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ARTICLE

Determinants of survival over 7 years for a natural cohort of sugar maple seedlings in a northern hardwood forest

Natalie L. Cleavitt, John J. Battles, Timothy J. Fahey, and Joel D. Blum

Abstract: The regeneration ecology of sugar maple (*Acer saccharum* Marsh.) has been impacted by acid rain leaching of base cations from the soils throughout much of its range. We tracked the survival and causes of death for a natural cohort of sugar maple seedlings across 22 sites in the Hubbard Brook Valley in New Hampshire, USA, where soil acidification has been documented. Survival over 7 years averaged 3.4%; however, significant differences in survival were observed among sites, which were classified into three main groups based on the shape of their survival curves. These site groups differed in position on the landscape, seedling nutrition and leaf size, and the prevalence of damage agents, but not in soil Ca. First-season mortality was high (71%), and the main damage agents were fungal infection (*Rhizoctonia* spp.) and caterpillar herbivory (Geometridae). Other principal causes of mortality in order of importance were winter injury, mechanical damage, and rodent (*Myodes gapperi* Vigors, 1830) tunneling, and all damage agents varied significantly in severity between years. This study highlights the importance of landscape-level variation in biotic factors for predicting sugar maple regeneration success. Predictions of sugar maple regeneration will require a better understanding of controls on initial seedling growth and the suite of biotic agents that damages seedlings.

Key words: Geometridae, Hubbard Brook Experimental Forest, mortality, *Rhizoctonia*, winter injury.

Résumé : Le lessivage des cations basiques du sol par les pluies acides a eu un impact sur l'écologie de la régénération de l'érable à sucre (*Acer saccharum* Marshall) presque partout dans son aire de répartition. Nous avons suivi la survie et les causes de mortalité d'une cohorte naturelle de semis d'érable à sucre dans 22 stations de la vallée de Hubbard Brook au New Hampshire, É.-U., où l'acidité du sol a été documentée. Sur une période de 7 ans, le taux moyen de survie a été de 3,4 %; cependant, des différences significatives ont été observées entre les stations qui ont été classées en trois groupes principaux sur la base de leur courbe de survie. Ces groupes de stations se distinguaient par leur position dans le paysage, la nutrition et la taille des feuilles des semis ainsi que par la prédominance des agents détériorateurs mais non par le Ca du sol. La mortalité a été élevée (71 %) durant la première saison et les principaux agents détériorateurs étaient les infections fongiques (*Rhizoctonia* spp.) et l'herbivorisme des chenilles (Geometridae). Les autres causes principales de mortalité étaient en ordre d'importance: les blessures hivernales, les blessures mécaniques et les galeries de rongeur (*Myodes gapperi* Vigors, 1830) et la sévérité des dommages causés par tous les agents détériorateurs était significativement différente d'une année à l'autre. Cette étude fait ressortir l'importance de la variation à l'échelle du paysage des facteurs biotiques pour prédire la réussite de la régénération de l'érable à sucre. Les prédictions concernant la régénération de l'érable à sucre nécessitent une meilleure compréhension des facteurs qui régissent la croissance initiale des semis et la série d'agents biotiques qui causent des dommages aux semis. [Traduit par la Rédaction]

Mots-clés : Geometridae, forêt expérimentale de Hubbard Brook, mortalité, *Rhizoctonia*, blessures hivernales.

Introduction

Temperate forests are confronted with an unprecedented combination of human-accelerated environmental changes, including climate warming (Dale et al. 2001), air pollution (Tomlinson 2003), and introduced pests and pathogens (Fischer et al 2013). These changes can have a profound influence on tree demography, including selective increases in canopy tree mortality and shifting rates of tree recruitment (St. Clair et al. 2008). Of these two processes, recruitment has received much less attention.

