Linking environmental gradients, species composition, and vegetation indicators of sugar maple health in the northeastern United States

Stephen B. Horsley, Scott W. Bailey, Todd E. Ristau, Robert P. Long, and Richard A. Hallett

Abstract: Sugar maple (*Acer saccharum* Marsh.) decline has occurred throughout its range over the past 50 years, although decline symptoms are minimal where nutritional thresholds of Ca, Mg, and Mn are met. Here, we show that availability of these elements also controls vascular plant species composition in northern hardwood stands and we identify indicator species of these nutrient thresholds. Presence and abundance of vascular plant species and data on 35 environmental variables were collected from 86 stands in New Hampshire and Vermont (NHVT) and Pennsylvania and New York (PANY). Nonmetric multidimensional scaling ordination was used to determine which variables affected presence and abundance of species; both measures gave similar results. A base cation – acid cation nutrient gradient on axis one accounted for 71.9% (NHVT) and 63.0% (PANY) of the variation in the nonmetric multidimensional scaling ordination. Measures of Ca, Mg, and pH formed the base end and Al, Mn, K, soil acidity, and organic matter the acid end in both subregions. In both subregions, sugar maple foliar Mg and Ca had the strongest association with the base end of axis 1; exchangeable Al in NHVT and foliar Mn in PANY were strongly associated with the acid end. McNemar's exact test and indicator species analysis were used to determine which species were present in stands that met the nutritional thresholds for Ca, Mg, and Mn foliar chemistry. McNemar's exact test identified 16 species in NHVT and PANY, 16 additional species in NHVT only, and 12 additional species in PANY only. Indicator species analysis identified a subset of these species with the highest frequency of occurrence. Indicator species could provide land managers with a diagnostic tool for determining where on the landscape sugar maple is "at risk" or likely to remain healthy in the face of stresses.

Résumé : Le dépérissement de l'érable à sucre (*Acer saccharum* Marshall) est survenu partout dans l'aire de répartition de cette essence au cours des 50 dernières années mais il y a très peu de symptômes de dépérissement aux endroits où les seuils nutritionnels pour Ca, Mg et Mn sont atteints. Nous montrons ici que la disponibilité de ces éléments régit également la composition en espèces de plantes vasculaires dans les peuplements de feuillus nordiques et nous identifions des espèces indicatrices des seuils pour ces nutriments. La présence et l'abondance des espèces de plantes vasculaires ainsi que 35 variables environnementales ont été mesurées dans 86 peuplements des États du New Hampshire et du Vermont (NHVT) ainsi que ceux de la Pennsylvanie et de New York (PANY). L'ordination de mesures multidimensionnelles non paramétriques a été utilisée pour déterminer quelles variables influencent la présence et l'abondance des espèces; les deux mesures ont produit des résultats similaires. Un gradient de nutriments allant des cations basiques à acides sur l'axe un expliquait 71,9% (NHVT) et 63% (PANY) de la variation dans l'ordination. Les mesures de Ca, Mg et de pH formaient la partie basique et Al, Mn, K, l'acidité du sol et la matière organique formaient la partie acide dans les deux sous-régions. Dans les deux sous-régions, le Mg et le Ca foliaire de l'érable à sucre était le plus étroitement associé à la portion basique de l'axe un; l'Al échangeable dans la sous-région NHVT et le Mn foliaire dans la sous-région PANY étaient fortement associés à la portion acide. Le test de McNemar et l'analyse des espèces indicatrices ont été utilisés pour déterminer quelles espèces étaient présentes dans les peuplements où les seuils nutritionnels pour Ca, Mg et Mn étaient atteints dans les feuilles. Le test de McNemar a identifié 16 espèces dans les deux sous-régions, 16 autres dans la sous-région NHVT et seulement 12 autres dans la sous-région PANY. L'analyse des espèces indicatrices a identifié un sous-ensemble des ces espèces dont la fréquence était la plus élevée. Les espèces indicatrices pourraient fournir aux aménagistes du territoire un outil de diagnostique pour déterminer à quel endroit le paysage d'érable à sucre est à risque et où il restera sain face aux stress. **Note** : l.7 de l'abstract, *saccharum* Marshall **au lieu de** *saccharum* Marsh.

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Introduction

Sugar maple (*Acer saccharum* Marsh.) is an important species in the northern hardwood forests of the northeastern and north-central United States and eastern Canada. During the past 50 years, episodes of sugar maple decline characterized by crown dieback and tree mortality have occurred throughout this range (Houston 1999; Horsley et al. 2002). The most recent of these declines began in northwestern and north-central Pennsylvania in the early to mid-1980s and continued through the mid-1990s (Kolb and McCormick 1993; Long et al. 1997). Studies of this decline episode have shown the importance of an interaction between imbalanced Ca, Mg, Al, and Mn and stress, particularly from insect defoliation, in the decline disease process (Horsley et al. 2000; Hallett et al. 2006). In a literature review comparing this decline episode with others reported throughout the species' range, Horsley et al. (2002) found that low supply of Ca and Mg (base cations) coupled with high availability of Al (a toxic, nonnutrient element) and Mn (a nutrient at trace levels) was a predisposing factor to decline in every event where these elements were studied. In this paper, we refer to Al and Mn as acid cations because their availability for plant uptake increases as soils become more acid and pH decreases.

Sugar maple develops best on sites high in base cations, but studies of its health and growth across the northeastern United States have given strong evidence that the quality of sites on which it occurs varies widely with respect to nutrition (Godman et al. 1990; Whitney 1990, 1999). Moreover, its ability to withstand stresses such as defoliation and drought and to repel organisms such as *Armillaria* spp. without declining is dependent on supplies of base cations (Marcais and Wargo 2000; Wargo et al. 2002). In previous work, we developed nutritional thresholds for Ca, Mg, and Mn and their interactions with defoliation stress (Horsley et al. 2000; Bailey et al. 2004). Trees with greater than threshold supplies of Ca and Mg or less than threshold supplies of Mn did not decline when the defoliation threshold was exceeded (Hallett et al. 2006). These relationships are consistent with improved vigor in trees treated with dolomitic limestone at sites with low base cation supplies (Long et al. 1997; Moore and Ouimet 2006).

Determination of nutritional status for large areas typically requires intensive soil and (or) foliar sampling, laboratory analysis, and interpretation. Expense of these procedures has prompted alternative approaches to site quality classification, such as vascular plant indicator species. Use of understory plants as indicators of site quality was pioneered by Cajander (1926) in Finland, Ellenburg (1950, 1988) and Schlenker (1950) in central Europe, Hills (1952) in Canada, Coile (1938) in the eastern United States, and Curtis (1959) in Wisconsin. Work on site relationships for vascular plants in northern hardwood forests has focused primarily on stand characteristics, soil moisture, and land form (Whitney 1991; Host and Pregitzer 1992). Soil chemistry has received only limited consideration as a site classification tool. Spies and Barnes (1985*a*) considered nutritional aspects of site quality using pH as an indicator of nutrition. Roberts and Christensen (1988) investigated soil chemistry in genetic horizons of partial profiles in a study of successional aspen stands in Michigan. Such relationships have not been examined across a broad region of the northern hardwood forest using multiple indicators of nutrition including whole-profile soil and foliar sampling. If site chemistry indicators can be developed over a broad area, assessment of vascular plant composition may provide an easily applied tool to assess site quality for base cation responsive species like sugar maple.

In this paper, our objectives were to determine (*i*) is a gradient of Ca, Mg, and Mn an important factor controlling vascular plant species composition in northern hardwood forests of the northeastern United States and (*ii*) which of these species closely mimic the sensitivity of sugar maple to thresholds for Ca, Mg, and Mn? To accomplish these objectives, we used northern hardwood stands in Pennsylvania, New York, Vermont, and New Hampshire on which our sugar maple decline studies were conducted and where data on a wide range of environmental variables were available (Horsley et al. 2000; Bailey et al. 2004; Hallett et al. 2006).

