



Experimental reversal of soil acidification in a deciduous forest: Implications for seedling performance and changes in dominance of shade-tolerant species



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ABSTRACT

Acer saccharum Marsh. (sugar maple) and the less valuable *Fagus grandifolia* Ehrh. (American beech) are the dominant shade-tolerant canopy species over large forest tracts in northeast North America. Negative effects of soil acidification on sugar maple could favor greater dominance of beech in the “zero-sum game” dynamics of closed-canopy forests. A watershed-level Ca addition experiment, reversing some effects of acidification (including pH and Ca availability), provided an opportunity to test effects on beech and sugar maple seedling performance over 5 yrs, under different canopy species. Ca addition almost doubled leaf area of sugar maple and increased that of beech by over 40%. However extension growth was increased only in sugar maple. Both the direction of effects and the relative performance of maple and beech were consistent across canopy species. We combine our results and other evidence into a conceptual model of how soil acidification and Ca depletion is shifting the competitive balance in the seedling stage toward beech, implying an increase in beech relative abundance in the canopy, unless compensated by other factors, such as beech bark disease. These findings, and mounting evidence of other negative effects of soil acidification, suggest re-examination of the cost-effectiveness of chemical remediation in some poorly buffered forested watersheds.

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1. Introduction

Acidification of poorly buffered forest soils in northeastern North America leads to depletion of essential cations and increased availability of other, potentially toxic elements. These changes may be causing declines in sensitive species, and increases in species more tolerant of soil acidification. Specifically, there is concern that Ca depletion and Al toxicity may contribute to decline in *Acer saccharum* (Marsh.), sugar maple (Juice et al., 2006), and a concomitant increase in the much less valuable *Fagus grandifolia* Ehrh. (American beech) (Duchesne and Ouimet, 2009). For brevity, we refer to these species as maple and beech. At the Hubbard Brook Experimental Forest (HBEF) in New Hampshire USA, where soil acidification is well documented (Gbondo-Tugbawa and Driscoll, 2003), Ca was added to an entire watershed in 1999 to experimentally reverse some of the changes due to soil acidification, and to test ecosystem and organism responses (Cho et al., 2010). Tree species that respond most positively to the experimental Ca addition should be those that suffer most from acidification and Ca

depletion, and would benefit most from reduction in air pollution that drives soil acidification. This logic is central to the development of this paper.

At the HBEF, in samples taken at similar elevation to our study site, the forest is heavily dominated by maple (33%), yellow birch (*Betula alleghaniensis*, 29%) and beech (23%), where percentages refer to total above and below ground biomass, calculated from data in Siccama et al. (2007). In this paper, we focus on maple and beech, which have similar shade-tolerant life-histories, and occur as the late successional co-dominants over large tracts of eastern North America (Braun, 1950). Their competitive balance in beech–maple forests has been the focus of numerous theoretical and empirical studies (reviewed in Takahashi et al., 2010). In closed-canopy forests, the dynamics of competing canopy species are constrained by available canopy space, such that losses in canopy dominance by one species are balanced by gains in other species (sometimes described as a “zero-sum game”).

Fig. 1 represents a logical and empirical framework to assess the consequences of soil acidification for changes in the relative success of maple and beech in gaining canopy dominance. Fig. 1A shows hypothesized effects (in pale gray) of reversal of acidification that would increase the overall performance (establishment, growth and survival) of maple relative to beech. The results of testing such hypotheses then determine the inferences (Fig. 1B)

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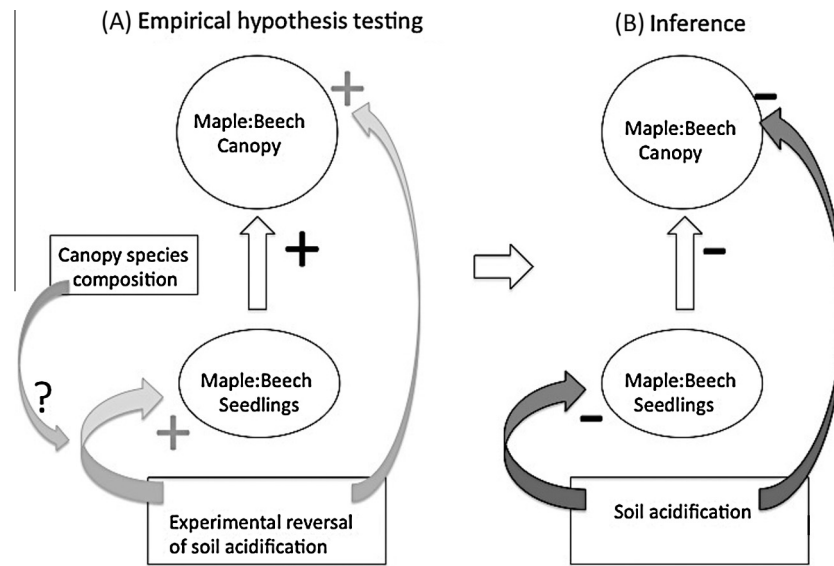