Our understanding of the early phases of tree recruitment is limited by the high spatial and temporal variability in seedling survival (Clark et al. 1999). Tracking the fate of new germinants in the field is a labor-intensive enterprise. To accommodate the typically steep decline in first-season seedling survival (Beckage et al. 2005; Cleavitt et al. 2011), many individuals must be marked at the outset. As a consequence, data are sparse. Beckage et al. (2005) applied an innovative Bayesian model of survival using seedling count data to characterize tree recruitment success. Their efficient approach appears to capture much of the information on annual survival patterns (Lavine et al. 2002). However, count data provide no insights regarding the causes of seedling mortality nor can they detect seasonal trends. Yet information on the determinants of seedling survival and subannual survival patterns is essential to assess potential limitations to recruitment associated with the ongoing environmental changes. Therefore, here we explicitly examine how survival, damage agents, and the relationship between these variables and site characteristics shift between the first season and the next 6 years for a natural cohort of marked sugar maple (*Acer saccharum* Marsh.) seedlings.

Sugar maple is of particular interest given current trends. The species has been in decline in areas of eastern North America with

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base poor soils as a result of acid rain exacerbated soil calcium deficiencies (Bailey et al. 2004), including effects on regeneration (Juice et al. 2006; Kobe et al. 2002). The relative concentrations of other soil cations, particularly Mg, Mn, and Al, have also been shown to be important in sugar maple ecology (St. Clair et al. 2008), and critical thresholds for these elements have been established (Hallett et al. 2006).

In the late 1990s, sugar maple decline was documented in Hubbard Brook Experimental Forest (HBEF) in northern New Hampshire, as evidenced by relatively slow growth rates, reduced recruitment across a wide elevation range, and unusually high mortality of mature sugar maple trees at higher elevations (Siccama et al. 2007). Sugar maple seedling densities are significantly lower at high elevations (Forcier 1973; Juice et al. 2006), well within the wider range of sugar maple distribution in the region. Recent studies demonstrated clearly that addition of Ca to the soils of an experimental watershed at HBEF, in an amount designed to replace the Ca lost from leaching by acid deposition in the 20th century, resulted in greatly enhanced sugar maple seedling survival (Cleavitt et al. 2011; Juice et al. 2006), as well as enhanced growth of mature sugar maples (Battles et al. 2014). Broader and longer term patterns of variation in sugar maple seedling survival at the HBEF have not been studied.

Previous studies of marked sugar maple seedlings have demonstrated the complexity of damage agents responsible for seedling mortality; however, these studies were all restricted in either the agents considered (Coyle et al. 2014) or the number of sites studied (Gardescu 2003; Cleavitt et al. 2011). In the present study, we observed damage agents on marked seedlings at 22 sites for a natural cohort resulting from the 2006 mast year; this mast event appears to have contributed to sugar maple regeneration across the region (Graignic et al. 2014). We compared survival and causes of damage for two periods: short term (from time of marking to leaf-off in the first fall) and longer term (up to leaf-off in year 7). The 22 sites across the Hubbard Brook Valley encompassed a range of elevation, soil fertility, and forest composition.

The objectives of the current study were to answer the following questions. (*i*) Does the first season exhibit the highest mortality? (*ii*) Does sugar maple seedling survival decrease with increasing elevation? (*iii*) Is increased survivorship associated with higher plant-available Ca soils? (*iv*) Do agents of damage show greater variation between sites or years? In addition, this study identifies factors that should be included in models seeking to predict sugar maple regeneration potential across complex landscapes such as the Hubbard Brook Valley.

Materials and methods

Study areas

The HBEF is located in north-central New Hampshire, USA (43°56′N, 71°45′W). Detailed descriptions of climate, hydrology, topography, and vegetation of the HBEF are presented in Likens and Bormann (1995). Soils are predominantly well-drained acid Spodosols (Haplorthods) of sandy-loam texture formed from glacial till. Soils generally decline in rooting depth with increasing elevation, but considerable variation in soil properties is associated with till characteristics, topographic position, and internal drainage (Bailey et al. 2014). Overstory vegetation is dominated by northern hardwoods: sugar maple, American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.), which comprise over 90% of the forest basal area, with a higher proportion of spruce–fir–birch at the highest elevations (van Doorn et al. 2011). The HBEF is mostly second-growth forest developed following logging in the late 19th and early 20th centuries, with most of the forest currently about 100 years old.