Methods

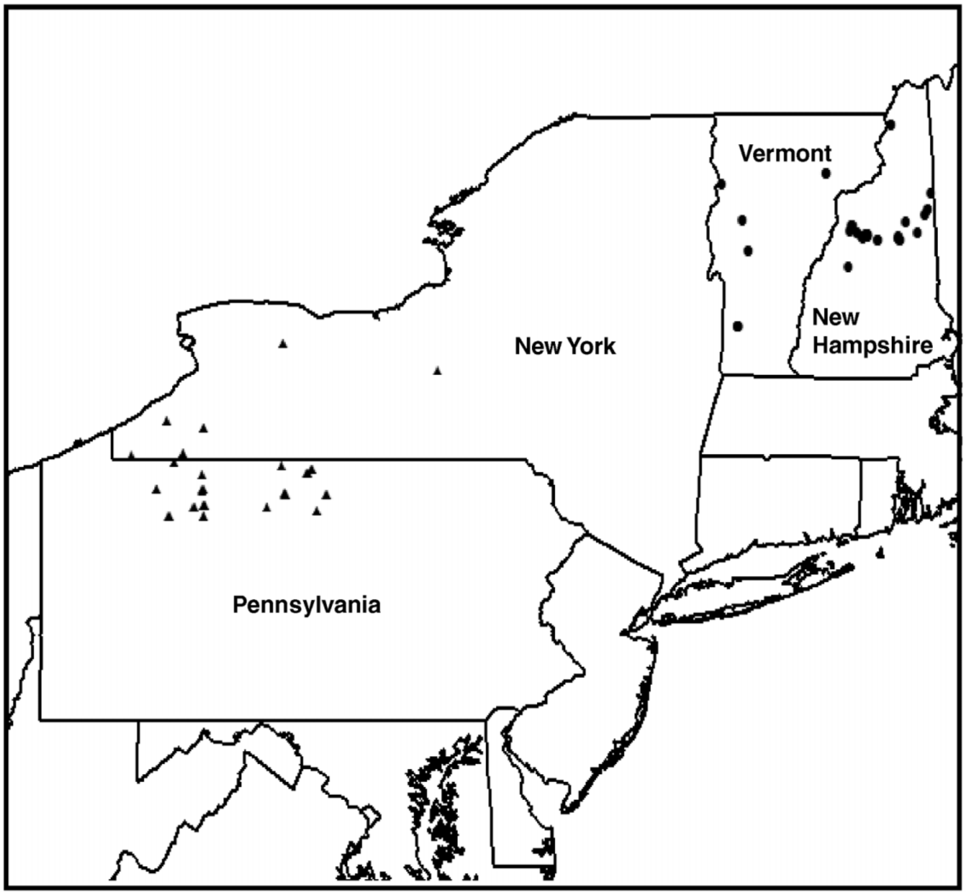
Study sites

Data were collected in 86 northern hardwood stands from western Pennsylvania to northern New Hampshire (Fig. 1). Forty-six stands were located on the northern Allegheny Plateau along topographic gradients in northwestern and north-central Pennsylvania and western New York (PANY) (23%–95% sugar maple) (Horsley et al. 2000). These stands were selected in 1995 and 1996 to include both stands containing trees with symptoms of sugar maple decline and stands containing trees with no decline symptoms, without knowledge of underlying soil conditions. The remaining 40 stands were located across New Hampshire and Vermont (NHVT) (25%–99% sugar maple) in 1997 and 1998. Details of species composition in all stands are found in Hallett et al. (2006). Little or no symptoms of sugar maple decline disease were observed in NHVT stands; stands were selected to include the range of soil and elevation where sugar maple was found in northern New England. The stands in both PANY and NHVT were part of a regional study to understand the causes of sugar maple decline (Hallett et al. 2006). Overall, study sites represented the major soil orders on which sugar maple is found (Spodosols, Inceptisols, Alfisols, and Ultisols) (Godman et al. 1990). Lithologic composition of bedrock and soil parent materials included granite, syenite, schist, phyllite, quartzite, amphibolite, marble, dolostone, sandstone, and shale. Most stands were mature second growth, originating following complete or nearly complete removal of overstory trees from 1880 to 1930 (Marquis 1975; Cogbill 2000).

Vegetation sampling

Species composition of each stand was determined by searching a 0.4 ha area surrounding a 20 m × 50 m sampling area. Presence of all vascular plant species was recorded in May and July 1999 (PANY) and in July 1999 and May 2000 (NHVT). Abundance data were collected on a 20 m × 50 m sampling area in each stand on 25 systematically located 1 m^2 plots. Duplicate analyses using presence–absence and abundance data gave similar results. Here, we present the

Fig. 1. Locations of study sites in the northeastern United States showing sites in Pennsylvania and New York (PANY) (triangles) and New Hampshire and Vermont (NHVT) (circles) Sites have one to three stands associated with them.



presence–absence results because they are easier for others to obtain and are more widely available. All plants were identified to species where possible. Nomenclature follows Gleason and Cronquist (1991).

Site chemistry variables

Thirty-five site chemistry, stand, and climatic variables were collected or calculated from each stand for analysis with species data (Table 1). Forest soils frequently have been sampled by depth rather than by genetic horizon. Thus, soil horizons developed under different pedogenic processes are mixed together, thereby increasing variability of samples (Bailey et al. 2005). We collected composite soil samples for chemical analysis by genetic horizon to a depth of 130 cm or bedrock from the four faces of a single pit, chosen after a reconnaissance of the site to be representative of the 0.4 ha sampling area. Samples were air-dried and sieved to remove particles >2 mm. Understory vegetation generally is presumed to draw most of its nutrition from surface soil horizons, although this rarely has been tested. Thus, we included soil chemical properties of three genetic horizons in the analysis: the Oa/A, the uppermost B, and the lowermost B horizons. Site chemistry variables by horizon were coded 1, 2, or 3, respectively. For example, pH of the Oa/A horizon is coded pH1, pH of the uppermost B horizon is pH2, and pH of the lowermost B horizon is pH3 (Table 1). We did not separate the Oa from the A horizon for this analysis due to the combined thin profile of the two horizons that would have resulted in insufficient sample for analysis. Samples were analyzed for pH in 0.01 mol·L^{-1} $CaCl_2$ (Robarge and Fernandez 1987). Organic matter content (om) was measured by loss on ignition (Robarge and Fernandez 1987). Exchangeable cations (exCa, exMg, and exK) were determined in 1 mol·L^{-1} NH_4Cl extracts (Blume et al. 1990). Exchangeable Al (exAl) was measured in 1 mol·L^{-1} KCl extracts. Exchangeable acidity (exacid) was determined by potentiometric titration (Thomas 1982). Concentrations of all cations in soil extracts were measured with inductively coupled plasma spectrophotometry (for details, see Bailey et al. 2004).

Sugar maple foliage was collected for chemical analysis because of the ability of foliar chemistry to integrate horizontal and vertical variation in soil chemistry within stands (Leaf 1973; Morrison 1985). We selected trees, defined as healthy by North American Maple Project vigor class 1, ≤10% crown dieback and foliage transparency, because they provided an integrated measure of site chemistry not affected by tree health issues (Cooke et al. 1996; Long et al. 1997). Within the 0.4 ha sampling area of each stand, foliage was collected from five dominant or codominant overstory sugar maples that were at least 25 cm in diameter at breast height (1.3 m above ground). A midcrown sample of 25 sun leaves was obtained from each tree during the last 2 weeks of August (1995 or 1996 in PANY, 1997 or 1998 in

Table 1. Site chemistry and stand and climatic variables and correlations with NMS axis 1 in New Hampshire and Vermont (NHVT) (*n* = 40) and Pennsylvania and New York (PANY) (*n* = 46) (variables with the highest positive and negative correlations in the NMS ordination are bolded).

		Range		Axis 1 correlation	
Abbreviation		NHVT	PANY	NHVT	PANY
Site chemistry variables					
exCa1	Exchangeable calcium, Oa/A ($cmol_c \cdot kg^{-1}$)	0.227–271	0.126–25.7	–0.554	–0.634
exCa2	Exchangeable calcium, upper B ($cmol_c \cdot kg^{-1}$)	0.196–21.6	0.044–9.02	–0.764	–0.565
exCa3	Exchangeable calcium, lower B ($cmol_c \cdot kg^{-1}$)	0.015–15.1	0.003–22.0	–0.723	–0.625
folCa	Foliar calcium ($mg \cdot kg^{-1}$)	2770–24100	3150–18000	**–0.881**	**–0.870**
exMg1	Exchangeable magnesium, Oa/A ($cmol_c \cdot kg^{-1}$)	0.080–27.2	0.016–4.41	–0.425	–0.626
exMg2	Exchangeable magnesium, upper B ($cmol_c \cdot kg^{-1}$)	0.018–3.07	0.014–3.97	–0.669	–0.388
exMg3	Exchangeable magnesium, lower B ($cmol_c \cdot kg^{-1}$)	0.002–2.58	0.002–7.56	–0.645	–0.480
folMg	Foliar magnesium ($mg \cdot kg^{-1}$)	457–3410	449–2870	**–0.868**	**–0.833**
pH1	pH, Oa/A	2.54–6.77	2.91–5.72	–0.807	–0.709
pH2	pH, upper B	3.14–7.04	3.22–5.71	-0.832	–0.576
pH3	pH, lower B	3.99–7.07	3.62–6.92	–0.768	–0.588
folP	Foliar phosphorus ($mg \cdot kg^{-1}$)	926–2450	952–2070	–0.142	–0.469
exAl1	Exchangeable aluminum, Oa/A ($cmol_c \cdot kg^{-1}$)	0.002–33.4	0.010–18.6	0.333	0.033
exAl2	Exchangeable aluminum, upper B ($cmol_c \cdot kg^{-1}$)	0.002–23.0	0.002–17.4	**0.677**	0.441
exAl3	Exchangeable aluminum, lower B ($cmol_c \cdot kg^{-1}$)	0.002–6.06	0.002–9.31	0.508	0.455
folMn	Foliar manganese ($mg \cdot kg^{-1}$)	122–3110	191–3740	0.508	**0.699**
exacid1	Exchangeable acidity, Oa/A ($cmol_c \cdot kg^{-1}$)	0.115–49.6	0.250–28.6	0.240	–0.042
exacid2	Exchangeable acidity, upper B ($cmol_c \cdot kg^{-1}$)	0.077–22.6	0.705–42.2	0.416	0.240
exacid3	Exchangeable acidity, lower B ($cmol_c \cdot kg^{-1}$)	0.048–10.7	0.563–20.2	0.266	0.276
exK1	Exchangeable potassium, Oa/A ($cmol_c \cdot kg^{-1}$)	0.079–5.47	0.010–2.561	0.111	0.040
exK2	Exchangeable potassium, upper B ($cmol_c \cdot kg^{-1}$)	0.027–0.390	0.046–0.384	0.226	0.055
exK3	Exchangeable potassium, lower B ($cmol_c \cdot kg^{-1}$)	0.003–0.250	0.030–0.319	–0.197	0.076
folK	Foliar potassium ($mg \cdot kg^{-1}$)	5190–11400	5420–11200	0.359	0.477
om1	Organic matter, Oa/A (%)	8.87–85.2	6.72–77.0	0.299	0.393
om2	Organic matter, upper B (%)	2.41–49.0	2.41–13.0	0.375	0.198
om3	Organic matter, lower B (%)	0.722–9.83	1.28–6.17	0.225	–0.038
folN	Foliar nitrogen ($mg \cdot kg^{-1}$)	11 800 – 22 600	15 100 – 21 600	–0.323	0.074
Stand variables					
Posit	Physiographic position	1–5	1–5	–0.266	–0.334
mottle	Depth to mottles (cm)	28–130	10–130	–0.238	–0.057
Pan	Depth to pan or bedrock (cm)	37–130	25–130	–0.360	0.152
Seep	Seep (absent or present)	0–1	0–1	–0.181	–0.128
Skel	Coarse fragments (%)	1–75	1–68	0.072	–0.297
totalba	Basal area (m^2)	23.8–47.3	15.2–45.1	–0.178	–0.263
Climatic variables					
anntemp	Mean annual temperature (°C)	3.6–7.3	6.3–8.7	–0.468	–0.045
precip	Mean annual precipitation (mm)	889–1604	898–1293	0.214	0.129

