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Soil Base Saturation Combines with Beech Bark Disease to Influence Composition and Structure of Sugar Maple-Beech Forests in an Acid Rain-Impacted Region

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ABSTRACT

Sugar maple, an abundant and highly valued tree species in eastern North America, has experienced decline from soil calcium (Ca) depletion by acidic deposition, while beech, which often coexists with sugar maple, has been afflicted with beech bark disease (BBD) over the same period. To investigate how variations in soil base saturation combine with effects of BBD in influencing stand composition and structure, measurements of soils, canopy, subcanopy, and seedlings were taken in 21 watersheds in the Adirondack region of NY (USA), where sugar maple and beech were the predominant canopy species and base saturation of the upper B horizon ranged from 4.4 to 67%. The base saturation value corresponding to the threshold for Al mobilization (16.8%) helped to define the species composition of canopy trees and seedlings. Canopy vigor and diameter at breast height (DBH) were positively correlated ($P < 0.05$) with base saturation for sugar maple, but unrelated for beech. However, beech occupied lower canopy positions than sugar maple, and as base saturation increased, the average canopy position of beech decreased relative to sugar maple ($P < 0.10$). In low-base saturation soils, soil-Ca depletion and BBD may have created opportunities for gap-exploiting species such as red maple and black cherry, whereas in high-base saturation soils, sugar maple dominated the canopy. Where soils were beginning to recover from acidic deposition effects, sugar maple DBH and basal area increased progressively from 2000 to 2015, whereas for beech, average DBH did not change and basal area did not increase after 2010.

Key words: sugar maple; American beech; beech bark disease; acidic deposition; soil calcium depletion; red spruce; base saturation; soil aluminum; base cation surplus.

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INTRODUCTION

Decades of acidic deposition (acid rain) have altered forest soils throughout eastern North America by decreasing the availability of calcium (Ca) while increasing the mobility of aluminum (Al) in the rooting zone (Johnson and others 2008; Warby and others 2009). Research on how these soil changes have affected forests has been limited largely to studies of individual tree species including sugar maple (*Acer saccharum* Marsh.), an abundant and highly valued species of northern hardwood forests in eastern North America. Sugar maple has a high Ca demand relative to most tree species in northern hardwood forests, but is nevertheless found over a wide range of soil chemistry, including soils where acidic deposition has substantially lowered Ca availability (Long and others 2009). Research on sugar maple has linked decreased soil Ca to elevated mortality, poor stand health, impaired regeneration, and reductions in growth in Quebec (Duchesne and others 2002) and the northeastern USA (Schaberg and others 2006; Long and others 2009; Sullivan and others 2013a). Because sugar maple is one of the most abundant species in northern temperate forests, acidic deposition effects on its growth and health are likely to play an important role in stand dynamics. However, little research has been done on how acidic deposition has affected the composition and structure of tree communities.

Throughout the period of acidic deposition (from about the mid-twentieth century to the present), beech bark disease (BBD) has been infecting American beech trees (*Fagus grandifolia* Ehrh.) over much of its northern range (Houston 1994) where it often grows abundantly in association with sugar maple (Burns and Honkala 1990). In the northeastern USA and eastern Canada, beech trees are considered to be in the aftermath of the initial infection wave of BBD (Cale and others 2015). The disease is spread by a non-native invasive insect that damages bark, allowing infection by one of two species of fungi that eventually kills the tree (Cale and others 2015). The mortality rate of BBD has been found to increase with tree size, but many trees survive long enough to grow into the canopy (Garnas and others 2011). The disease often results in aggressive beech regeneration through root sprouts and seed production that create a dense understory of seedlings and saplings (Giencke and others 2014) and has led to a shift toward smaller beech trees in the aftermath forest that are sufficiently abundant to maintain the pre-infection basal area of the species despite the BBD-induced mortality (Garnas and others 2011).

A few studies have addressed possible detrimental and beneficial effects of BBD on sugar maple abundance and growth, but results are limited and inconsistent. In Quebec forests, where soil Ca depletion was linked to sugar maple decline, relative basal area of dead sugar maple was positively correlated with live basal area of beech (Duchesne and Ouimet 2009, 2011). The absolute and relative basal area of beech was also found to be inversely correlated with soil Ca concentrations. These factors suggested that loss of sugar maple from soil Ca depletion was contributing to the expansion of beech in Quebec. However, in forests in southeastern New York (NY), formerly co-dominated by beech and sugar maple, a shift toward sugar maple dominance was found to be positively correlated with severity of BBD. This shift in species coincided with an increase in exchangeable base cation concentrations in the forest floor, which was suggested as a positive feedback for sugar maple through improved soil nutrition (Arthur and others 2017).

Further investigation is needed to resolve how acidic deposition and BBD combine to influence the widespread forests of eastern North America where sugar maple and beech grow together. Because acidic deposition effects on forests are mediated through soils, appropriate measurements are needed to relate acidic deposition effects on soils to measurements of tree condition. Much of the currently available information on this subject has been derived from controlled experiments done with manipulated soils that do not well represent natural forest soils (Cronan and Grigal 1995). The ratio of Ca/Al in soil solutions has received the most attention as a stress indicator because (1) Ca is an important nutrient, and (2) certain forms of Al are often harmful to plants, causing problems such as increased mortality of fine roots (Godbold and others 2003) and impairment of Ca uptake (Cronan and Grigal 1995). Furthermore, as exchangeable Ca decreases from acidic deposition, buffering in soils shifts from Ca to Al at a threshold seen in modeling of cation exchange equilibria (Reuss 1983), site comparison studies (Cronan and Schofield 1990), and long-term monitoring of forest soils (Lawrence and others 2005). In well-buffered soils, base saturation may or may not decrease from acidic deposition, but base saturation will remain sufficiently high to prevent Al mobilization.

Despite the relationships observed between Ca/Al ratios of soil solutions and tree stress, the difficulties of measuring Al concentrations in natural forest soil solutions have limited the application of this indicator. Base saturation, a more easily measured soil characteristic than soil-water Al concentrations, could provide a useful alternative to Ca/Al ratios. The base saturation value at which the Al mobilization threshold occurs was estimated from exchange equilibria equations to be between 15 and 20%, regardless of cation exchange capacity (Reuss 1983). Limited field data also support Al mobilization in soil solutions below a base saturation of 20% (Cronan and Schofield 1990). These factors suggest that measurements of soil base saturation could be used as a practical substitute for Ca/Al ratios for assessing acidic deposition effects on forests.

Additional research is needed to better understand how acidic deposition has affected forests, but as this work continues, consideration must also now be given to soil changes associated with recovery. Decreased mobilization of Al and stabilized Ca concentrations were evident in the most recent soil monitoring data available for eastern North America (Lawrence and others 2015). At this time, it remains uncertain how acidic deposition decreases are guiding the processes and rates of soil recovery, although these soil changes may already be affecting forest communities.