Twenty-two study sites were chosen in the HBEF in spring 2007 (Fig. 1). Sites were chosen based on (*i*) the presence of sugar maple seedlings from the 2007 cohort at the site, (*ii*) variation in soil Ca status, and (*iii*) variation in topographic position (Fig. 1). At each site, elevation, aspect, slope, sugar maple overstory abundance (circular 10 m radius plot), seedling density (1 m wide × 30 m long belt transect), and relative abundance of leaf litter by species (10 point counts of fresh leaf litter per seedling transect) were quantified. The sampling was centered on the marked sugar maple seedlings to describe their environment. Aspect was decomposed into measures of eastness and northness. Eastness was calculated as the sin(aspect), ranging from 1 for due east to –1 for due west. Northness was calculated as cos(aspect), ranging from 1 for due north to –1 for due south.

Soil sampling

Soil samples were collected at 19 of the 22 sites from 21 August to 2 September 2008 (soil analysis using similar methods was available for three of the sites from Schwarz et al (2003)). Five soil samples per site were taken with a 5 cm diameter split PVC corer and separated by horizon in the field. The horizon depths were measured to the nearest 0.5 cm, and samples were taken back to the lab for pH measurements on the organic and B horizons. Based on findings of Bailey et al. (2004), we used the top 5 cm of the B horizon to assess soil Ca status. The sample was homogenized and left to air dry. In the lab, 5 g of soil was extracted with 1 mol·L^{-1} ammonium chloride and run as 1:10 dilutions using an inductively coupled plasma optical emission spectrometer (ICP-OES; PE-3300 DV, Perkin Elmer, Norwalk, Connecticut).

Seedling samples for chemistry and mycorrhizal scoring

Seedlings were collected from all the sites for plant biomass and chemical analyses. In July 2007, 20 whole seedlings were carefully excavated from each of 22 sites. Ten of these seedlings were immediately frozen for chemical analysis. The remainder were pooled by site and dried at 60 °C for 48 h, and leaves, stem, and root were weighed separately to obtain a site average biomass for the first-season seedlings. For chemical analysis, whole seedlings (i.e., including above- and below-ground parts) were finely ground in a ball mill and analyzed for concentrations of Al, Ca, Fe, K, Mg, Mn, and P following combustion of 0.1 g subsamples at 550 °C for 4 h. After adding 0.5 mL of 50% H_2O_2, samples were re-heated to 550 °C for 2 h. Ash was dissolved in 5 mL of 50% ultra-pure HNO_3 and brought to a final volume of 10 mL with deionized H_2O. Solutions were analyzed by ICP-OES.

In June 2007, 10 sugar maple seedlings were collected randomly from each of the 22 study sites to quantify colonization by arbuscular mycorrhizal fungus (AMF). Roots were clipped from 10 of the seedlings and stored in 10% ethanol for AMF assessment. Fine roots were cleared and stained for AMF analysis using a modification of the Brundrett et al. (1994) ink and vinegar approach. Lateral roots were cleared using 10 mL of 10% KOH in a 90 °C water bath, with KOH changed every 30 min until no pigment was visible in the solution. Roots were rinsed with distilled water and acidified with 10% HCl, stained with 0.05% Parker Quink ink (Parker Pen Products, Newhaven, East Sussex, UK) in 1:1 glycerol–vinegar for 9–12 h, and stored in a de-stain solution of 1:1 glycerol–vinegar until observation under a compound microscope at 200× magnification.

For each sample, observations were taken at 1 mm intervals on a grid (n = 100), with colonization scored on the basis of intersection of fungal structures with the grid. Fungal structures scored included nonstaining septate hyphae, blue-staining hyphae, and AMF structures (appressoria, arbuscules, coils, and vesicles). Percent colonization was calculated from the proportion of total observations of each structure relative to total observations.