NHVT) by shooting small branches from the periphery of the crown with a shotgun (Morrison 1985). Samples were dried to constant mass at 65 °C, dry ashed at 485 °C, taken up in 10% HCl, and analyzed for P, K, Ca, Mg, and Mn by inductively coupled plasma spectroscopy. Total Kjeldahl N was determined with a Lachat autoanalyzer (for details, see Horsley et al. 2000). Measures of foliar (fol) elements are expressed as concentrations (mg kg^{-1}) of folN, folP, folK, folCa, folMg, and folMn (Table 1).

Stand variables

Local physiography (posit) of each stand was classified using a system similar to that used by the North American Maple Project (Cooke et al. 1996). Summit and shoulder physiographic positions were grouped together and coded 1; these generally represented sites with the least moisture and nutrient retention. Upper backslopes were coded 2, middle backslopes were coded 3, and lower backslopes were coded 4. Code 5 represented sites with the most potential moisture and nutrient retention and included stands on foot- or toe-slopes, benches, or any topographic position with concave topography.

Stand soil physical properties included depth (cm) to mottles (mottle) and to a root restrictive layer or bedrock (pan); presence of seeps (seep) was noted and expressed categorically as present or absent. Mottle and seep were interpreted as measures of soil drainage in our analysis, although seeps may also act as a delivery mechanism for nutrients generated by mineral weathering in the subsoil and bedrock (Bailey et al. 2004). Volumetric coarse fragment content

(%) (skel) of each soil horizon was estimated visually by horizon from pit faces and averaged for the profile (Bailey et al. 2005).

Stand density (the cross-sectional area of all stems >2.5 cm diameter at breast height) was measured as basal area ($m^2 \cdot ha^{-1}$) (totalba). We interpreted totalba as a measure of understory light availability (Marquis 1973).

Climatic variables

Climatic parameters included 30-year normal mean annual temperature and mean precipitation downloaded from the NRCS, National Cartography and Geospatial Center (www.ncgc.nrcs.usda.gov/). Parameter values for the study stands were extracted from a raster coverage of climate values calculated using the PRISM (parameter-elevation regressions on independent slopes model) for interpolation between climate monitoring stations (Daly et al. 1994).

Data analysis

Nonmetric multidimemsional scaling (NMS) ordination (Kruskal 1964) was used to investigate environmental gradients in the data and species associated with these gradients. NMS is an ordination technique well suited to ecological data that typically are not normally distributed; it currently is considered one of the most robust ordination techniques. Use of ranked distances tends to linearize the relationships between distances measured in species space and distances in environmental space. This relieves the ‘‘zero-truncation problem’’ that plagues all ordinations of heterogeneous community data sets (McCune and Grace 2002). PC-ORD version 5.01 was used to calculate the ordinations based on two sets of matrices, one for NHVT and one for PANY (McCune and Mefford 2006). A presence–absence (1, 0) species matrix contained all species that were present in five or more stands (NHVT, 112 species; PANY, 122 species). An environmental matrix included all 35 site chemistry, stand, and climatic variables listed above and in Table 1. We analyzed the NHVT and PANY subregions separately because some taxa were relatively common in one subregion and uncommon in the other, resulting in a regional ordination with no significant environmental variables.

Initial runs of NMS in ‘‘autopilot’’ mode were used to determine an appropriate number of dimensions using scree plots. In five subsequent iterations, the run with minimum stress was used for NMS ordination. Clarke’s (1993) ‘‘rules of thumb’’ were used to interpret the reliability of the ordination results. Ecological community data typically have Clarke values between 10 and 20; values <15 are ‘‘quite satisfactory’’ for ecological community data (McCune and Grace 2002). Resulting ordinations were rotated as necessary so that the environmental vectors with the highest correlation coefficients were parallel to axis 1. Correlation coefficients with axis 1 were used to determine the most important environmental variables.

Because our goal was to determine species that responded to environmental gradients in a way similar to sugar maple, we used a multistep procedure to develop a list of indicator species including the NMS matrix of species scores for axis 1 and McNemar’s exact test. In our previous studies of sugar maple decline, we found that folCa ≥5500 $mg \cdot kg^{-1}$, folMg ≥700 $mg \cdot kg^{-1}$, or folMn ≤1900 $mg \cdot kg^{-1}$ were associated with stands that remained healthy even when exposed to stress (Horsley et al. 2000; Hallett et al. 2006). To account for analytical and interannual variability in nutrient determination and make our judgments more conservative, we increased the thresholds for Ca and Mg by 10% and decreased the threshold for Mn by 10%. Thus, our revised thresholds for folCa and folMg were ≥6050 and ≥770 $mg \cdot kg^{-1}$, respectively; folMn was ≤1710 $mg \cdot kg^{-1}$. These thresholds were combined into a single index value (CaMgMn index) as follows: folCa + folMg – folMn (6050 + 770 – 1710 = 5110). Stands with a CaMgMn index value >5110 were considered to have adequate nutrition. McNemar’s exact test of symmetry in SAS version 9.1 (SAS Institute Inc. 2003) was used to determine species whose presence is sensitive to this threshold. For each species, a 2 × 2 confusion matrix was used to summarize counts (a, b, c, d) of presence or absence of a species where the CaMgMn index was above or below the threshold value for sugar maple health (Fielding and Bell 1997). McNemar’s exact test calculates the measure

$$(b - c)^2/(b + c)$$

that yields an approximate χ^2 value with 1 degree of freedom. A significant χ^2 ($P \leq 0.05$) indicates that the species was not present or was present only a few times when the CaMgMn index was below the threshold. The value of c, the number of false positive classifications, was regarded as excessive when values of 2 or more were obtained and used to cull species as indicators, even if McNemar’s exact test was significant. The list of candidate species was culled further by retaining only those species that were primarily associated with the nutritional axis in the NMS ordination by comparing correlation coefficients on the NMS ordination axes.

The indicator species analysis of Dufrene and Legendre (1997) in PC-ORD version 5.01 was used as an additional test to evaluate species presence in relation to the CaMgMn index (McCune and Mefford 2006). For each species, relative abundance and relative frequency are calculated. The product of relative abundance (the number of sites on which a species occurred in each of the two groups defined by the CaMgMn index relative to the total number of occurrences in both groups expressed as a percent) and relative frequency (the number of plots on which the species occurred divided by the sum of numbers of plots for all species) is the indicator value. Statistical significance of the indicator value for each species is evaluated by a Monte Carlo method with 1000 randomizations. A P value ≤0.05 in the Monte Carlo test of significance and a ≥95% perfect indication value in the indicator species test were used to identify indicator species. In practice, only species with both high relative abundance and high relative frequency are selected by indicator species analysis.

Results

Environmental factors controlling species presence

In NHVT, NMS ordination accounted for 93.3% of the variation among environmental variables on three axes with a final stress value of 12.25; 71.9% of the variability was associated with axis 1. NMS ordination of PANY data accounted for 87.2% of the variability on three axes with a final stress value of 13.94; 63.0% of the variability was associated with axis 1. Thus, Clarke's "rules of thumb" suggest that we can have confidence that a reliable ordination was made. The nutritional gradient on axis 1 was the strongest environmental gradient in both subregions (Table 1; Fig. 2). Measures of Ca, Mg, and pH formed the base end of the gradient in both subregions, while measures of Al, Mn, K, soil acidity, and organic matter formed the acid end of the gradient. In both subregions, folMg (r = –0.868 in NHVT, r = –0.833 in PANY) and folCa (r = –0.881 in NHVT, r = –0.870 in PANY) had the strongest association with the base end of axis 1; exAl2 in NHVT (r = 0.677) and folMn in PANY (r = 0.699) were most strongly associated with the acid end of the gradient. Other variables strongly associated with axis1 in both subregions were foliage or soil measures of Ca, Mg, Mn, Al, and pH (Table 1).