To investigate possible effects of acidic deposition and BBD on hardwood forests, we have related available data on soil and stream chemistry to stand characteristics in 21 watersheds throughout the Adirondack region in northeastern NY. This region well represents the large areas of eastern North America that have experienced decades of both acidic deposition and beech bark disease, but are showing signs of recovery from acidic deposition. The primary objectives of this paper are to: (1) verify the relationship of base saturation to the Al mobilization threshold, (2) determine if the species composition of sugar maple-beech forests is related to base saturation, (3) evaluate how base saturation and BBD combine to influence the stand composition and structure, and (4) investigate temporal dynamics of a sugar maple-beech forest in an intensively monitored watershed where BBD is severe and soil shows the beginnings of recovery from acidic deposition.

METHODS

The study was located in the western and central parts of the Adirondack region of New York, where extensive research has been conducted on the effects of acidic deposition on surface waters and soils. Atmospheric wet deposition data for this analysis were obtained from the National Atmospheric Deposition Program (NADP) Site NY29, which is centrally located within the Adirondack region. (http://nadp.sws.uiuc.edu/data/sites/sitedetails.aspx?id=NY20&net=NTN; accessed July 6, 2016).

Study Design for Soil and Vegetation Analyses

This analysis utilized soil and vegetation data collected in watersheds previously studied in the Adirondack Sugar Maple Project (ASMP). Previous results of the ASMP, published in Sullivan and others (2013b) and Bishop and others (2015), focused exclusively on sugar maple. Repeated soil sampling to evaluate possible changes in soils from acidic deposition was not done within the ASMP watersheds, but Sullivan and others (2006), Johnson and others (2008), and Warby and others (2009) each documented acidic deposition effects on soils with repeated soil sampling conducted throughout the ASMP study region.

In the ASMP study design, two or three plots (20 by 50 m) were established in each of 20 small watersheds (< 1 km^2) that were selected to provide a wide range of Ca availability based on the chemistry of streams and soils determined in previous Adirondack studies (Lawrence and others 2008a; Page and Mitchell 2008). Plots contained approximately 50 trees larger than 10 cm diameter at breast height (DBH). Each of the fifty total plots contained three or more sugar maple trees that were (1) greater than 35 cm DBH and (2) of suitable form for coring. These criteria ensured that sugar maple trees were common in all study plots. Beech was also common in all 20 watersheds and occurred in all but one of the 50 plots. Photographs taken for general plot information in the ASMP showed BBD in 43 of 50 plots and all 20 watersheds. Although some photographs did not include clear views of beech trees, it was unlikely that BBD was absent from any of the plots other than the single plot that did not have any beech trees. The initial killing front of BBD reached the Adirondack region by the early 1970s (Houston 1994), so the beech in the study plots represented the aftermath forest, as described by Giencke and others (2014). Watersheds were also selected to avoid areas with evidence of logging within the past three to four decades. Plots were located within watersheds to avoid existing gaps in the canopy and to represent the two or three predominant landscape types with respect to vegetation (conifer or hardwood) and topography (hillslopes or relatively level terrain) within each watershed. General landscape characteristics (including slope, hillslope position, aspect, and forest composition) were evaluated through the use of geographic databases, satellite imagery, and field reconnaissance to select plot locations that were generally representative of each watershed.

This analysis also used soil and vegetation data from the 52-ha South Tributary subwatershed of the Buck Creek Long-Term Monitoring Watershed (hereafter the South Buck Watershed) located in the western part of the Adirondack region, near Inlet, NY. More information on the South Buck Watershed is available in Lawrence (2002) and (2011).

Vegetation Measurements

On the ASMP plots, species, DBH, crown position, and canopy vigor were recorded for all trees larger than 10 cm DBH, following the protocols of the North American Maple Project (Cooke and others 1998). Vigor classes were rated as healthy (4), slight decline (3), moderate decline (2), and severe decline (1), with an assumed acceptable error of plus or minus one vigor class. Note that the vigor class ratings used in this paper have been reversed from the North American Maple Project protocols, in which a rating of 1 was the highest vigor (healthy). Crown positions were rated as: dominant (3), codominant (2), intermediate (1), and crowns entirely below the main canopy (0). Trees with DBH above 10 cm and a crown position of 0 were referred to as subcanopy trees. Note that the crown position ratings used in this paper have been reversed from the North American Maple Project protocols, in which a rating of 1 was the dominant canopy position. One 10 by 10 m subplot was established within each plot for enumeration, by species, of saplings between 1 cm and 10 cm DBH. At each of five predetermined locations at 10-m increments along the centerline of the plot, a 1 m by 1 m subplot was established within which the number and species of each tree seedling were recorded. To be counted, the seedling needed to be at least 5 cm tall, have at least two fully formed leaves, and have DBH below 1 cm. All measurements were done during June–July, 2009.

Vegetation measurements in the South Buck Watershed were taken in 15 circular plots (9 m radii) distributed along 7 transects approximately perpendicular to the stream channel. All trees within the plots with DBH of at least 5 cm were identified and measured for DBH at a fixed tag approximately 1.4 m from the ground, in the growing seasons of 2000, 2005, 2010, and 2015. Counts of saplings by species (>1 m high with DBH < 5.0 cm) were also made in 2015. Virtually all trees above 10 cm DBH were infected with BBD.

All vegetation measurements collected in the ASMP and South Buck Watershed plots are available in Lawrence and others (2017a).

Soil Sampling and Analysis

Soils in all study watersheds were classified as Spodosols. All ASMP soil sampling was done in June–July 2009. Three to five shallow reconnaissance soil pits were opened in each plot to evaluate the variation in profile characteristics within the plot. A representative pit was selected for full excavation and mineral soil sampling. The selected pit location was excavated into the C horizon or until an impenetrable layer was reached. The full profile was then described following National Resource Conservation Service (NRCS) protocols (Schoeneberger and others 2012). Profile descriptions are available in Lawrence and others (2017b). Representative soil samples from the upper 10 cm of the B horizon were collected from the pit face. This study focused on the upper 10 cm of the B horizon because fine roots were common in this depth increment, and by keeping the thickness constant, comparability among sampled locations was maximized. Furthermore, the upper B horizon is the layer within the soil profile where Al mobilization from acidic deposition is most prevalent, affecting both this horizon and organic-rich overlying horizons (Lawrence and others 1995). An additional soil pit was also sampled in 10 plots (each in a separate watershed) to assess local variability of soil properties. Analysis of data between replicate pits is available in Sullivan and others (2013b). A comparison was also made between average watershed values for base saturation of the upper B horizon (determined by one or two sampling points per plot) and the A horizon (determined by up to 5 sampling points per plot, depending on horizon presence). The base saturation of these two horizons would be expected to be correlated if variability in each horizon was sufficiently characterized. A high correlation found between the base saturation of the A and B horizons ($R^2 = 0.81$) indicated that the soil variability of the upper B horizon was characterized adequately with this sampling design (Supplemental Figure 1).

Soil samples in the South Buck Watershed were collected from the upper 10 cm of the B horizon in 1998 and again in 2014. Unused portions of the soil samples collected in 1998 were archived, and 27 samples (9 per horizon) were reanalyzed with the samples collected in 2014. Results were compared to evaluate possible biases between analyses of the different collections and to adjust data as needed following the method described in Lawrence and others (2016). Further details of this analysis are provided in supplemental methods along with original and reanalysis data (Supplemental Table 1).