Field seedling surveys

The survival of marked seedlings from the 2007 cohort at each of the 22 study sites was followed from the time of marking in June–July 2007 through fall 2013. Seedlings were double-marked

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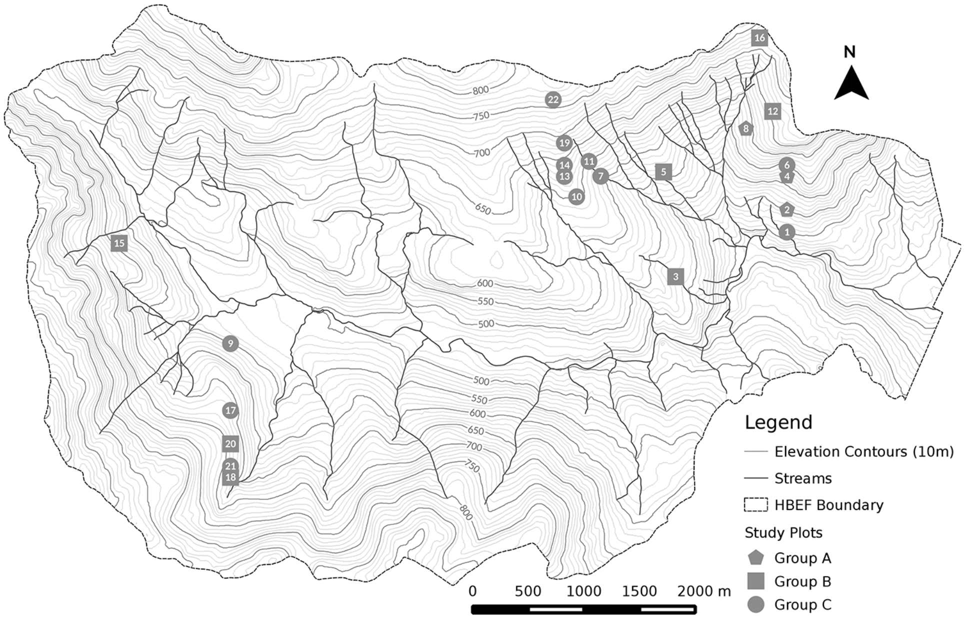
Fig. 1. Location of 22 study areas within the Hubbard Brook Valley, Woodstock and Ellsworth, New Hampshire. Sites are numbered 1–22 by increasing elevation corresponding to the order in Supplementary Tables S2 and S4. Sites are further coded by symbol to indicate group membership based on survival curves.

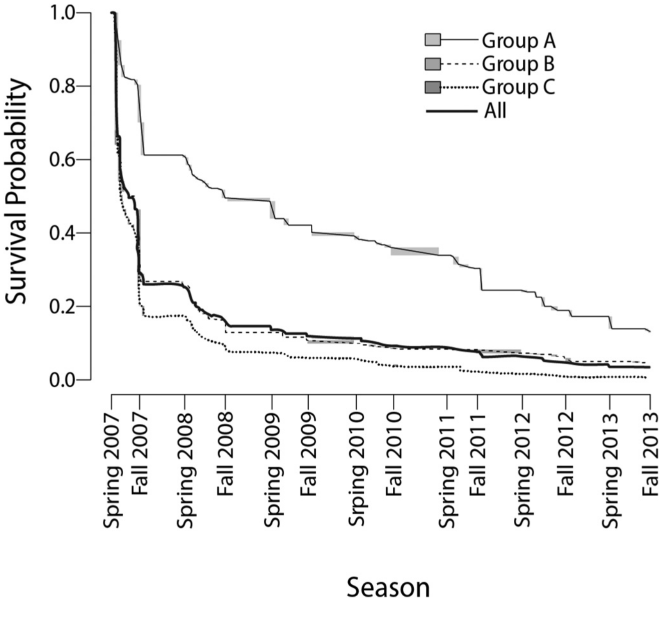


with a numbered flag and a uniquely colored ground-level marker. There were originally 2200 marked seedlings, but 20 of these were lost prior to 2012, leaving 2180 seedlings for most analyses. Sometime after the last survey visit for the season in October 2011, one of the sites (site 6) was destroyed by a black bear, resulting in 23 additional lost seedlings (hence, 43 lost in total). First-season survival is from June–October 2007. In 2007 and 2008, seedlings were visited biweekly during the snow-free season. In 2009, seedlings were visited three times (May, July, October), and from 2010 to 2013, the surviving seedlings were visited monthly from the start of the growing season to leaf-off in the fall (six to seven survey times per season).