Fig. 1. Hypotheses and inferences, regarding effects of soil acidification on the relative performance of sugar maple and beech at Hubbard Brook Experimental Forest (HBEF), NH. Figure includes information from the literature as well as findings from this study. Maple:beech represents performance of maple relative to beech, in the canopy and seedling layers (see details in text). Pale gray, filled arrows on left (A) represent hypotheses. Dark gray, filled arrows on right (B) represent inferences from testing those hypotheses. Black, unfilled arrows in both A and B represent logical connections: increased (relative) maple performance at the seedling stage leads to higher (relative) recruitment of maple to the canopy, unless compensatory trends occur between seedling and canopy stages. Black, unfilled arrow in center connects the testing of effects of reversal of soil acidification (on left, A), with inferences (on right, B) regarding anthropogenic soil acidification effects. Reversal of soil acidification enhanced relative performance of maple both in seedlings (this study and evidence from literature) and in the canopy (evidence from literature). Effects of reversal of acidification on maple:beech seedling performance did not depend on the identity of the canopy species above (this study), so Canopy Species Composition is omitted from inferences on right (B). Overall, findings from this and other studies imply that soil acidification is reducing maple dominance relative to beech.

regarding the effects of anthropogenic soil acidification on the relative dominance of maple and beech.

If reversal of soil acidification increases the seedling performance of maple relative to beech (Fig. 1A, lower left, gray “+” arrow), the representation of maple relative to beech in the canopy would be increased (center, black unfilled “+” arrow) unless compensatory trends occur between the seedling and canopy stages. A potential complicating factor (left gray arrow, marked “?” because there is no a priori directional hypothesis) is that the species of canopy tree dominating a local area could influence whether and how Ca addition to the soil affects the seedling performance of beech and/or maple seedlings under its canopy. The empirical research in this paper addresses these hypotheses (lower two gray arrows in Fig. 1A).

Reversal of soil acidification can also affect canopy trees directly: the right, gray “+” arrow in Fig. 1A represents the hypothesis that Ca addition favors the performance of canopy maple relative to canopy beech. In Section 4, we summarize the evidence from original research from this study, along with other relevant evidence from the HBEF and other northern hardwood sites, to assess the support for the hypotheses in Fig. 1A (reversal of soil acidification, all three gray arrows). On that basis, we develop inferences regarding the effects of anthropogenic acidification of forest soils in northern hardwood forests on the competitive balance between maple and beech (Fig. 1B).

In the remainder of Section 1, and in Sections 2 and 3, we focus on testing the hypothesis that reversal of soil acidification favors maple seedlings relative to those of beech. To do so, we compare the seedling performance (focusing on extension growth and growth in leaf area) of maple and beech, in both Ca-added and control sites.

Further, we test whether the performance of seedlings depends on which species occupies the canopy above them. The species of canopy tree dominating a local site influences the quantity and quality of litter on the forest floor and key aspects of nutrient dynamics, as demonstrated for northern hardwoods forest by

Finzi et al. (1998) in a study that included both beech and maple. There is also evidence from northern hardwood forests that the species identity of a canopy tree results in plant-soil feedbacks via soil biota under its canopy, which in turn can drive strong species-specific effects on seedling performance (McCarthy-Neumann and Ibáñez, 2012). Thus, to evaluate the implications of seedling performance for canopy replacement and forest dynamics, it is important to test whether the seedling performance of maple relative to beech differs under different canopy species. Specifically, we test whether canopy species identity influences the response of seedlings to Ca addition, which would manifest as a significant interaction between canopy species and Ca treatment. To date, research on the effects of soil acidification (and partial reversal of those effects via Ca addition) on seedling performance have not included assessment of canopy species effects.

For maple, the most abundant species, with known sensitivity to soil acidification, we tested seedling performance under canopy trees of all four of the most abundant canopy species at our research site, i.e. yellow birch and white ash (*Fraxinus americana*), in addition to the focal species, maple and beech. For beech seedlings, for which previous research leads to the expectation of little or no effect of Ca addition, we focus on the beech–maple interaction, comparing beech seedling performance under beech and maple canopies.

2. Methods

The HBEF is an intensively studied northern hardwoods forest in the White Mountains of the northeastern USA, described in detail in Likens and Bormann (1995). Several drainage basins within the HBEF have been designated as experimental watersheds and identified by numbers (e.g. Watershed 1). In 1999, a slow-release form of wollastonite (CaSiO_3) was applied aerially at $0.85 \text{ Mg Ca ha}^{-1}$ to the entire Watershed 1 (Peters et al., 2004). The substantial increases in pH and Ca content in the forest floor, which apparently peaked in 2002–2004, are described in Groffman et al. (2006) and

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