All soil samples were analyzed in the US Geological Survey New York Water Science Center Laboratory (USGS NY Laboratory) for moisture content (oven drying at 65 and 105°C for organic and mineral samples, respectively), exchangeable Ca, Mg, Na, and K (unbuffered 1 M NH_4Cl vacuum extraction), and pH (0.01 M $CaCl_2$ slurry) following USEPA standard methods (Blume and others 1990). Exchangeable Al was determined by 1 M KCl batch extraction and measurement by inductively coupled plasma optical spectrometer (ICP). Exchangeable acidity was determined by 1 M KCl batch extraction and measurement by titration (Thomas 1982). Exchangeable H was calculated by subtracting exchangeable Al from exchangeable acidity. Effective cation exchange capacity was calculated as the sum of exchangeable acidity and exchangeable base cations (Ca, Mg, K, and Na). All data from these chemical analyses are available in Lawrence and others (2017a). Effective base saturation (hereafter base saturation) was calculated as the sum of exchangeable base cations divided by the effective cation exchange capacity. In the calculation of base saturation, Ca was the dominant factor in the numerator and Al was the dominant factor in the denominator so base saturation provided a useful way to express the Ca–Al relationship in these soils. Also, because base saturation incorporates six measurements of soil exchange chemistry, most of the other measurements exhibited covariance with base saturation. For these reasons, base saturation was chosen in this study to serve as the measure to relate to stand composition and structure.

Stream Water Collection and Chemical Analysis

The harmful forms of Al released by acidic deposition into soil water not only affect forests, but are also discharged into streams (Driscoll and others 2001). This enables the chemistry of headwater streams to be used in assessing Ca buffering and Al mobilization in forest soils. A chemical index of stream water termed the base cation surplus (BCS) has been developed to quantify the status of watersheds with respect to the Al mobilization threshold in soils (Lawrence and others 2007). For values of BCS greater than zero, stream water Al concentrations are essentially zero, which indicates that Al mobilization is minimal or not occurring in the watershed. Values of BCS less than zero correlate linearly with stream concentrations of inorganic monomeric Al, the forms of Al that are mobilized by acidic deposition. Therefore, the BCS value of zero defines the threshold of Al mobilization.

The BCS had not yet been quantitatively related to measurements of base saturation in forest soils so data were compiled from several previous and ongoing USGS Adirondack projects to provide paired soil and stream data for 26 watersheds. Soil data were available from the 20 ASMP watersheds plus four watersheds sampled in 2004 in the Western Adirondack Stream Survey (WASS), and the North and South Buck watersheds (sampled in 1997 and 1998, respectively). The WASS and Buck Creek soil samples were also analyzed in the USGS NY Laboratory following the same chemical analysis methods described above.

Stream samples were collected from 19 watersheds in late March 2004 through the WASS (Lawrence and others 2008a). These stream samples were analyzed in the laboratory of the Adirondack Lakes Survey Corporation (ALSC) for concentrations of constituents needed to calculate the BCS (Ca^{2+}, Mg^{2+}, Na^+, K^+, $SO_4{}^{2-}$, $NO_3{}^-$, Cl^-, and dissolved organic carbon [DOC]), following USEPA-approved methods described elsewhere (Burns and others 2006). Additional stream samples were collected in May 2011 in four ASMP watersheds that did not overlap with the WASS watersheds, and data from early April 2004 were included from the North and South Buck watersheds. Water samples from the four ASMP and two Buck Creek watersheds were analyzed in the USGS NY Laboratory following the methods described in Lawrence and others (2011). Standard operating procedures for water analyses done by the USGS NY Laboratory are available at: https://www.sciencebase.gov/catalog/item/55ca2fd6e4b08400b1fdb88f (accessed August 4, 2017). A total of 155 stream samples collected from 2006 to 2008 were analyzed in both the ALSC and USGS NY laboratories to evaluate consistency of results. Mean differences between laboratory results were less than 5% for constituents used to calculate BCS, with the exception of Ca^{2+} (12%) and $NO_3{}^-$ (7.3%). All stream chemistry data are available at USGS Water Data for the Nation accessed June 1, 2017, at http://waterdata.usgs.gov/nwis/ (site codes listed in Supplemental Table 2), except for data from ASMP site S14, which were obtained from Christopher and others (2006).

Values of BCS were calculated as described in Lawrence and others (2007) from the following equation using chemical concentrations expressed in μeq L^{-1}.

$$\mathrm{BCS} = (\mathrm{Ca}^{2+} + \mathrm{Mg}^{2+} + \mathrm{Na}^{+} + \mathrm{K}^{+}) - (\mathrm{SO}_4^{2-} + \mathrm{NO}_3^{-} + \mathrm{Cl}^{-} + \mathrm{RCOO}_s^{-})$$

where RCOO_s^{-} = the concentration of strongly acidic organic anions.

The concentrations of strongly acidic organic anions were estimated from: $\mathrm{RCOOs}^{-} = 0.071(\mathrm{DOC}) - 2.1$ (Lawrence and others 2007), based on Adirondack stream water samples. Further application and discussion of the BCS is provided elsewhere (Lawrence and others 2008b, 2013).

Analysis of inorganic monomeric Al was also done on stream samples collected in the 20 ASMP watersheds and South Buck Watershed in spring 2004 to provide specific information on acidic deposition effects within the study watersheds. Analysis was done in the ALSC laboratory following USEPA-approved methods described elsewhere (Burns and others 2006). The threshold relationship between the BCS and inorganic monomeric Al described in Lawrence and others (2007) was apparent in the stream chemistry data for the 21 watersheds in this study (Supplemental Figure 2). The occurrence of this form of Al in stream water is a strong indication of Al mobilization in soil by acidic deposition (Lawrence and others 2007). Results presented in Supplemental Figure 2 illustrate the variations in acid buffering among the study watersheds.

Data Analyses

Annual mortality (percent y^{-1}) for beech in the South Buck Watershed was computed as:

$$\text{Mortality rate} = \left[1 - (S/N_0)^{(1/ny)}\right] * 100$$

where S equals number of surviving trees, N_0 equals the initial number of trees, and ny equals the total number of years (Forrester and others 2003).

All soil and vegetation measurements collected in the fifty ASMP plots (2–3 plots per watershed) were analyzed by watershed. Possible correlations between soil and vegetation measurements were evaluated with Pearson product-moment correlation or Spearman's rank correlation if normality was disproven. Statistical differences between groups of watersheds defined by base saturation of the upper B horizon were evaluated using two-tailed t tests, unless normality was disproven, in which case the Mann-Whitney rank sum test was used. Linear regression was used to test for significant trends. Values of $P < 0.10$ were considered to indicate a statistically significant effect. Specific P values are presented where $0.01 < P < 0.10$.