By the end of the first growing season, more than 70% of the seedlings in the spring cohort had died (Fig. 2). Given the goals of this study, namely to track determinants of seedling survival through multiple seasons and years, we needed to maintain a minimum sample size. Thus in late September and early October of 2007 (i.e., the end of the first growing season), we marked and measured additional seedlings to bring the sample back to 100 individuals at each site prior to winter 2007–2008. We marked more seedlings at two sites (sites 10 (*n* = 200) and 16 (*n* = 300)) to accommodate high site heterogeneity due to local topography. Therefore, this data set initially included 2500 seedlings (638 of these seedlings were survivors that had been marked originally). Thus, we created two distinct data sets that served different purposes: a 2007 "summer cohort" composed of the originally marked seedlings and a 2007 "fall cohort" sample of seedlings that were present during the September–October 2007 remark period. We limit inferences regarding population dynamics to the summer cohort. We use the fall cohort exclusively to document the causal agents of mortality after the first growing season.

At the initial observation time in 2007, leaf expansion class, leaf number, and leaf damage estimates (visual percentage) were recorded for each seedling. Damaged leaves were inspected to determine the causal agent, which with time could be assigned to several categories (Supplementary Table S1).[1] There is often a lag in assigning causes of death to insure that the seedling is truly dead or because the seedling survives in a suboptimal condition for some time into the growing season. Therefore, many seedling deaths eventually attributed to winter agents have death dates into the next growing season.

Fig. 2. Fitted survival curves of sugar maple seedlings at HBEF based on Kaplan–Meier estimators. The lines represent the interpolated functions. The grey rectangles denote the range of possible values given the censoring in the data. Error boxes around the "All" sites curve were omitted for clarity.



Survival analysis

We used nonparametric maximum likelihood estimators to quantify the survivorship of sugar maple seedlings from the initial

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0177.

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summer cohort. For practical reasons (e.g., seedlings buried by winter snows, sampling effort), we did not maintain a constant census interval over the course of this longitudinal field study. Thus, our data included two kinds of censoring. Some seedlings ($n = 75$) survived the entire 7 years (right censored). For the remainder ($n = 2082$), we knew only the interval in which they died (i.e., interval censored). As noted above, the length of the intervals ranged from 14 days during the growing season to more than 5 months over the winter. We used Turnbull's (1976) procedure for the Kaplan–Meier estimator to calculate survivorship curves and the weighted logrank test from the "interval" package in R (Fay and Shaw 2010; R Core Team 2013) to quantify differences among sites.

Major goals were to identify the patterns and determinants of survival of naturally occurring sugar maple seedlings in Hubbard Brook Valley. We used conditional inference trees (CIT; introduced as random forests by Breiman 2001) for two purposes: (*i*) to detect any difference in survivorship among the 22 sites and (*ii*) to identify the most important variables related to survival outcomes. CIT is an extension of classification and regression trees (CART; Brieman et al. 1984), a nonparametric binary recursive partitioning method. CART partitions data into homogeneous subsets in terms of the explanatory variables. We chose the CIT implementation of random forests because this method can handle survival data with censored responses (Strobl et al. 2008). In addition, CIT is unbiased towards different variable types while also accommodating the autocorrelation among potential predictors (Strobl et al. 2008).

To classify differences in survivorship among the sites, we used the ctree function in the "party" package in R (Strobl et al. 2009; R Core Team 2013). The goal was to search for any consistent similarities in survival curves among the 22 sites. Groups identified by ctree were subsequently tested using the weighted logrank test described above.

To explore determinants of survival, we measured a broad suite of potential biological and environmental variables (described above) and then used CIT to identify the most important variables for survival outcomes. Specifically, we applied the cforest function (Strobl et al. 2009; R Core Team 2013). This function employs random subsampling without replacement. We selected 1000 classification trees and five predictors. CIT is referred to as an ensemble technique, with results for each predictor averaged across all the trees. Ecological studies are increasingly using CIT (Cutler et al. 2007).