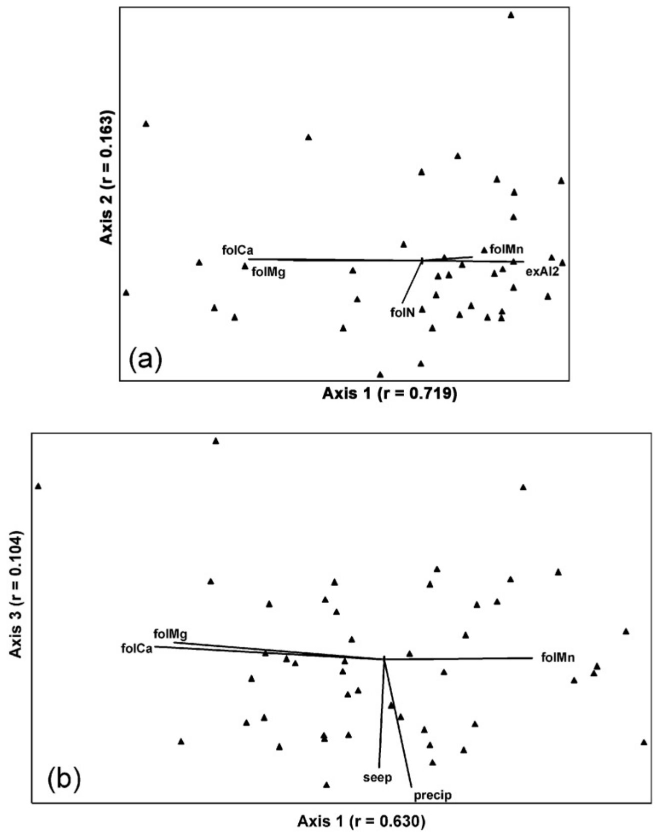
Axes 2 and 3 accounted for a relatively small proportion of the variability in both subregions. In NHVT, axes 2 and 3 accounted for 16.3% and 5.1% of the variability, respectively, while in PANY, they accounted for 13.8% and 10.4% of the variability, respectively. Environmental variables had weaker relationships (lower r values) with NMS axes 2 and 3. In NHVT, the strongest variable was folN on axis 2 (r = –0.442) and anntemp on axis 3 (r = 0.494); in PANY, the strongest variables were seep (r = –0.600) and precip (r = 0.650) on axis 3.

Species associated with base cation and acid cation site conditions

Table 2 shows species having $P \leq 0.05$ and one or less false positive in McNemar's exact test that were associated with axis 1 of the NMS ordination. A total of 50 of the original 234 species from both subregions met these conditions; all were associated with the base cation end of NMS axis 1. Most species were always included in the above CaMgMn threshold group, although a few species had one false positive occurrence in NHVT or PANY. Sixteen species occurred in both subregions, while an additional 16 species were associated with NHVT only and 18 species were associated with PANY only. Species correlation coefficients with axis 1 generally were higher in NHVT than in PANY. All of the species selected by NMS ordination and McNemar's exact test have value as indicators of sites at the high end of the base cation nutrient gradient on northern hardwood sites. Relative frequency of occurrence in our stands ranged from 12% (*Carex laxiflora*) to 72% (*Caulophyllum thalictroides*).

Indicator species analysis designated a subset of the species selected by McNemar's exact test and NMS axis 1 as indicators; no taxa were selected by indicator species analysis that were not selected by McNemar's exact test. Three species occurred region-wide (*Adiantum pedatum*, *Athyrium thelypteroides*, and *Caulophyllum thalictroides*), three species were designated in NHVT only (*Ostrya virginiana*, *Ribes cynosbati*, and *Tilia americana*), and six species were selected in PANY only (*Actaea alba*, *Carex plantaginea*, *Cardamine concatenata*, *Hepatica acutiloba*, *Taraxacum officinale*, and *Trillium grandiflorum*) (Table 2). Species identified by indicator species analysis had a minimum of 86% relative abundance in both subregions; minimum relative frequency was 31% in NHVT and 28% in PANY. Thus, species selected by indicator species analysis represent the indicator species most likely to be found because of their frequent occurrence on sites with relatively high base cation nutrition.

Fig. 2. NMS ordination results for (*a*) NHVT and (*b*) PANY. Study stands are represented by triangles. Environmental variables correlated with NMS axis 1 are shown as vectors. Values in parentheses on the axes are Pearson correlation coefficients. For clarity, only the variables with the highest correlation coefficients are shown. See Table 1 for a complete list.



Discussion

Environmental gradients controlling vascular plant composition of northern hardwood forests

Most forest site classification studies contain limited soil and foliar chemistry data. We were particularly interested in acid and base cation chemistry gradients because of their role as predisposing factors to sugar maple decline and our ultimate goal to develop an easily applied practical tool for evaluating site quality for sugar maple health using vegetation species composition. The first goal of our study was to determine whether a gradient of Ca, Mg, and Mn was an important control of species composition in northern hardwood forests of the northeastern United States. Use of detailed soil and foliar chemistry revealed strong acid and base cation relationships in two subregions of the northeastern United States that cover the range of soils on which sugar maple occurs in northern hardwood forests of the region. Axis 1 (the axis with the highest correlation coefficient by rotation)

Table 2. Selection of indicator species using McNemar's exact test, NMS ordination, and indicator species analysis.

	NHVT					PANY				
			Indicator species analysis					Indicator species analysis		
Latin name and uuthority	McNemar no. of false positives	NMS axis 1 correlation	*P*	Relative abundance	Relative frequency	McNemar no. of false positives	NMS axis 1 correlation	*P*	Relative abundance	Relative frequency
Region-wide										
Adiantum pedatum L.	0	–0.821	**0.016**	**100**	**35**	0	–0.447	**0.020**	**100**	**34**
Asarum canadense L.	0	–0.659	0.138	100	19	0	–0.312	0.300	100	16
Athyrium thelypteroides (Michx.) Desv.	1	–0.741	**0.031**	**86**	**42**	1	–0.314	**0.001**	**90**	**66**
Botrychium virginianum (L.) Sw.	0	–0.670	**0.015**	**100**	**35**	0	–0.321	0.080	100	25
Carex laxiflora Lam.	1	–0.439	1.000	62	12	0	–0.225	**0.037**	**100**	**28**
Carya cordiformis (Wangenh.) K. Koch.	0	–0.776	0.144	100	19	0	–0.551	**0.006**	**100**	**47**
Caulophyllum thalictroides (L.) Michx.	0	–0.821	**0.016**	**100**	**35**	0	–0.617	**<0.001**	**100**	**72**
Circaea lutetiana L.	0	–0.712	0.141	100	19	0	–0.395	0.085	100	22
Dryopteris marginalis (L.) Gray	1	0.736	0.121	83	35	0	–0.676	**0.009**	**100**	**41**
Epipactis helleborine (L.) Crantz	0	–0.769	0.072	100	27	0	–0.368	0.307	100	16
Hydrophyllum virginianum L.	0	–0.739	0.139	100	19	0	–0.333	0.082	100	25
Osmorhiza claytonii (Michx.) C.B. Clarke	0	–0.672	**0.016**	**100**	**38**	0	–0.230	0.079	100	22
Panax quinquefolius L.	0	–0.676	0.073	100	23	1	–0.233	1.000	64	13
Ranunculus abortivus L.	0	–0.769	0.145	100	19	1	–0.390	0.072	84	38
Thalictrum dioicum L.	1	–0.617	0.642	68	15	0	–0.435	0.085	100	22
Viola pubescens Ait.	0	–0.667	0.070	100	27	0	–0.470	**0.005**	**100**	**47**
NHVT only										
Actaea rubra (Ait.) Willd.	1	–0.482	0.128	83	35					
Aster divaricatus L.	1	–0.698	0.123	83	35					
Aster lateriflorus (L.) Britton	0	–0.562	0.144	100	19					
Cardamine diphylla (Michx.) Wood	0	–0.635	0.074	100	23					
Carex deweyana Schwein.	0	–0.125	0.147	100	19					
Carex pedunculata Muhl. ex Willd.	0	–0.483	0.140	100	19					
Dicentra canadensis (Goldie) Walp.	0	–0.635	0.074	100	23					
Eupatorium rugosum Houttuyn	0	–0.738	0.072	100	23					
Impatiens pallida Nutt.	0	–0.659	0.148	100	19					
Laportea canadensis (L.) Weddell	0	–0.743	0.074	100	27					
Matteuccia struthiopteris (L.) Todaro	0	–0.524	0.076	100	23					
Ostrya virginiana (P. Mill.) K. Koch	0	–0.694	**0.017**	**100**	**38**					
Ribes cynosbati L	0	–0.798	**0.035**	**100**	**31**					
Tilia americana L.	0	–0.735	**0.032**	**100**	**31**					
Ulmus rubra Muhl.	0	–0.774	0.145	100	19					
Viola canadensis L.	0	–0.717	0.068	100	27					
PANY only										
Actaea alba (L.) Miller						0	–0.708	**0.001**	**100**	**63**
Agrostis capillaris L.						0	–0.268	0.296	100	16
Aralia nudicaulis L.						0	–0.331	0.151	100	19
Carex plantaginea Lam.						1	–0.423	**0.038**	**86**	**44**
Carpinus caroliniana Walt.						0	–0.346	0.081	100	22
Cardamine concatenata (Michx.) Sw.						0	–0.519	**0.022**	**100**	**34**
Crataegus L.						1	–0.398	0.243	80	28
Galium asprellum Michx.						1	–0.231	0.135	81	31

Table 2 (*concluded*).

