Calcium Depletion as a Limitation to Tree Growth and Carbon Sequestration within the Northern Forest

Theme #2

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Key Results:

• Long-term calcium (Ca) addition improved the crown condition and growth (increased carbon (C) sequestration) of sugar maple trees, but had little influence on co-occurring American beech.
• Long-term aluminum (Al) addition produced signs of stress (e.g., membrane damage in roots) in sugar maple trees, whereas sympatric beech showed few signs of stress and actually increased in growth.
• Differential responses of sugar maple and beech to changes in soil cation nutrition could favor beech over sugar maple if acidic inputs continue to deplete Ca and increase the availability of Al.

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Project Summary

- **Rationale**: continued inputs of acid deposition are depleting Ca and increasing the availability of potentially phytotoxic Al in regional soils.

- **Methods**: we evaluated the radial growth and physiology of sugar maple and American beech trees in a long-term Ca- or Al-addition study to see how these species responded to changes in these cations that reflect the influences of continued acid inputs.

- **Major findings**: The response of trees varied with treatment, tree species and measurement parameter. In general, sugar maple trees had a positive response to Ca addition (e.g., increasing their radial growth) and a negative response to Al treatment (e.g., showing increased root damage). In contrast, beech experienced no benefit from Ca addition, and showed a recent positive response (e.g., increased growth) to Al addition.

- **Implications for the Northern Forest**: Differential responses of sugar maple and beech to changes in soil cation nutrition could favor beech over sugar maple if acidic inputs continue to deplete Ca and increase the availability of Al.
Background and Justification

Numerous reports indicate that inputs of acidic deposition and other anthropogenic factors are depleting Ca from forest soils within the Northern Forest and elsewhere. Because Ca is a biologically essential element, anthropogenic alterations of this cation may have serious implications to forest health and productivity. Indeed, Ca depletion has been implicated in the decline (crown thinning, reduced growth and increased mortality) of at least two tree species in the Northern Forest - red spruce and sugar maple. Ca is an important structural component of woody cell walls and its availability modulates aspects of carbohydrate metabolism including photosynthesis and respiration, and the formation and/or breakdown of various carbohydrates. Considering these functions, likely consequences of tree Ca deficiencies include reductions in structural C gains (woody growth/biomass) and alterations in non-structural carbohydrates (including spring sucrose levels that fuel woody growth and leaf formation, and are the foundational basis for the maple syrup industry). Additionally, Al mobilization by acidic inputs competitively inhibits Ca uptake, and can be independently toxic. The goal of our project was to test the hypothesis that soil Ca depletion and increased soil Al may be reducing tree growth and C sequestration within hardwood trees of the Northern Forest.
Methods

We tested this hypothesis by measuring above ground woody annual increments and stored shoot carbohydrates (starch and soluble sugars) for dominant and codominant sugar maple and American beech trees growing in the NuPert Study - a long-established and replicated Ca- and Al-addition study at the Hubbard Brook Experimental Forest (HBEF) in Thornton, NH. This study provided multiple advantages for evaluating the potential influence of Ca depletion on C sequestration, including: 1) soil Ca depletion was well documented in this area, and 2) Ca manipulation treatments were long-standing and have had time to influence tree physiology. Indeed, Ca addition in this study has already significantly increased growth for smaller sugar maple trees, and there is emerging data showing that Al addition has influenced tree physiology at the site. Because the study design compares ambient Ca depletion (control plots) to potential further Ca depletion (reduced Ca availability on Al-addition plots) relative to historically more typical levels of Ca availability (Ca-addition plots), it provides an indication of contemporary and possible future impacts of Ca depletion in comparison to simulated pre-pollution levels of Ca availability. This unique design increases the policy relevance of study findings and has bearing on the management of forests to preserve health, productivity and C sequestration.
Methods – soil-based measures

• Root cation concentrations (ICP-AES)

• Root injury (relative electrolyte leakage: REL)

• Extracellular Enzyme Activity (EEA: a measure of soil enzymes of plant and microbial origin)
Root Measurements

- Fine roots (≤ 2 mm) were collected for each of the five dominant sugar maple trees/plot.
- Membrane integrity of fine roots was measured using a conductivity bridge to assess relative electrolyte leakage (REL).
- Cation concentrations were assessed using ICP-AES analysis (see foliar methods).
Soil Collection for EEA

• Cores collected Fall 2007 & Spring 2008.
• 3 random samples per plot interior. (n = 36 per date)
• Packed in dry ice for transport.
• Kept at - 80°C in lab until analyses.
Methods – Soil EEA

- Frozen soil cores thawed & processed immediately.
- Samples homogenized in buffer sol’n at ambient soil pH.
- Micropipetted into 96-well plates with MUF substrates, then incubated.
- EEA was measured fluorometrically.
Methods – Soil EEA

• Integrative measure.
• Measures the activity of enzymes that catalyze decomposition & mineralization.
• EEA assayed: Phosphatase, Sulphatase, β-glucosidase, β-cellobiosidase, Xylosidase, Chitinase, & Serine Protease.
Methods – above-ground physiology

• Woody growth – xylem increment cores
• Foliar cation nutrition – ICP analysis
• Foliar antioxidant enzyme activity
• Foliar and shoot soluble carbohydrates (sugars and starch)
Tree Sample Collection

- Foliar enzymes and foliar/shoot carbohydrates.
- Sun-lit foliage & woody shoots collected with shotguns.
- Packed in dry ice for transport.
- Kept at -80°C in lab until analyses.
Methods – Foliar Elemental Analysis

• Foliage was dried, ground, and digested using sulphuric acid.
• Elemental analysis was conducted by ICP-AES.
• Cation concentrations of Al, Ca, K, Fe, Mg, Mn, and P determined.
Methods – Foliar Antioxidants

• Leaf tissue frozen in liquid N, ground, homogenized in an extraction solution, and centrifuged.