Multivariate changes in species composition relative to soil chemical factors were analyzed using non-metric multidimensional scaling (NMS) in PC-ORD (v. 6.19, McCune and Mefford 2011). Species composition was characterized using proportional species abundance (basal area) in each watershed (ranging from 0 to 1; relative to the total basal area) to account for the variation in the total basal area across all watersheds. Following Peck (2010), NMS was run using autopilot setting set to slow and thorough using Sorensen distances, with a 2-dimensional solution selected based on the scree plots and the stress plot showing statistically significant reduction of stress ($P < 0.05$) to an acceptable stress value (< 15). The effects of species on the ordination, and the potential effects of base saturation on species composition, were explored using joint plots (biplots) based on a second matrix with either species or base saturation data; vectors in joint plots were scaled in proportion to correlation coefficients and shown when $R \geq 0.2$ for the clarity of presentation.

RESULTS

Base saturation in the upper B horizon of 26 watersheds located throughout the Adirondack region was found to be strongly correlated ($P < 0.01$) with BCS values measured in the streams of these watersheds. Linear regression indicated that a BCS value of 0.0 μeq L^{-1}, the value that defines the Al mobilization threshold, approximated a base saturation value of 16.8% (Figure 1). Confidence intervals showed that the intersection of base saturation with a BCS of 0.0 μeq L^{-1} ranged from 13.0 to 20.8% at $P < 0.05$.

Species composition across the watersheds was broadly characterized by two compositional axes (NMS axis 1 and 2; explaining 84.4% of the variation in composition in total) that correlated well with the main environmental gradient along axis 1 described by the concentrations of Ca and Al (Figure 2). Axis 1 (71.2% of the variation) described primarily the gradient from forests dominated by sugar maple (*Acer saccharum*), hophornbeam (*Ostrya virginiana* (Mill.) K. Kock), basswood (*Tilia americana* L.), and white ash (*Fraxinus americana* L.) to forests dominated by American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis*

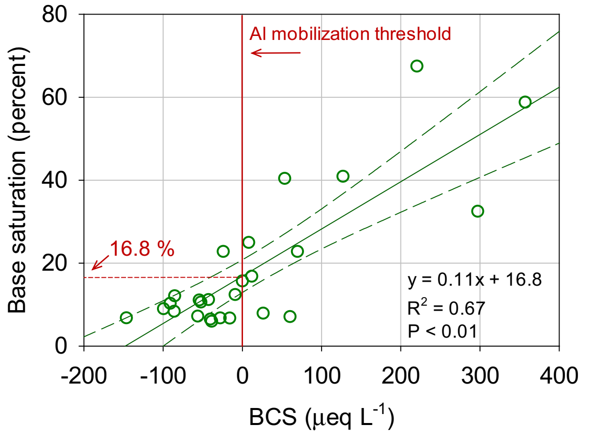

Figure 1. Base saturation of the upper 10 cm of the B horizon as a function of the base cation surplus (BCS) in stream water. Negative BCS values indicate Al mobilization. Confidence interval ($P < 0.05$) is indicated by dashed lines.

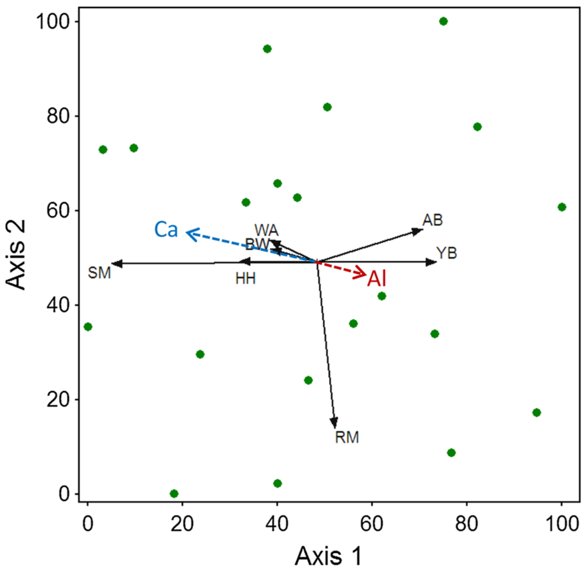

Figure 2. NMS ordination showing differences in tree species composition across the 20 studied watersheds (full circles) and correlations (vectors) of watershed tree species abundance (solid black lines), calcium (Ca, dashed blue line), and exchangeable aluminum (Al, dashed red line) with the ordination axes. Species abundance was expressed as proportional basal area of each species. SM: sugar maple; AB: American beech; YB: yellow birch; RM: red maple; WA: white ash; BW: basswood; HH: hophornbeam.

Britt.). These compositional changes arrayed primarily along the soil acidification gradient described by decreasing Ca and increasing exchangeable Al from left to right (Figure 2). Axis 2 (13.2% of the variation) described primarily the gradient of increasing proportion of red maple (*Acer rubrum* L.). NMS ordination also showed a distinct difference between proportional basal area of sugar maple and beech for individual watersheds when related to base saturation of the upper B horizon (Supplemental Figure 3). Sugar maple proportional basal area was substantially greater in watersheds with relatively high-base saturation, whereas beech showed the opposite relationship.

Soils in all watersheds exhibited low cation exchange capacity, ranging from 1.8 to 10.7 cmol_c kg^{-1} (Lawrence and others 2017b), which reflected the coarse texture of soils typical of the Adirondack region. Values of base saturation in the upper B horizon varied widely among watersheds from 5.9 to 67.4% (Table 1). Eleven of the watersheds had base saturation values of approximately 12% or less and were therefore likely to be subject to Al mobilization. Two watersheds had values that approximated the threshold value of 16.8% (between 15 and 17%), and seven watersheds had base saturation values sufficiently high (above 22%) to prevent Al mobilization.

Total basal area (all species) showed a strong positive relationship with base saturation based on linear regression ($P < 0.01$; $R^2 = 0.44$), and DBH in plots with base saturation in the Al mobilization range were significantly less ($P < 0.01$) than in plots with base saturation high enough to buffer against Al mobilization (Table 1). Sugar maple and beech dominated all of the study watersheds in terms of number of trees, comprising an average of 44 and 40% of all measured trees greater than 10 cm DBH, respectively (Table 1). The abundance (number of trees per ha) of sugar maple, beech, red spruce (*Picea rubens* Sarg.), and yellow birch (*Betula allegheniensis* Britton) were not related to base saturation ($P > 0.10$). However, red maple (*Acer rubrum* L.) and black cherry (*Prunus serotina* Ehrh.) were not found in plots with base saturation values above the threshold of 16.8% base saturation, and white ash, basswood (*Tilia americana* L.), and hophornbeam (*Ostrya virginiana* (Mill.) K. Kock) were not found in plots with base saturation values below 16.8%, with the exception of white ash in one plot with an average base saturation of 12.3 (Table 1).

The DBH of all canopy trees averaged by watershed did not vary with base saturation ($P > 0.10$). When averaged by species, the DBH of sugar maple was positively correlated with base saturation ($P < 0.01$; $R = 0.64$) and the DBH in watersheds with base saturation less than 16.8 were substantially less than those greater than 16.8 ($P < 0.01$), but there was no correlation between these factors for any other species ($P > 0.10$). There was also no relationship between the DBH ratio of beech to sugar maple (plot averages of beech DBH/plot averages of sugar maple DBH) and base saturation ($P > 0.10$).