Latin name and uuthority	NHVT McNemar no. of false positives	NHVT NMS axis 1 correlation	NHVT Indicator species analysis *P*	NHVT Indicator species analysis Relative abundance	NHVT Indicator species analysis Relative frequency	PANY McNemar no. of false positives	PANY NMS axis 1 correlation	PANY Indicator species analysis *P*	PANY Indicator species analysis Relative abundance	PANY Indicator species analysis Relative frequency
Geranium maculatum L.						0	–0.368	0.154	100	19
Hepatica acutiloba DC.						1	–0.370	**0.009**	**88**	**53**
Mitella diphylla L.						0	–0.359	0.080	100	22
Oxalis stricta L.						1	–0.204	0.410	72	19
Streptopus roseus Michx.						0	–0.265	0.086	100	22
Taraxacum officinale G.H. Weber ex Wiggers						1	–0.331	**0.017**	**87**	**50**
Trillium grandiflorum (Michx.) Salisb.						0	–0.348	**0.045**	**100**	**28**
Uvularia grandiflora J.E. Smith						0	–0.396	0.307	100	16
Veronica officinalis L.						0	–0.143	0.307	100	16
Viola rostrata Pursh						0	–0.299	0.089	100	25

Note: Number of false positive indications in McNemar's exact test and Pearson's correlation coefficient with NMS axis 1 are shown region-wide for species that passed in both NHVT and PANY. Species that passed in only one subregion are shown as NHVT or PANY only. For indicator species analysis, *P* values from a Monte Carlo test, relative abundance, and relative frequency are shown. Species selected by indicator species analysis are shown in bold for each regional category.

of the NMS ordination was dominated by a gradient of acid and base cation availability including foliar Ca, Mg, and Mn and various measures of exchangeable Ca, Mg, Al, and pH, suggesting that this gradient was the most important regional control of vascular plant composition of the northern hardwood forests in our study. Among the chemical measures, foliar concentrations of Ca, Mg, and Mn were highly correlated with axis 1, supporting the concept that trees integrate vertical and lateral soil variability and cation abundance (Leaf 1973). Recently, Bailey et al. (2004) found that B horizon (horizons 2 and 3 in this study) expressions of Ca and Mg availability were the best predictors of foliar Ca and Mg, accounting for 63%–76% of the variability in foliar chemistry in regression equations.

The health of sugar maple and the distribution of vascular plants that are indicators of its potential health can be understood in terms of processes that govern the availability of Ca and Mg and their antagonistic cations Mn and Al in the soil. On the northern Allegheny Plateau in PANY, variation in site quality for sugar maple can be understood by considering the nature of parent materials, the location of weathering reactions in the soil, the effect of topographic position on delivery of weathering products to the root zone of vascular plants, and processes that result in accumulation of organic matter or leaching of nutrients from the site. Soils on unglaciated sites typically are highly acidic and are dominated by primary minerals like quartz and muscovite, which resist weathering and are poor in Ca and Mg, and secondary minerals like kaolinite and illite, which are relatively stable in the soil environment and also are not sources of Ca and Mg. Weatherable minerals are confined to subsoil and bedrock, typically well below the rooting zone of vascular plants. Thus, plants growing on the Plateau top in summit, shoulder, and upper back slope topographic positions only have access to low supplies of Ca and Mg and typically have high foliar concentrations of Mn. Sugar maple growing in these upper topographic positions on unglaciated sites are the most susceptible to decline when they experience two or more moderate to severe defoliations in the preceding 10 years (Horsley et al. 2000). Trees growing in lower topographic positions may have access to higher supplies of Ca and Mg ions via water flowpaths, such as seeps and lateral flow, that bring weathering products generated in the subsoil or bedrock to the rooting zone and recharge base cation supplies on the soil exchange complex. Soil pH in lower topographic positions often is higher as a result. Lower topographic positions also benefit from accumulation of leaf litter and organic matter generated upslope, especially on portions of hill slopes with concave topography. Sugar maple growing on unglaciated mid- and lower back slope topographic positions typically have higher foliar concentrations of Ca and Mg and lower foliar concentrations of Mn and remain healthy even when they experience more than threshold amounts of stress. Soil Al also is less available.

By contrast, on the glaciated portion of the northern Allegheny Plateau, much of the highly weathered regolith was removed by glaciation. Soil parent materials developed from glacially quarried and transported drift derived from relatively unweathered bedrock. Thus, there is less contrast in availability of Ca and Mg and pH between upper and lower topographic positions in the rooting zone. Sugar maple growing in upper and lower topographic positions on glaciated sites have health responses similar to those of trees growing on the lower topographic positions of unglaciated sites.

Since at least the mid-1960s, there has been a significant change in soil chemistry that has impacted low base cation sites on the northern Allegheny Plateau. Comparison of archived 1967 soil samples removed by genetic horizon from the upper 120 cm of unglaciated summit topographic position sites with new samples taken from the same sites in 1997 showed significant decreases in pH and exchangeable Ca and Mg and a significant increase in exchangeable Al (and presumably also Mn, which was not measured) (Bailey et al. 2005). Thus, unglaciated upper slope sites, which already were low in exchangeable Ca and Mg, have become less suitable for sugar maple and for vascular plants that are indicators of site nutritional quality for sugar maple.

In NHVT, soil parent materials are derived from glacial drift, similar to the glaciated portion of the Allegheny Plateau. However, glacial till quality in NHVT is quite diverse in comparison with the portion of PANY considered in this study, where glacial drift is derived from a relatively narrow range of lithologies, consisting of a mix of sandstone, siltstone, and shale. By contrast, in NHVT, glacial drift is composed of a broad mix of metamorphic and igneous lithologies, resulting in soils that span a range in chemistry similar to the range in chemistry in PANY (Table 1). Parent materials dominated by quartzites and certain schists and granitic rocks are quite low in weatherable Ca and Mg minerals, whereas parent materials dominated by amphibolites and marble generated the soil at the sites with the highest concentrations of these nutrients. As in PANY, local modification in geologic influence is seen where seeps are present or where concave topography and low landscape positions allow the colluvial accumulation of litter and buildup of soil organic matter.

Thus, northern hardwood forests of the northeastern United States are underlain by a wide range of lithologies. Where soil availability of Ca, Mg, and pH is in the upper end and of Mn and Al is in the lower end of their ranges and where weathering products of these richer lithologies reach the rooting zone of plants, site nutritional quality for sugar maple is highest and a distinctive array of vascular plants develops that can be used to indicate these rich site conditions. This association often is referred to as rich mesic forest or rich mesophytic forest.

Which species are most sensitive to environmental gradients?

The second goal of our study was to determine which species closely mimic the sensitivity of sugar maple to thresholds for Ca, Mg, and Mn. Northern hardwood forests occur on mesic sites with a wide range of fertility and support a wide range of vegetation; some species are generalists and occur under a variety of site conditions, while others have specific site requirements and occur only when these requirements are met. In Table 3, we compare the species selected as indicators of sites where sugar maple can remain healthy, even under stress, with those associated with rich mesic forests by others. Some of these studies are compilations of species encountered during census of rich mesic forests, while others offer data on site chemistry. In the text below, references are designated by state and author (e.g., MA-A) as shown in Table 3. There is a remarkable similarity between rich mesic species in the northern hardwood forests of the northeast and Lake States and those identified using extensive nutritional data in our study.

Early work in northern hardwood forests by several investigators identified species found on mull humus that they associated with rich mesic forests. In the Adirondacks of New York, Romell and Heiberg (1931) identified a distinctive array of vascular plants that they associated with the mull humus type formed on mesic sites that were "rich in lime" and underlain by loam or clay soils. Soil pH between 4.6 and 6.5 was most common for crumb mull humus associated with northern hardwood sites (Table 3, NY-J). Lutz (1932) extended the Romell and Heiberg (1931) study to unglaciated northern hardwood sites with grain mull humus on the Allegheny Plateau in northwestern Pennsylvania in the vicinity of many of our sites (Table 3, PA-F).

Weatherbee and Crow (1992) (Table 3, MA-B) and Bellemare et al. (2005) (Table 3, MA-A) associated rich mesophytic forest in western Massachusetts with sites influenced by calcareous bedrock, alkaline groundwater, and mull humus. Whitney (1991) described indicator species of north-central Massachusetts rich coves at the high end of the soil fertility gradient using landscape position and soil substrate (Table 3, MA-C). Sperduto and Nichols (2004) associated rich mesic forests in New Hampshire with high base saturation of bedrock and soil, topographic position (including colluviation), and hydrologic flow through soil and fractured bedrock (Table 3, NH-D). In Vermont, Thompson and Sorenson (2000) associated rich northern hardwood forests with Ca-rich bedrock and locations where colluvial processes move mineral-rich soil and bedrock downslope (Table 3, VT-E). Fike (1999) listed the vernal flora of rich mesic sugar maple – basswood (*Tilia americana*) forests in western Pennsylvania (Table 3, PA-G), while Edinger et al. (2002) characterized the sugar maple – basswood rich mesic forest of the Great Lakes Plain ecozone in New York (Table 3, NY-H). Both used census data. Kudish (1992) listed species associated with soil pH >5.0 in the Adirondacks of New York (Table 3, NY-I).