• Enzyme activities of APX, GR, and CAT measured spectrophotometrically and activity expressed as μmol product min\(^{-1}\)mg\(^{-1}\).
Methods – Soluble Carbohydrates

- Foliar cuticular waxes were removed.
- Pith, bark, phloem and cambium were removed from shoot samples.
- Extracted into 80% ethanol, centrifuged.
- Total sugars, sucrose, glucose, fructose, xylose, & raffinose determined using a Waters HPLC.

Carbohydrate peaks
Tree Sample Collection

• Xylem increment cores.
• 2 cores/tree.
• Dominant sugar maple, co-dominant/intermediate sugar maple and beech.
• Growth assessed as basal area increment (BAI).
Statistical Analyses

- ANOVA
- Nested design for tree measures
- Nested design for individual EEA measures
- Crossed design for soil assays across EEA systems (plot means)
- Correlations among leaf-based measures
Sugar maple trees in treated plots had greater root concentrations of Ca and Al, consistent with treatment application. This suggests that roots are a better indicator of Al treatment and uptake than foliar-based measures, which appeared unresponsive to Al treatment.

Membrane leakage of sugar maple fine roots (an indicator of stress) was significantly reduced for trees in Ca-addition plots, and greatest in Al-addition plots, suggesting that Ca:Al balance is critical to maintaining root health.

Soil extracellular enzyme activities (EEA: a measure of enzyme activity from both roots and microbes) highlight treatment-induced alterations to generalized soil processes. Across soil enzyme systems EEA levels were greatest in Al-addition plots in fall, but were elevated in Ca-addition plots in spring compared with ambient conditions. This suggests a differential impact of treatment to soil communities across the seasons.

The impacts of soil Ca and Al treatment were evident at the root and broader soil community level (as indicated by EEA data). However, soil treatments also translated into significant changes in the above-ground function of trees (see next slide).
We measured foliar elemental concentrations, foliar antioxidant enzyme activities, foliar and woody shoot carbohydrates in sugar maple trees. Ca additions were associated with greater Ca concentrations in foliage compared to leaves from trees in control and Al-addition plots. Al additions were associated with lower foliar phosphorus concentrations in comparison with foliage from trees in Ca-addition plots. Although Al concentrations in leaves appeared unaffected by soil Al-treatment, additions of Al to soil were associated with higher antioxidant enzyme (glutathione reductase and ascorbate peroxidase) activities in foliage and lower shoot sugar (total sugars, sucrose, glucose and fructose) concentrations relative to trees in Ca-addition and control plots.
Results/Project outcomes
Radial Growth of Maple and Beech

• Dominant sugar maple experienced sharp declines in growth for two years following the 1998 ice storm, and declines were indistinguishable among soil treatments.

• Co-dominant and intermediate sugar maple and American beech experienced the inverse response to the ice storm – increased radial growth, presumably due to canopy release after dominant trees experienced ice-associated branch loss.

• Dominant maples on Ca-addition plots tended to have greater growth than similar trees on Al-addition and control plots, but treatment differences were not significant, presumably as a result of increased variability in growth following the ice-storm.

• Co-dominant and intermediate sugar maple experienced greatest radial growth in trees on Ca-addition plots through 2007 compared to Al-addition and control plots.

• American beech growth was not affected by treatment until 2007 and 2008 when trees growing on Al-addition plots experienced greater radial growth than those on control and Ca-addition plots.
In general, Ca addition had positive influences on sugar maple growth and carbon relations, but shows no signs of influencing beech growth.

There are indications that Al addition is negatively impacting sugar maple health, but beech on Al-addition plots have experienced increased growth in recent years.

Differential responses of sugar maple and beech to changes in soil cation nutrition could favor beech over sugar maple as acidic inputs continue to deplete Ca and increase the availability of Al.

Because our Ca treatment reflects pre-pollution soil Ca levels and Al treatment mimics soil cation status projected with future pollution loading, our treatments provide an indication of possible impacts over time.
Future directions

• We plan to continue monitoring tree productivity and physiology at the NuPert plots to evaluate long-term impacts of Ca and Al addition – especially relative to ambient controls, which are a surrogate for regional native forests and often show impacts intermediate to Ca and Al treatments.

• We also plan to expand monitoring at NuPert to assess treatment impacts beyond the tree – including higher trophic levels.

• Plans are also underway to relate results from the NuPert plots to the broader landscape via collaboration with scientists that map and model pollution inputs, critical loads, and exceedance levels.
List of products
Presentations at Scientific Conferences


List of products
Theses/Dissertations


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Manuscripts in preparation for submission to scientific journals


Questions?

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