The canopy vigor rating (which increases with improving canopy condition) averaged by watershed was positively correlated with base saturation for sugar maple ($P = 0.03$; $R = 0.50$) and was significantly higher (indicating better health) at base saturation values above 16.8% than below ($P = 0.016$). The canopy vigor rating for beech was not correlated with base saturation nor were there differences when watersheds were grouped based on the Al mobilization threshold ($P > 0.10$). The canopy vigor rating did tend to be higher for beech than sugar maple in most watersheds, and this relationship was statistically significant in 6 of 11 watersheds with base saturation values below 16.8%, but in only 2 of 7 watersheds with base saturation values above 16.8% (Table 1).

The average crown position rating of beech was lower than for sugar maple in all watersheds (Figure 3). Linear regression also showed that the average crown position rating of beech decreased with increasing base saturation ($P = 0.050$), but that the crown position ratings for sugar maple and red maple were not related to base saturation ($P > 0.10$). There was no linear relationship between base saturation and crown position of beech when values were grouped above or below the Al threshold (Figure 3). However, when expressed as a ratio of beech to sugar maple, a t test showed higher values in watersheds where base saturation values were below the Al mobilization threshold than above the threshold ($P = 0.028$). Overall, these findings indicated that the average crown position of beech was lower in the canopy relative to sugar maple in watersheds with soils buffered against Al mobilization than where Al mobilization occurred. Below the base saturation value at which Al mobilization occurred, red maple had higher average crown position ratings than sugar maple or

Table 1. Watershed Averages of Base Saturation (percent) of the Upper B Horizon, Basal Area ($m^2\ ha^{-1}$), Number of Trees ($trees\ ha^{-1}$) with Diameter at Breast Height > 10 cm, and Canopy Vigor Rating (Color table online).

Watershed Code	Base Sat.	Basal Area	Number of Trees with DBH > 10 cm									Canopy Vigor Rating	
			SM	AB	YB	RS	RM	BC	WA	BW	HH	SM	AB
31009	5.9	34.5	150	283	70	13	17	7				2.18	2.45
17002	6.6	25.8	297	107	17		27	23				1.99	***2.81***
30009	6.6	32.5	220	343	7	10		3				2.02	***2.41***
13008	6.7	30.0	170	350	10		20					2.35	***2.81***
29012	7.0	27.2	320	110			25	30				1.84	***3.45***
26008	7.8	30.6	235	185	20	5	60	20				2.43	***2.95***
35014	8.3	34.3	175	240	20	20	110					2.03	2.15
27019	10.2	30.0	163	183	117		33					2.51	2.29
22019	10.5	32.0	210	210	5	5	45					1.95	2.26
12003	11.1	31.6	333	83	30		53	3				2.38	2.28
9006	12.3	33.6	193	223	33		3	37	10			1.81	***2.33***
28037	15.6	35.8	410	210	50	20	55	80				2.62	2.76
7001	16.7	33.7	257	83	13		3	50				2.25	2.36
AMP	22.7	42.4	90	185	20	20					5	2.33	2.46
WF	24.9	39.2	203	213	23	10						2.69	2.63
N1	32.4	29.5	200	233	10	10			7			2.68	2.76
NW	40.3	45.3	245	155	10				90	20	15	2.24	2.26
28030	40.8	38.0	140	383	3	3						2.17	***2.83***
S14	58.7	47.2	190	185	15	10			35	35	10	2.29	***3.14***
24001	67.4	36.4	290	90					5		15	2.91	2.94

Shading indicates soils in which Al mobilization occurred (yellow), soils at or near the Al mobilization threshold (gray), and soils buffered to prevent Al mobilization (green). SM: sugar maple; AB: American beech; YB: yellow birch; RS: red spruce; RM: red maple; BC: black cherry; WA: white ash; BW: basswood; HH: hophornbeam. Bold italicized font indicates that the canopy vigor rating of AB was higher than SM ($P < 0.05$). Canopy vigor rating increases as canopy condition improves.

beech (Figure 3), whereas in watersheds with base saturation sufficiently high to buffer against Al mobilization, red maple trees (DBH > 10 cm) were absent within and below the canopy.

The total number of canopy trees of all species combined was not related to base saturation ($P > 0.10$) although some species were totally absent either above or below the threshold base saturation of 16.8. There was also no relationship between base saturation and density of saplings plus subcanopy trees for any species when expressed as percent of total saplings plus subcanopy trees. The total percentage of beech saplings and subcanopy trees averaged 77% of the total of saplings and subcanopy trees for all species, with a maximum of 100%, and was less than 50% in only two watersheds. In contrast, the total number of beech in the canopy as a percent of total canopy trees averaged 36%, with a maximum of 65%, and was only greater than 50% in five watersheds. However, the ratio of saplings plus subcanopy trees to canopy trees was consistently higher for beech than sugar maple and this difference was substantially greater ($P < 0.01$) in watersheds where Al mobilization did not occur than where Al mobilization did occur (Supplemental Figure 4). This ratio was not correlated to base saturation for sugar maple ($P > 0.10$), but was positively correlated with base saturation for beech ($P = 0.018$; $R = 0.52$).

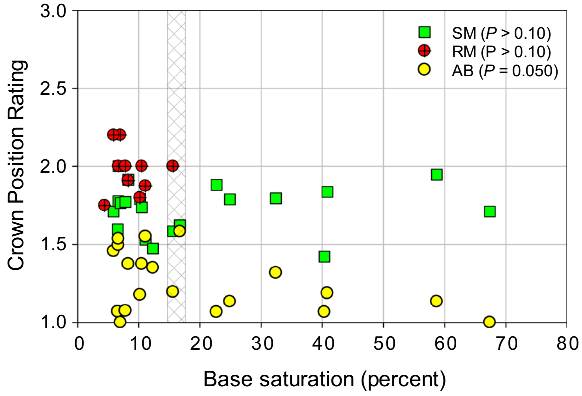

Figure 3. Average crown position rating in each watershed for sugar maple (SM), red maple (RM), and American beech (AB) trees growing in the canopy as a function of base saturation in the upper 10 cm of the B horizon. A higher crown position rating indicates a higher crown position in the canopy. The base saturation where the Al mobilization threshold occurs is indicated by vertical cross-hatching that encompasses the two sites with base saturation values that closely approximate the threshold value of 16.8. Two plots with a single red maple tree were not included in the red maple data presented.

Like the abundance of canopy trees, and saplings plus subcanopy trees, seedling abundance of beech was not related to base saturation (Figure 4). However, seedling abundance for sugar maple was substantially higher in watersheds with base saturation values that prevented Al mobilization ($P < 0.01$), than in watersheds with base saturation values that indicated Al mobilization, and was positively correlated with base saturation ($P = 0.056$; $R = 0.43$). In sharp contrast, red maple seedling abundance was substantially higher where base saturation values indicated Al mobilization, than where base saturation buffered against Al mobilization ($P < 0.01$), and was negatively correlated with base saturation ($P < 0.01$; $R = -0.57$). Red maple seedlings were nearly absent in the watersheds where base saturation buffered against Al mobilization (Figure 4).

