. 1-2 mm) in three elevation zones of reference and treated (WS1) watersheds before (1998) and 14 years after treatment (2013) with calcium silicate. Mean +/- standard errors (n = 12).

A. <1 mm roots		Fine root biomass (g/m ²)			
		1998		2013	
		REF	W1	REF	W1
Low	FF + 0-5	289.8 ± 39.9	230.4 ± 28.1	257.9 ± 27.7	196.1 ± 21.2
	5-10	67.7 ± 3.8	155.4 ± 17.3	122.0 ± 18.9	85.0 ± 8.7
	10-15	54.8 ± 9.3	96.2 ± 11.3	62.0 ± 9.2	86.5 ± 11.8
	15-20	45.5 ± 9.8	91.3 ± 14.6	45.5 ± 12.8	69.7 ± 8.5
	Total	457.6 ± 58.6	573.3 ± 32.5	487.5 ± 48.2	437.3 ± 29.2
Mid	FF + 0-5	194.8 ± 24.5	316.4 ± 42.2	187.7 ± 25.4	218.5 ± 22.3
	5-10	74.4 ± 18.4	131.0 ± 26.0	86.3 ± 7.9	93.5 ± 5.6
	10-15	55.5 ± 12.6	85.5 ± 9.2	77.9 ± 11.0	78.3 ± 6.0
	15-20	47.0 ± 7.8	117.1 ± 48.1	56.0 ± 11.5	84.0 ± 10.4
	Total	371.6 ± 34.4	650.0 ± 52.2	407.9 ± 29.3	474.3 ± 33.5
High	FF + 0-5	221.9 ± 50.2	178.3 ± 27.5	239.3 ± 35.5	139.5 ± 18.6
	5-10	106.9 ± 17.1	90.2 ± 11.3	80.4 ± 9.0	52.0 ± 6.5
	10-15	90.3 ± 15.9	66.9 ± 9.6	64.3 ± 8.8	43.7 ± 3.6
	15-20	49.7 ± 13.2	110.9 ± 33.0	69.9 ± 11.6	38.6 ± 4.0
	Total	468.9 ± 36.9	446.2 ± 24.0	453.9 ± 42.1	273.7 ± 23.8
B. 1-2 mm roots		Fine root biomass (g/m ²)			
		1998		2013	
		REF	W1	REF	W1
Low	FF + 0-5	120.4 ± 18.5	67.9 ± 17.2	52.09 ± 10.7	66.0 ± 17.2
	5-10	31.1 ± 4.8	31.1 ± 7.7	27.6 ± 4.5	27.4 ± 5.0
	10-15	34.9 ± 8.8	39.8 ± 13.4	23.6 ± 7.5	29.5 ± 5.6
	15-20	13.3 ± 6.1	58.6 ± 18.7	23.1 ± 14.2	31.7 ± 8.2
	Total	199.8 ± 24.0	197.4 ± 8.4	126.5 ± 6.9	154.6 ± 9.1
Mid	FF + 0-5	40.7 ± 15.9	64.1 ± 17.3	44.4 ± 8.3	68.8 ± 14.6
	5-10	43.2 ± 7.8	49.6 ± 14.4	46.6 ± 9.0	31.6 ± 6.4
	10-15	34.7 ± 9.3	55.4 ± 12.1	40.0 ± 5.7	27.2 ± 6.7
	15-20	21.4 ± 3.7	40.6 ± 8.6	38.8 ± 9.9	53.7 ± 13.4
	Total	140.0 ± 4.9	209.7 ± 5.0	169.7 ± 1.8	181.2 ± 9.7
High	FF + 0-5	96.2 ± 25.4	61.8 ± 18.1	93.5 ± 17.0	41.5 ± 4.0
	5-10	16.4 ± 5.3	28.2 ± 8.9	33.2 ± 10.3	13.3 ± 5.1
	10-15	25.2 ± 9.3	28.6 ± 5.9	34.8 ± 6.1	18.6 ± 3.9
	15-20	10.7 ± 8.0	24.1 ± 5.1	27.6 ± 6.5	12.0 ± 3.5
	Total	148.5 ± 19.9	142.7 ± 8.8	189.2 ± 15.5	85.4 ± 6.9