In the Lake States, Pregitzer and Barnes (1984) used soil biophysical properties along with soil pH, total N, P, and K to identify rich mesic sites in upper Michigan northern hardwood stands (Table 3, MI-K). Spies and Barnes (1985*a*) also used soil biophysical properties along with soil moisture and soil pH to classify vegetation in upland northern hardwood–hemlock (*Tsuga canadensis*) stands in the upper peninsula of Michigan (Table 3, MI-L). In a similar study, Spies and Barnes (1985*b*) developed a multifactor ecological classification in northern hardwood forests of the upper peninsula of Michigan including data on physiographic position, soil organic matter, pH, exchangeable Ca, Mg, and K, and total N for the upper 150 cm of soil to characterize vascular understory plants indicative of fertile to very fertile sites (Table 3, MI-M). Host and Pregitzer (1992) investigated the relationship between landform and vascular species composition in forests of northwestern lower Michigan.

Comparison of the species that were selected in both NHVT and PANY in our study with Tables 2 and 3 shows

Table 3. Species described as distinctive of rich mesic forests from the literature and species identified as indicators of sugar maple health in our study (in bold).

	Indicator species		"Rich mesic" forest literature[a]					
Species	NHVT	PANY	MA	NH	VT	PA	NY	MI
***Actaea alba* (L.) Miller**	**0**	**1**	**A, B**		**E**	**F, G**	**H, J**	**N**
***Actaea rubra* (Ait.) Willd.**	**1**	**0**	**A, B**					
***Adiantum pedatum* L.**	**1**	**1**	**A, B**	**D**	**E**		**H, I**	**K, L, M, N**
***Agrostis capillaris* L.**	**0**	**1**						
Allium tricoccum Ait.	0	0	A, B	D	E	F, G	H	L, M, N
***Aralia nudicaulis* L.**	**0**	**1**						
Arisaema triphyllum (L.) Schott	0	0				F, G	I, J	L, M
***Asarum canadense* L.**	**1**	**1**	**A, B**	**D**	**E**	**G**	**H, J**	
***Aster divaricatus* L.**	**1**	**0**						
***Aster lateriflorus* (L.) Britton**	**1**	**0**						
Athyrium filix-femina (L.) Roth	0	0		D			H	
***Athyrium thelypteroides* (Michx.) Desv.**	**1**	**1**		**D**	**E**		**H, I**	
***Botrychium virginianum* (L.) Sw.**	**1**	**1**	**B**	**D**	**E**	**F, G**		**K, L, M, N**
***Cardamine concatenata* (Michx.) Sw.**	**0**	**1**	**A, B**			**F, G**	**J**	
***Cardamine diphylla* (Michx.) Wood**	**1**	**0**	**A, B**			**F**	**H, J**	
***Carex deweyana* Schwein**	**1**	**0**	**B**					
***Carex laxiflora* Lam.**	**1**	**1**		**D**				
***Carex pedunculata* Muhl ex Willd.**	**1**	**0**						
***Carex plantaginea* Lam.**	**0**	**1**	**A, B**	**D**	**E**	**F**	**H, I, J**	**N**
***Carpinus caroliniana* Walt.**	**0**	**1**					**H, I**	
***Carya cordiformis* (Wangenh.) K. Koch.**	**1**	**1**	**A, C**		**E**		**H**	
***Caulophyllum thalictroides* (L.) Michx.**	**1**	**1**	**A, B**	**D**	**E**	**F, G**	**H, I, J**	**L, M, N**
***Circaea lutetiana* L.**	**1**	**1**					**J**	
Claytonia virginica L.	0	0				G	H	
Cornus alternifolia L.f.	0	0			E		H, I	L, M
***Crataegus* L.**	**0**	**1**						
***Dicentra canadensis* (Goldie) Walp.**	**1**	**0**	**A, B**	**D**	**E**	**F**	**H, I, J**	
Dicentra cucullaria (L.) Bernh.	0	0	A, B	D	E		H, I, J	
***Dryopteris marginalis* (L.) Gray**	**1**	**1**	**A, C**			**G**	**I**	
***Epipactis helleborine* (L.) Crantz**	**1**	**1**						
Erythronium americanum Ker-Gawl.	0	0				F	H	
***Eupatorium rugosum* Houttuyn**	**1**	**0**		**D**	**E**			
Fraxinus americana L.	0	0	A, C	D	E	G	H, I	
***Galium asprellum* Michx.**	**0**	**1**						
Galium triflorum Michx.	0	0				F	I	
***Geranium maculatum* L.**	**0**	**1**				**G**		
Geranium robertianum L.	0	0			E		H	
***Hepatica acutiloba* DC.**	**0**	**1**	**A, B**		**E**	**F, G**	**J**	**N**
***Hydrophyllum virginianum* L.**	**1**	**1**	**A, B**		**E**		**H, J**	
***Impatiens pallida* Nutt.**	**1**	**0**			**E**			
***Laportea canadensis* (L.) Weddell**	**1**	**0**	**B**		**E**			
***Matteuccia struthiopteris* (L.) Todaro**	**1**	**0**						**L, M**
Milium effusum L.	0	0	B		E			
***Mitella diphylla* L.**	**0**	**1**				**F, G**		**N**
***Osmorhiza claytonii* (Michx.) C.B. Clarke**	**1**	**1**	**A, B**			**F**	**I, J**	**L, M, N**
Osmunda claytoniana L.	0	0					I, J	
***Ostrya virginiana* (P. Mill.) K. Koch**	**1**	**0**	**A, C**	**D**	**E**		**H**	
***Oxalis stricta* L.**	**0**	**1**						
***Panax quinquefolius* L.**	**1**	**1**	**B**		**E**	**F**		
Panax trifolius L.	0	0				F	J	
Polystichum acrostichoides (Michx.) Schott	0	0	C		E			
Prenanthes altissima L.	0	0					J	
Prunus virginiana L.	0	0					I	
***Ranunculus abortivus* L.**	**1**	**1**	**B**				**J**	
***Ribes cynosbati* L.**	**1**	**0**						

Table 3 (*concluded*).

Species	Indicator species NHVT	PANY	"Rich mesic" forest literature[a] MA	NH	VT	PA	NY	MI
Sambucus racemosa L.	0	0			E			
Smilacina racemosa (L.) Desf.	0	0				G	H, I	
Solidago flexicaulis L.	0	0	B		E			
***Streptopus roseus* Michx.**	**0**	**1**						
***Taraxacum officinale* G.H. Weber ex Wiggers**	**0**	**1**						
***Thalictrum dioicum* L.**	**1**	**1**	**A, B**				**H**	
Tiarella cordifolia L.	0	0				F	H	N
***Tilia americana* L.**	**1**	**0**	**A, C**	**D**	**E**	**G**	**H, I, J**	
Trillium erectum L.	0	0				F	H, J	
***Trillium grandiflorum* (Michx.) Salisb.**	**0**	**1**		**D**			**J**	
***Ulmus rubra* Muhl.**	**1**	**0**						
***Uvularia grandiflora* J.E. Smith**	**0**	**1**	**B**					**L, M**
***Veronica officinalis* L.**	**0**	**1**						
***Viola canadensis* L.**	**1**	**0**	**B**	**D**	**E**	**F**	**I, J**	**N**
***Viola pubescens* Ait.**	**1**	**1**	**A**	**D**			**J**	**K, L, M**
***Viola rostrata* Pursh**	**0**	**1**						
Viola rotundifolia Michx.	0	0	B		E	F		
Waldsteinia fragarioides (Michx.) Tratt.	0	0	B					

Note: Only those species present on five or more plots in our analysis are included from the literature. A zero under an indicator species means that it is not an indicator; a 1 means that the species was an indicator in that subregion.

[a]A, Bellemare et al. 2005; B, Weatherbee and Crow 1992; C, Whitney 1991; D, Sperduto and Nichols 2004; E, Thompson and Sorenson 2000; F, Lutz 1932; G, Fike 1999; H, Edinger et al. 2002; I, Kudish 1992; J, Romell and Heiberg 1931; K, Pregitzer and Barnes 1984; L, Spies and Barnes 1985*a*; M, Spies and Barnes 1985*b*; N, Host and Pregitzer 1992.

that species in our study with moderate to high relative frequency (greater than ~20%) typically were the ones that had the widest range of occurrence in rich mesic northern hardwood forests. These included *Adiantum pedatum*, *Athyrium thelypteroides*, *Botrychium virginianum*, *Caulophyllum thalictroides*, *Dryopteris marginalis*, *Osmorhiza claytonii*, and *Viola pubescens*. These also were the species selected by indicator species analysis in either one or both subregions. *Asarum canadense*, *Hydrophyllum virginianum*, *Ranunculus abortivus*, and *Thalictrum dioicum* have a wide range of occurrence in rich mesic northern hardwood forests but occurred with lower relative frequency on our study sites and therefore were not selected by indicator species analysis. Nevertheless, they are important indicators of sites where sugar maple will remain healthy under stress. Among the remaining species selected in both subregions of our study, *Carex laxiflora*, *Carya cordiformis*, *Circaea lutetiana*, *Epipactis helleborine*, and *Panax quinquefolius*, all are widely distributed in the eastern United States (Gleason and Cronquist (1991) but generally occurred with the lowest relative frequency in our study. *Epipactus helleborine* is a Eurasian weed naturalized in the United States since 1879 (Luer 1979); its range is still expanding. *Panax quinquefolius* is heavily collected for its roots (Eaton and Schrot 1987) and is highly preferred by deer to the extent that its population viability may be threatened in some areas (McGraw and Furedi 2005). In Pennsylvania, overbrowsing by white-tailed deer (*Odocoileus virginianus* Zimm.) has impacted vegetation for more than 80 years (Horsley et al. 2003; Latham et al. 2005). This may account for the low relative frequency of occurrence (13%) of *Panax quinquefolia* in PANY in our study.