Soil sampling in the South Buck Watershed in 1998 and 2014 spanned the time period when acidic deposition decreased at the fastest rate observed in the deposition monitoring record, which dated back to 1980 (Supplemental Figure 5). Between 1998 and 2014, wet deposition of SO_4 decreased by half and wet deposition of inorganic N showed a significant decrease ($P < 0.05$) that was not observed in the prior record ($P > 0.10$). Between the original soil sampling and resampling, several marked changes in soils were documented (Figure 5). In the Oe horizon, exchangeable Ca increased, exchangeable Al decreased and base saturation increased from 1998 to 2014 ($P < 0.01$). In the Oa horizon, exchangeable Ca and base saturation were not significantly different ($P > 0.10$) between sampling years, but exchangeable Al decreased ($P < 0.01$). In the upper 10 cm of the B horizon, exchangeable Ca was not significantly different ($P > 0.10$), but exchangeable Al increased ($P < 0.01$) and base saturation decreased ($P < 0.01$).

Vegetation measurements in the South Buck Watershed showed that in 2000 beech, sugar maple, and yellow birch comprised, respectively, 61, 15, and 18%, of total basal area of trees at least 5 cm DBH. The average DBH of sugar maple increased progressively over the four measurements ($P < 0.01$), as did yellow birch ($P = 0.041$), but no significant change in average DBH of beech ($P > 0.10$) was observed due to mortality offset by growth and addition of small trees as they grew to 5 cm DBH (Figure 6a). The mortality rate for all beech trees was 0.72% y^{-1}, but for beech > 20 cm DBH, the mortality rate was 1.4% y^{-1}. Over the

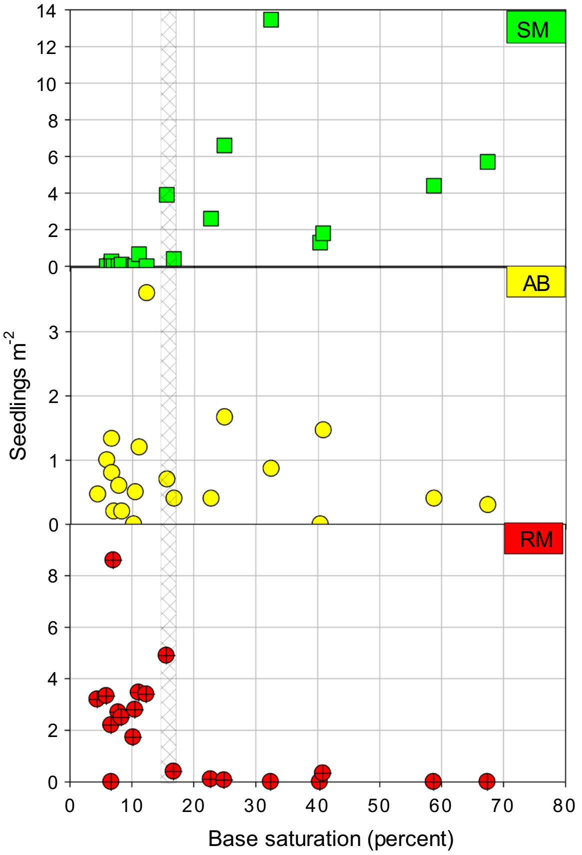

Figure 4. Seedling abundance as a function of base saturation of the upper 10 cm of the B horizon for sugar maple (SM), American beech (AB), and red maple (RM). The base saturation where the Al mobilization threshold occurs is indicated by vertical cross-hatching that encompasses the two sites with base saturation values that closely approximate the threshold value of 16.8.

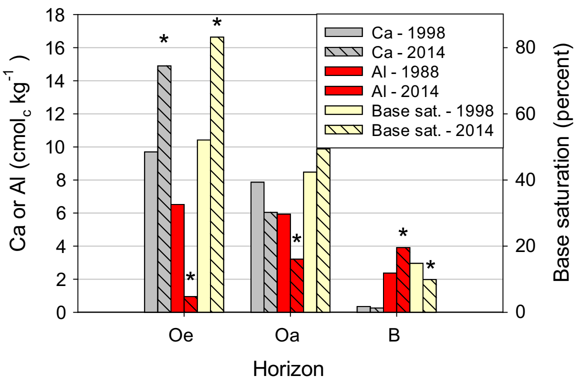

Figure 5. Concentrations of exchangeable Ca, exchangeable Al and base saturation (base sat.) in Oe and Oa horizons, and the upper 10 cm of the B horizon in 1998 and 2014 in South Buck Watershed. Asterisks indicate a significant difference ($P < 0.01$) between sampling years.

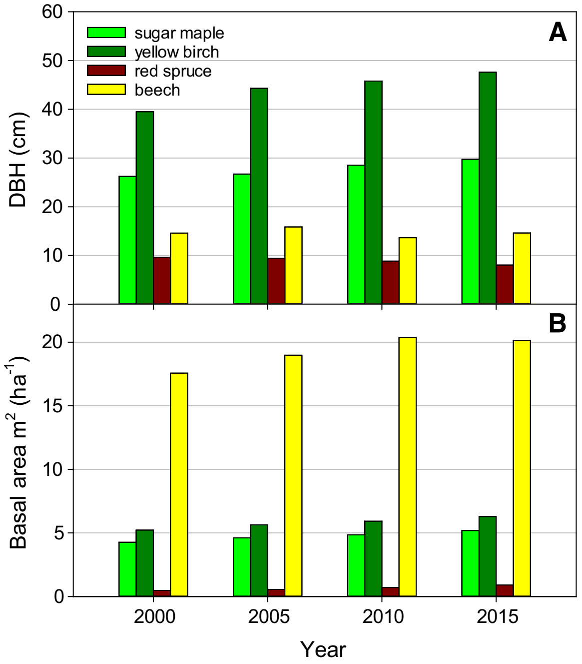

Figure 6. Average diameter at breast height (DBH) (a) and basal area (b) for sugar maple, yellow birch, red spruce, and beech in the South Buck Watershed from 2000 to 2015.

15-year measurement period, 19% of beech trees with DBH above 20 cm died, which equated to 26.5% of the basal area of beech in this size range. There was no mortality of the 35 sugar maple and yellow birch trees larger than 6 cm DBH. Basal area of sugar maple and yellow birch also increased progressively through the measurement period ($P < 0.01$), as did beech for the first three measurements before leveling off in the fourth measurement period (Figure 6b). The beech measurements showed an overall increasing trend in basal area ($P = 0.084$).

Red spruce were rare in the canopy (2.7% of basal area in 2015), but the number of trees reaching 5 cm DBH increased from 5 between 2000 and 2005, to 11 between 2005 and 2010, to 25 between 2010 and 2015. The addition of trees growing into the measurement range caused the average DBH to progressively decrease ($P = 0.30$) from 9.6 to 8.0 cm (Figure 6a). Red spruce also showed strong basal area growth, nearly doubling from 2000 to 2015 (1.9 to 3.6 m^2 ha^{-1}).