584 Table 4. Analysis of variance table for best model of log (fine root biomass, g m^{-2}) comparing
 585 reference and treated (WS1) forest at three elevations (low, mid, high) before and 14 years
 586 after (Time) treatment with wollastonite (calcium silicate). Treatment effect in BACI design is
 587 indicated by Treatment:Time interaction.

Coefficients	Estimate	Std. Error	T value	Pr (> t)
(Intercept)	5.92821	0.07856	75.465	< 2e-16
Treat	-0.17968	0.08963	-2.005	0.047061
Time	-0.14034	0.09214	-1.523	0.130170
Elevlow	0.25928	0.07872	3.294	0.001275
Elevmid	0.16209	0.07606	2.131	0.034968
Treat:Time	0.42763	0.12664	3.377	0.000968

588

589 **Note:**

590 Residual standard error: 0.3686 on 130 degrees of freedom

591 Multiple R-squared: 0.1605, Adjusted R-squared: 0.1283

592 F-statistic: 4.972 on 5 and 130 DF, p-value: 0.0003364

Table 5. Analysis of variance table for best model of fine root:leaf biomass ratio comparing reference and treated (WS1) forest two years and 14 years after treatment with wollastonite (calcium silicate). Treatment effect in BACI design is indicated by Treatment:Time interaction.

Coefficients	Estimate	Std. Error	T value	Pr (> t)
(Intercept)	0.034213	0.002908	11.767	< 2e-16
Time	0.006659	0.004238	1.571	0.11855
Treat	0.013630	0.004112	3.315	0.00118
Treat:Time	-0.019575	0.005994	-3.266	0.00139

Note:
Residual standard error: 0.01745 on 132 degrees of freedom
Multiple R-squared: 0.09549, Adjusted R-squared: 0.7493
F-statistic: 4.645 on 3 and 132 DF, p-value: 0.004035

602 Table 6. Relative change (%) in aboveground live biomass by species and elevation zones
 603 between the beginning of treatment (2001/2002) and 2011/2012 in reference (WS6) and Ca-
 604 treated (WS1) watersheds at the HBEF. Relative change calculated as the difference in biomass
 605 between earlier and later inventory. Includes all trees ≥ 2 cm.

	Low	Mid	High
WS6 (2002 to 2012)			
Beech	-20.1	16.2	10.1
Sugar maple	-2.8	-12.5	-13.8
Yellow birch	-0.7	-8.4	5.7
All	-3.2	-6.9	0.7
WS1 (2001 to 2011)			
Beech	-4.2	-0.1	15.2
Sugar maple	2.1	10.1	24.3
Yellow birch	-9.7	-11.3	-2.8
All	2.7	1.3	5.1

606

FIGURE CAPTIONS

Figure 1. Fine root (< 1mm diameter) biomass in a. treated (Watershed 1) and b. reference northern hardwood forests in three elevation zones before (1998) and 14 years after treatment (2013) with calcium silicate. Error bars indicate standard errors (n = 12).

Figure 2. Ratio of fine root (< 1 mm) mass (g/m²) to leaf litterfall mass (g/m²) in a. treated (Watershed 1) and b. reference northern hardwood forests in three elevation zones two years (2001) and 14 years after treatment (2013) with calcium silicate. Error bars indicate standard errors (n = 12).

Figure 3. Depth distribution of fine roots in a. treated (Watershed 1) and b. reference northern hardwood forests in the high elevation hardwood zone before (1998 dashed) and 14 years after treatment (solid) with calcium silicate. Shaded areas indicate 95% confidence intervals around the regression lines.

FIGURE 1

FIGURE 2

FIGURE 3