Selection of a species in one subregion of our study but not in the other usually occurred because the species was not found in sites of both subregions. In a few instances, this was due to range limitations. For example, *Actaea rubra*, selected in NHVT, is not found in the flora of northwestern or north-central Pennsylvania, and *Cardamine concatenata*, *Geranium maculatum*, and *Viola rostrata*, which were selected in PANY, are at the edge of their range in NHVT (USDA NRCS. 2007). Another reason for nonselection in one subregion but not in the other was that axis 1 was not the strongest axis for the species in both subregions. *Actaea alba* and *Streptopus roseus* were strongly associated with axis 1 in PANY but were more strongly associated with axis 3 and axis 2, respectively, in NHVT. Likewise, *Laportea canadensis* was strongly associated with axis 1 in NHVT but was found on axes 3 and 2 in PANY. In two instances, nonselection of a species as an indicator may have resulted from our inability to separate two co-occurring species. Both *Impatiens pallida* and *Impatiens capensis* occurred in the PANY flora but were not in bloom at the time of data collection; *Impatiens pallida* was found in the NHVT flora. The same was true of *Dicentra canadensis* and *Dicentra cucullaria* in PANY; both species were identified in NHVT. A few species that were selected as indicators in one subregion were not selected in the other because they had more than the one false positive (number shown in parentheses) in McNemar's exact test. This was true of *Aster divaricatus* (3), *Cardamine diphylla* (3), *Dicentra canadensis* (3), *Ostrya virginiana* (3), *Tilia americana* (4), and *Viola canadensis* (2) that were selected as indicators in NHVT but not in PANY and *Aralia nudicaulis* (12) that was selected as an indicator in PANY but not in NHVT. A few species were not selected as indicators in either subregion for the same reason. These included *Allium tricoccum* (NHVT 1, PANY 2), *Dicentra cucullaria* (NHVT 2), *Osmunda claytoniana*

(PANY 0, NHVT 4), *Podophyllum peltatum* (PANY 2), *Tiarella cordifolia* (NHVT 3, PANY 2), and *Trillium erectum* (NHVT 13, PANY 3). Species that were close to the one false positive threshold may be associated with rich mesic forest but did not meet our conservative criteria for indicating nutritional quality of sites for sugar maple.

The authors cited in Table 3 list a number of other taxa as distinctive of rich mesic forests that are not included in Table 3 because they occurred on less than five plots in our study. Examples include *Aralia racemosa*, *Carex albursina*, *Carex platyphylla*, *Cystopteris bulbifera*, *Dryopteris goldiana*, *Oryzopsis racemosa*, *Podophyllum peltatum*, and *Sanicula trifoliata*. These plants were restricted to plots with foliar nutrient concentrations in the healthy range for sugar maple. However, they were too infrequent to form the basis of an indicator tool for assessing sugar maple site quality. In addition, a number of taxa listed by the authors cited in Table 3 as distinctive of rich mesic forests were relatively common in our study but did not pass statistical tests as indicators of sugar maple health. This includes some common vernal ephemeral species, such as *Allium tricoccum*, *Claytonia virginica*, *Dicentra cucullaria*, *Erythronium americanum*, and *Panax trifolius*. Other species on this list include *Arisaema triphyllum*, *Cornus alternifolia*, *Fraxinus americana*, *Milium effusum*, *Polystichum acrostichoides*, and *Tiarella cordifolia*. Many of these are taxa that prefer moist site conditions and are often found in lower landscape positions or along stream courses. However, we suggest that these taxa are less restricted to high base cation conditions than the other taxa that passed the indicator tests.

Four species selected as indicators in PANY, *Agrostis capillaris*, *Oxalis stricta*, *Taraxacum officinale*, and *Veronica officinalis*, as well as *Epipactis helleborine*, selected in both subregions, are widespread naturalized Eurasian weeds. There is recent evidence that weed species are more likely to invade rich as opposed to poor nutritional habitats (Funk and Vitousek 2007). Most of the sites in PANY where these weeds became established were close to forest roads, trails, or fields. Most NHVT plots tended to be further from roads, which may have contributed to less colonization by exotic species. *Taraxacum officinale*, which had a relative frequency of 50% in PANY, was selected by indicator species analysis in addition to NMS and McNemar's exact test.

Value of indicator species to forest land managers

Choosing sites with high nutritional quality is important to insure continued health of sugar maple in the face of inevitable stress events such as defoliation, drought, or deep soil freezing (Horsley et al. 2002). Even without stress events, imbalanced Ca, Mg, and Mn nutrition is sufficient to cause a decrease in sugar maple health (Hallett et al. 2006). Use of indicator species provides a diagnostic tool allowing forest land managers to determine where in the landscape sugar maple may be "at risk" or likely to remain healthy. Searches for indicator species can be incorporated into land management cruises to define high-quality sites. The species identified by indicator species analysis define a few easily found species. Additional indicators that are useful in decision making were found using NMS ordination and McNemar's exact test. Indicator species can be combined with data on stress history of the site. Most public forestry organizations maintain records derived from aerial surveillance that show the geographic location of insect buildups and defoliation events. Stress history combined with site nutritional quality data can help land managers make a more informed decision about whether an insect suppression program is needed. For example, in Pennsylvania, records of insect buildups and defoliations are maintained on federal forest land by the State and Private Forestry branch of the US Forest Service. On state forest land, the Pennsylvania Department of Conservation and Natural Resources maintains a digitized database of defoliation events over time. Even if stress history is not available, a manager faced with an area where an insect outbreak is expected can still use indicator species information to prioritize suppression activities. Use of such an integrated system would help managers focus scarce suppression and control resources on the most vulnerable sugar maple stands, which will help maintain the health of sugar maple in northern hardwood forests of the northeastern United States.

Conclusions

This study demonstrates the utility of vegetation as an indicator of site quality for sugar maple in northern hardwood stands across the northeastern United States. NMS ordination demonstrated that base and acid cation availability is an important factor determining whether rich mesic flora is present in northern hardwood forests of the northeastern United States. This conclusion was based on the integration of vascular plant records (234 species) with a large database containing intensive measurements of foliar and soil chemistry and other site, stand, and climatic variables. The similarity in indicator species between the NHVT and PANY subregions suggests the importance of base and acid cation nutrition to ecological processes in the northeastern region. Some differences in indicator species did occur. These seem to be the result of differences in species lists and in frequency of species in the NHVT and PANY data sets. Our results suggest that indicator species of site suitability for sugar maple (Table 2) largely overlap with flora that has been recognized as typical of the rich mesic hardwood community. This provides land managers with a diagnostic tool for determining where in the landscape sugar maple is "at risk" or likely to remain healthy in the face of stresses such as excessive defoliation, drought, or deep soil freezing, the primary stresses associated with sugar maple decline.

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References

Bailey, S.W., Horsley, S.B., Long, R.P., and Hallett, R.A. 2004. Influence of edaphic factors on sugar maple nutrition and health on the Allegheny Plateau. Soil Sci. Soc. Am. J. **68**: 243–252.

Bailey, S.W., Horsley, S.B., and Long, R.P. 2005. Thirty years of change in forest soils of the Allegheny Plateau, Pennsylvania. Soil Sci. Soc. Am. J. **69**: 681–690. doi:10.2136/sssaj2004.0057.

Bellemare, J., Motzkin, G., and Foster, D.R. 2005. Rich mesic forests: edaphic and physiographic drivers of community variation in western Massachusetts. Rhodora, **107**: 239–283. doi:10.3119/0035-4902(2005)107[0239:RMFEAP]2.0.CO;2.

Blume, L.J., Schumacher, B.A., Schaffer, P.W., Cappo, K.A., Papp, M.L., van Remortel, R.D., Coffey, D.S., Johnson, M.G., and Chaloud, D.J. 1990. Handbook of methods for acid deposition studies laboratory analysis for soil chemistry. EPA/600/4-90/023. USEPA, Environmental Monitoring Systems Laboratory, Las Vegas, Nev.

Cajander, A.K. 1926. The theory of forest types. Acta For. Fenn. **29**: 1–108.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. **18**: 117–143.

Cogbill, C.V. 2000. Vegetation of the pre-settlement forests of northern New England and New York. Rhodora, **102**: 250–276.

Coile, T.S. 1938. Forest classification: classification of forest types with special reference to ground vegetation. J. For. **36**: 1062–1066.

Cooke, R., Pendrel, B., Barnett, C., and Allen, D. 1996. North American maple project cooperative field manual. USDA Forest Service, Northeastern Area, State and Private Forestry, Durham, N.H.

Curtis, J.T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wis.

Daly, C., Neilson, R.P., and Phillips, D.L. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteorol. **33**: 140–158. doi:10.1175/1520-0450(1994)033<0140:ASTMFM>2.0.CO;2.

Dufrene, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. **67**: 345–366.