Beech saplings dominated the understory in 2015 with a density of 10,478 stems ha^{-1}, but spruce saplings were also abundant (4,715 stems ha^{-1}). No sugar maple or yellow birch saplings were observed in the plots.

DISCUSSION

Verification of a Base Saturation Value that Defines the Al Mobilization Threshold

The base saturation for Al mobilization of 16.8% shown in Figure 1 falls within the range of 15–20% suggested by the work of Reuss (1983) and Cronan and Schofield (1990). Because previous analysis of Adirondack stream chemistry demonstrated that a BCS value less than zero indicated Al mobilization by acidic deposition (Lawrence and others 2007), this result strengthens the interpretation that a base saturation value of 16.8% corresponds to the approximate threshold of Al mobilization. However, the use of base saturation in assessing recovery was complicated by soil results in the South Buck Watershed where an increase in base saturation occurred in the Oe horizon, but a decrease in the upper B horizon was observed. These apparently contrasting results may both be tied to recovery as movement of Al in the soil profile changed as a result of the large decreases in acidic deposition (Lawrence and others 2015). The decrease in exchangeable Al in Oe and Oa horizons is a likely reflection of decreased Al mobilization within the upper B horizon, which would decrease upward transport into the organic horizons through hydrologic and biocycling processes, as detailed in Lawrence and others (1995, 2015). Furthermore, the large decrease in exchangeable Al in the organic horizons suggests the downward transport of Al out of these horizons, leading to Al deposition in the upper B. This would be a reversal of the pattern that occurred when acidic deposition levels were high—namely mobilization of solid-phase Al forms within the B that were transported into organic soil horizons (Lawrence and others 1995; Warby and others 2009) as well as into surface waters (Cronan and Schofield 1990). Further work is needed to understand the changes occurring in forest soils under conditions of decreasing acidic deposition. Nevertheless, by defining the base saturation value that corresponds to the Al mobilization threshold, this analysis demonstrated the value of base saturation as a measure for assessing acidic deposition effects and recovery in forest ecosystems. This analysis also demonstrated the benefit of incorporating aquatic and terrestrial data to interpret ecosystem effects of acidic deposition.

Relationships Between Soil Base Saturation and Stand Composition

Base saturation appeared to be an important factor in determining the presence of some species of trees, but not others. White ash, basswood, and hophornbeam, species recognized as calciphilic (Mitchell and others 2003), occurred only in watersheds with base saturation values high enough to prevent Al mobilization (with the exception of white ash in one watershed), whereas red maple and black cherry, species considered to favor acidic soils (Burns and Honkala 1990), were found only in watersheds where Al mobilization occurred. The occurrence of sugar maple, beech, and yellow birch in almost all watersheds, over nearly the full range of base saturation, indicated that these species were likely to have been common to abundant in all these watersheds before acidic deposition, although some degree of elevated mortality of sugar maple in the past seem likely in the low-base soils, based on studies such as Hallett and others (2006). The current stand composition likely reflects a combination of varying soil chemical tolerances and competitive species interactions. Despite the occurrence of mature sugar maple throughout the range of base saturation, lower canopy vigor, and smaller DBH where base saturation was less than 16.8% suggested that Al mobilization played a role in suppressing sugar maple growth. Basal area growth of sugar maple was found to be inversely correlated with exchangeable Al concentrations for these same study sites by Bishop and others (2015).

The percent abundance of beech saplings in the understory was considerably greater than that of beech trees in the canopy, similar to results of other studies of stands affected by BBD (Duchesne and Ouimet 2009; Bannon and others 2015). Also similar to the study of Bannon and others (2015), we found no relationship between base saturation and the abundance of any sapling species as a percent of total saplings although Ca concentrations were considerably lower in our study. Duchesne and Ouimet (2009) did observe a negative correlation between beech sapling basal area and soil exchangeable Ca and Mg in soils with a base status similar to Bannon and others (2015).

In beech, the lack of direct relationships to base saturation in terms of canopy vigor, DBH, and regeneration suggests that its stronger presence in low-base soils is more a response to the decline of other species than a preference of beech for more acidic soils. However, the strong effects of BBD on growth and regeneration may have obscured more subtle soil-related responses. Yellow birch has received little study in relation to soil chemistry or acidic deposition effects, but has not been considered to be sensitive to soil acidity levels (Burns and Honkala 1990). Red spruce over 10 cm DBH were not numerous, but like sugar maple, beech, and yellow birch, they were found over nearly the full range of base saturation. Widespread red spruce declines have been strongly linked to Ca depletion and Al mobilization, which were found to have a number of negative physiological effects that included predisposing the trees to winter injury (Shortle and Smith 1988; Hawley and others 2006; Schaberg and others 2011). Red spruce growth declines in the 1960s–1970s were documented over much of its range in the Northeast, including the Adirondacks (Hornbeck and Smith 1985), and high mortality of canopy trees in the Adirondacks was noted at both upper and lower elevations in the Adirondacks (Lawrence and others 1997). These past declines in red spruce may have contributed to gap formation in the study watersheds where base saturation was low and Al mobilization occurred. More recent information suggests that red spruce decline in the Northeast has lessened or perhaps ended. Pontius and others (2016) suggested that a resurgence of red spruce in the White Mountains of New Hampshire (NH) at elevations similar to this study may be related to the decreases in acidic deposition, and Engel and others (2016) considered decreased acidic deposition as a possible factor in the pronounced increases in basal area growth that they measured in red spruce in Vermont and NH from the late 1990 s up to 2010.

Combined Effects of Beech Bark Disease and Base Saturation on Stand Composition and Structure

The numerical dominance of beech in the sapling stratum (beech thickets) without dominant crown positions, recorded in all study watersheds, is consistent with the effect of BBD on beech regeneration in our study region (Giencke and others 2014). The low crown position of beech relative to sugar maple where Al mobilization did not occur, and to red maple, and sugar maple to a lesser extent, where Al mobilization did occur, also suggested that BBD reduced the ability of beech to compete with other species for upper canopy positions (Garnas and others 2011). Nevertheless, beech remains a major component in the study watersheds, and decades of BBD undoubtedly played a role in shaping the composition and structure of these stands.

The repeated measurements in South Buck Watershed provided data on the types of effects that can result from BBD. Due the numerical dominance of beech in the canopy of this watershed, the high percentage of mortality in beech larger than 20 cm DBH produced canopy gaps that may have contributed to the release of understory red spruce. Despite this mortality, total basal area of beech showed an overall increase without an increase in average DBH. This occurred as the size distribution of beech trees shifted toward more numerous small trees and fewer large trees. During the same period, the average DBH of sugar maple and yellow birch increased, which suggested a diminishing canopy position for beech. A similar shift in beech toward more abundant small trees and fewer large trees was observed in an Adirondack sugar maple-beech forest infected with BBD studied by Forrester and others (2003) and Giencke and others (2014).

Results from the ASMP watersheds suggested that the effects of BBD varied with Ca availability due to differences in the sensitivity of sugar maple and beech to soil Ca depletion. In soils with low base saturation, a lack of sensitivity to soil chemistry may have provided some benefit to beech in relation to Al-intolerant sugar maple, which is consistent with the smaller difference in crown position in these soils. In Quebec, Duchesne and Ouimet (2009) similarly found that beech showed a low sensitivity to soil base status and may have benefited from sugar maple decline in low-base soils, and in sugar maple-dominated low-Ca soils at the Hubbard Brook Experimental Forest, NH, beech showed greater increase in growth in soils treated with Al than with Ca whereas subdominant canopy sugar maple responded positively to Ca additions (Halman and others 2015).

Measurements were collected in the ASMP watersheds in a single year so data on gap formation were not available. Nevertheless, mortality from the first wave of BBD, as well as aftermath mortality, plus acidic deposition effects on sugar maple and red spruce, was likely to have increased the rate of gap formation in watersheds where base saturation was below the Al mobilization threshold. Regenerating beech would be expected to have filled a fraction of these gaps, but red maple and black cherry, species considered to be effective at exploiting gaps (Burns and Honkala 1990; Abrams 1998), were important components of the canopy. The tolerance of red maple and black cherry to acidic soils undoubtedly played a role in their common occurrence in the watersheds where Al mobilization occurred.

Some level of gap production from BBD can also be assumed in the watersheds where base saturation was high enough to prevent Al mobilization. In these watersheds, sugar maple appeared to benefit from favorable soil conditions, as suggested by the strong positive relationship between soil base saturation, and canopy vigor and DBH, which was not seen in beech, and the improved crown position of sugar maple relative to beech. The potential effect of sugar maple causing soil changes favorable to its growth, as seen in southeastern NY (Arthur and others 2017), would help to maintain its dominance. These factors and the absence of fast-growing gap-exploiting species (other than white ash common in two watersheds) suggested that sugar maple competed effectively for gaps in the watersheds where soil Ca availability buffered against Al mobilization.

Despite the advantage of sugar maple in the canopy, the understory dominance of beech has been suggested as an impediment to the regeneration of sugar maple (Pontius and others 2016). High seedling abundance and some occurrence of saplings in the study watersheds where base saturation buffered against Al mobilization suggests the potential for sugar maple to regenerate in this type of stand. However, shading caused by beech saplings has been shown to have a negative effect on sugar maple seedling survival (Hane 2003). Further research is needed to evaluate effects of BBD on sugar maple regeneration.

Effects of Soil Recovery in South Buck Watershed

The previous soil resampling studies conducted in the Adirondack region (Sullivan and others 2006; Johnson and others 2008; Warby and others 2009) all showed decreases in exchangeable Ca concentrations up through 2004, and the two studies that evaluated exchangeable Al (Johnson and others 2008; Warby and others 2009) recorded increases. However, the more recent soil resampling data presented for South Buck Watershed (1998–2014) show the beginnings of soil recovery in this beech-sugar maple watershed, although stream chemistry indicated some degree of Al mobilization up through 2014 (US Geological Survey, 2016 Water Data for the Nation, accessed June 10, 2012, at http://waterdata.usgs.gov/nwis/. The South Buck Watershed results were similar to indications of soil recovery identified at multiple sites throughout the northeastern USA and eastern Canada (Lawrence and others 2015).

Pronounced decreases in exchangeable Al coupled with increases or no change in exchangeable Ca resulted in base saturation increases from 52 to 83 and 42 to 49% in the Oe and Oa horizons, respectively, although the increase in the Oa horizon was not significant ($P > 0.10$). However, base saturation in the upper B horizon decreased from 15 to 9.9% from no change in exchangeable Ca, and an increase in exchangeable Al. The exchangeable Al increase could suggest a worsening of soil chemistry, but is more likely related to the recovery occurring in the overlying organic layers as Al moved downward out of these horizons to be deposited in the upper B horizon (Lawrence and others 1995, 2015).

The soil changes in South Buck Watershed led to substantial increases in Ca availability in the Oe and Oa horizons, which may have contributed to the increase in watershed basal area for sugar maple, yellow birch, and red spruce. The decrease in base saturation in the upper B horizon probably did not have a large effect on Ca availability because of the substantial increases in Ca and decreases in Al (Figure 5) in the horizons of maximum fine root density. Furthermore, Ca concentrations of the Oe and Oa horizons were higher than in the upper B horizon by more than a factor of 10

The composition of the forest in this watershed prior to depletion of Ca is uncertain, but some loss of canopy sugar maple and red spruce during the period of high acidic deposition is probable (Lawrence and others 1997; Hallett and others 2006). The question now becomes whether these species can expand their importance within the current stand structure with beech dominating the understory. The relatively high sapling density and low canopy density of red spruce indicates that this species can compete well in the understory with beech. This, and the strong growth of canopy trees, suggests that red spruce will become more common within the canopy over the next few decades, which is counter to literature speculation that trending climate will decrease the future abundance of red spruce (Beckage and others 2008). Expansion of red spruce in low-base soils could represent an additional limiting factor in the regeneration of sugar maple. In a recent study of seedling nutrition in mixed stands of sugar maple and conifers (including spruce), soil acidification resulting from conifer litter lowered foliar concentrations of Ca and Mg in sugar maple seedlings to levels of nutritional deficiency (Collin and others 2016).

CONCLUSION

This analysis identified base saturation and BBD as key factors in determining stand composition and structure in the Adirondack hardwood forest. Study results also showed that base saturation was related to the geochemical threshold of Al mobilization, a key process in determining the extent of acidic deposition effects on soils. The importance of identifying thresholds to better understand how ecosystems respond to environmental drivers was detailed by Groffman and others (2006). In study watersheds where Al mobilization occurred, lowering of base saturation by acidic deposition sometime in the past is probable (Lawrence and others 1987, 2007). Although this study does not present a direct link between Al mobilization and stand characteristics, the negative sensitivity of sugar maple to base saturation below the Al mobilization threshold suggests that acidic deposition was a factor in shaping stand characteristics as well.

Marked decreases of harmful Al forms in Adirondack lakes (Lawrence and others 2013) support the likelihood that Al mobilization in soils is on a downward trend. However, the ongoing dominance of beech in the understory and competition from more acid-tolerant species for canopy gaps may limit expansion of sugar maple in watersheds with base saturation below the Al mobilization threshold, even with favorable changes in soil chemistry. These conditions could promote the expansion of red spruce, which, like sugar maple, has experienced prior decreases in abundance as a result of acidic deposition, but may be more tolerant of low base saturation and compete more effectively with understory beech than sugar maple. Where base-rich soils occur, sugar maple may further increase their dominance as BBD continues to weaken the ability of beech to compete for upper canopy space, providing that sugar maple seedlings and saplings can provide regeneration in the presence of the dense beech understory. Because these factors coexist in much of the forests of eastern North America, results of this study are applicable across a large region.

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