Eaton, S.W., and Schrot, E.F. 1987. A flora of the vascular plants of Cattaraugus County, New York. Bull. Buffalo Soc. Nat. Sci. Vol. 31. Buffalo Society of Natural Sciences, Buffalo, N.Y.

Edinger, G.J., Evans, D.J., Gebaner, S., Howard, T.G., Hunt, D.M., and Olivero, A.M. (*Editors*). 2002. Ecological communities of New York State. New York State Department of Environmental Conservation, Albany, N.Y.

Ellenburg, H. 1950. Unkrautgemeinschaften als zeiger fur klima und boden. Landwirtschaftliche Pflanzensoziologie I. Verlag Eugen Ulmer, Stuttgart, W. Germany. p. 141S.

Ellenburg, H. 1988. Vegetation ecology of central Europe 4th edition. Cambridge University Press, Cambridge, U.K.

Fielding, A.H., and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. **24**: 38–49.

Fike, J. 1999. Terrestrial and palustrine plant communities of Pennsylvania. Pennsylvania Department of Conservation and Natural Resources, Harrisburg, Pa.

Funk, J.L., and Vitousek, P.M. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature (Lond.), **446**: 1079–1081. doi:10.1038/nature05719. PMID:17460672.

Gleason, H.A., and Cronquist, A. 1991. Manual of vascular plants of the northeastern United States and adjacent Canada. 2nd ed. New York Botanical Garden, New York.

Godman, R.M., Yawney, H.W., and Tubbs, C.H. 1990. *Acer saccharum* Marsh. Sugar maple. *In* Silvics of North America. Vol. 2. Hardwoods. *Edited by* R.M. Burnes and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 250. pp. 78–91

Hallett, R.A., Bailey, S.W., Horsley, S.B., and Long, R.P. 2006. Influence of nutrition and stress on sugar maple at a regional scale. Can. J. For. Res. **36**: 2235–2246. doi:10.1139/X06-120.

Hills, G.A. 1952. The classification and evaluation of soil for forestry. Ont. Dept. Lands For. Res. Rep. No. 24.

Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A., and Hall, T.J. 2000. Factors associated with decline disease of sugar maple on the Allegheny Plateau. Can. J. For. Res. **30**: 1365–1378. doi:10.1139/cjfr-30-9-1365.

Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A., and Wargo, P.M. 2002. Health of eastern North American sugar maple forests and factors affecting decline. North. J. Appl. For. **19**: 34–44.

Horsley, S.B., Stout, S.L., and deCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. **13**: 98–118. doi:10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2.

Host, G.E., and Pregitzer, K.S. 1992. Geomorphic influences on ground-flora and overstory composition in upland forests of northwestern lower Michigan. Can. J. For. Res. **22**: 1547–1555. doi:10.1139/x92-205.

Houston, D.R. 1999. History of sugar maple decline. *In* Sugar maple ecology and health: Proceedings of an International Symposium, Warren, Pa. *Edited by* S.B. Horsley and R.P. Long. U.S. For. Serv. Gen. Tech. Rep. NE-261. pp. 19–26.

Kolb, T.E., and McCormick, L.H. 1993. Etiology of sugar maple decline in four Pennsylvania stands. Can. J. For. Res. **23**: 2395–2402. doi:10.1139/x93-296.

Kruskal, J. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika, **29**: 115–129. doi:10.1007/BF02289694.

Kudish, M. 1992. Adirondack upland flora: an ecological perspective. The Chauncy Press, Saranac, N.Y.

Latham, R.E., Beyea, J., Benner, M., Dunn, C.A., Fajvan, R.R., Freed, M., Grund, M., Horsley, S.B., Rhoades, A.F., and Shissler, B.P. 2005. Managing white-tailed deer in forest habitat from an ecosystem perspective: Pennsylvania case study. Report by the Deer Management Forum for Audubon Pennsylvania and Pennsylvania Habitat Alliance, Harrisburg, Pa.

Leaf, A.L. 1973. Plant analysis as an aid in fertilizing forests. *In* Soil testing and plant analysis. *Edited by* L.M. Walsh and J.D. Beaton. Soil Science Society of America, Madison, Wis. pp. 426–454.

Long, R.P., Horsley, S.B., and Lilja, P.R. 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. Can. J. For. Res. **27**: 1560–1573. doi:10.1139/cjfr-27-10-1560.

Luer, C.A. 1979. The native orchids of the United States and Canada, excluding Florida. New York Botanical Garden, New York, N.Y.

Lutz, H.J. 1932. Notes on plant indicators of mull forest soil in northwestern Pennsylvania. Proc. Pa. Acad. Sci. **6**: 125–127.

Marçais, B., and Wargo, P.M. 2000. Impact of liming on the abundance and vigor of *Armillaria* rhizomorphs in Allegheny hardwoods stands. Can. J. For. Res. **30**: 1847–1857. doi:10.1139/cjfr-30-12-1847.

Marquis, D.A. 1973. The effect of environmental factors on regeneration of Allegheny hardwoods. Ph.D. dissertation, Yale University, New Haven, Conn.

Marquis, D.A. 1975. The Allegheny hardwood forests of Pennsylvania. U.S. For. Serv. Gen. Tech. Rep NE-15.

McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Ore.

McCune, B., and Mefford, M.J. 2006. PC Ord 5.0. MjM Software, Gleneden Beach, Ore.

McGraw, J.B., and Furedi, M.A. 2005. Deer browsing and population viability of a forest understory plant. Science (Washington, D.C.), **307**: 920–922. doi:10.1126/science.1107036. PMID: 15705851.

Moore, J.-D., and Ouimet, R. 2006. Ten-year effect of dolomitic lime on the nutrition, crown vigor, and growth of sugar maple. Can. J. For. Res. **36**: 1834–1841. doi:10.1139/X06-081.

Morrison, I.K. 1985. Effect of crown position on foliar concentrations of 11 elements in *Acer saccharum* and *Betula alleghaniensis* trees on a till soil. Can. J. For. Res. **15**: 179–183. doi:10.1139/x85-031.

Pregitzer, K.S., and Barnes, B.V. 1984. Classification and comparison of upland hardwood and conifer ecosystems of the Cyrus H. McCormick Experimental Forest, upper Michigan. Can. J. For. Res. **14**: 362–375.

Robarge, W.P., and Fernandez, I. 1987. Quality assurance methods manual for laboratory analytical techniques. USEPA, Corvallis, Oreg.

Roberts, M.R., and Christensen, N.L. 1988. Vegetation variation among mesic successional forest stands in northern lower Michigan. Can. J. Bot. **66**: 1080–1090.

Romell, L.G., and Heiberg, S.O. 1931. Types of humus layer in the forests of northeastern United States. Ecology, **12**: 567–608. doi:10.2307/1929001.

SAS Institute Inc. 2003. SAS version 9.1. SAS Institute Inc., Cary, N.C.

Schlenker, G. 1950. Forstliche standortskartierung in Wurttemberg. Allg. Forstztg. **41**: 1–4.

Sperduto, D.D., and Nichols, W.F. 2004. Natural communities of New Hampshire. New Hampshire Natural Heritage Bureau, Concord, N.H.

Spies, T.A., and Barnes, B.V. 1985*a*. A multifactor ecological classification of the northern hardwood and conifer ecosystems of the Sylvania Recreation Area, Upper Peninsula, Michigan. Can. J. For. Res. **15**: 949–960. doi:10.1139/x85-152.

Spies, T.A., and Barnes, B.V. 1985*b*. Ecological species groups of upland northern hardwoods – hemlock forest ecosystems of the Sylvania Recreation Area, Upper Peninsula, Michigan. Can. J. For. Res. **15**: 961–972. doi:10.1139/x85-153.

Thomas, G.W. 1982. Exchangeable cations. *In* Methods of soil analysis. Part 2. 2nd ed. *Edited* by A.L. Page et al. Agron. Monogr. 9. American Society of Agronomy and Soil Science Society of America, Madison, Wis.

Thompson, E.H., and Sorenson, E.R. 2000. Wetland, woodland, wildland. A guide to the natural communities of Vermont. University Press of New England, Hanover, N.H.

USDA NRCS. 2007. The PLANTS database (http://plants.usda.gov, 17 December 2007). National Plant Data Center, Baton Rouge, La.

Wargo, P.M., Minocha, R., Wong, B.L., Long, R.P., Horsley, S.B., and Hall, T.J. 2002. Measuring changes in stress and vitality indicators in limed sugar maple on the Allegheny Plateau in north-central Pennsylvania. Can. J. For. Res. **32**: 629–641. doi:10.1139/x02-008.

Weatherbee, P.B., and Crow, G.E. 1992. Natural plant communities of Berkshire County, Massachusetts. Rhodora, **94**: 171–209.

Whitney, G.G. 1990. The history and status of the hemlock–hardwood forests of the Allegheny Plateau. J. Ecol. **78**: 443–458.

Whitney, G.G. 1991. Relation of plant species to substrate, landscape position, and aspect in north central Massachusetts. Can. J. For. Res. **21**: 1245–1252. doi:10.1139/x91-173.

Whitney, G.G. 1999. Sugar maple: abundance and site relationships in the pre- and post settlement forest. *In* Sugar maple ecology and health. *Edited by* S.B. Horsley and R.P. Long. Proc. of an International Symposium. U.S. For. Serv. Gen. Tech. Rep. NE-261. pp. 14–18.