We used permutation importance to rank the variables that best predict survival. Variable importance is a measure of prediction accuracy for observations before and after permuting, averaged over all classification trees (Strobl et al. 2008, 2009). A challenge with this technique is identifying the most relevant variables as there is no standard statistical criterion (Boulesteix et al. 2012). To provide some guidance, we designed a simple Monte Carlo approach. We generated 100 iterations in which survival probabilities for each seedling were generated at random (binomial distribution in which the probability of survival equals 50%). We then calculated variable importance for each iteration to develop a null distribution of variable importance values. We used the 99th percentile of the null distribution of importance values as a guide to relevant factors.

Damage agent analysis

For the first season (summer 2007 cohort), the presence or absence of the two main damage agents (caterpillar herbivory and fungal infection) were analyzed for their relationship to site-level variables using logistic regression. We followed the model-building procedure of Hosmer and Lemeshow (1989) in which univariate models were constructed and all variables with a p value of 0.25 or less were included in further multivariate models. The multivariate model possibilities were then compared using the change in log-likelihood (LL) between models containing different combinations of the variables. The best models were determined based on significance of the variables in the model and deviance reduction between models. For all models, $N = 2180$ seedlings. Model details are given in the Supplementary tables.

For putative death causes scored for the subsequent 6 years (remarked fall cohort), contingency analysis was used to test for differences in the importance of agents between sites and years ($N = 2127$ as 198 seedlings were still alive, 112 had uncertain cause of death, and 63 were lost). There were six death agent categories that were separated by the main timing of damage between winter (late fall herbivory, freeze damage, and rodent tunneling) and growing season (fungal damage, caterpillar herbivory, and mechanical damage) (also see Supplementary Table S1). Damage analyses were run using JMP 10 Pro (SAS Institute Inc., Cary, North Carolina, USA).

Results

Site and seedling measures

The study sites ranged in elevation from 350 to 800 m, encompassing the range over which sugar maple is abundant in the HBEF. Soils were all highly acidic with B horizon pH ranging from 3.68 to 4.96 (Supplementary Table S2). Extractable soil Ca in the top of the B horizon exhibited a nine-fold range across the sites. The depth of the organic layer was greater on west-facing sites ($r = -0.616$, $p = 0.0023$), and soil pH was higher on steeper sites ($r = 0.601$, $p = 0.0031$) (Supplementary Table S3). The abundance of sugar maple in the overstory canopy and the proportion of sugar maple leaf litter varied markedly among the sites, as did the initial density of sugar maple seedlings in the 2007 cohort (Supplementary Table S2). Sugar maple abundance was positively related to seedling Ca ($r = 0.612$, $p = 0.0025$) and initial seedling densities ($r = 0.715$, $p = 0.0002$) (Supplementary Table S3).

Seedling Ca concentration in July 2007 indicated that seedlings from 10 of the study sites were below the critical foliar levels for Ca (5500 $\mu g \cdot g^{-1}$) suggested by Hallett et al. (2006) (Supplementary Table S4). Seedlings at all sites were above the critical values for Mg and below the toxic level for Mn (Supplementary Table S4). Seedling P, Mg, and K were all closely correlated (Supplementary Table S3). Colonization of seedling roots by AMF was best described by the percentage of arbuscules in spring 2007. Arbuscules ranged from 5%–48% colonization of the seedling roots among sites (Supplementary Table S4).

Seven-year survival and site groupings

Survivorship of the 2007 summer cohort at 22 sites for 7 years was 3.4%. The survival curve shows a steep drop in the number of living seedlings in the first growing season (71% mortality) (Fig. 2). The second growing season (8.9% mortality) and the first winter (3% mortality) were also important times of higher mortality. The conditional inference tree using survival curves as the response variable divided the sites into three distinct groups ($p < 0.001$), a classification that was confirmed by the logrank tests on group differences ($p < 0.001$): group A (three sites) had higher survival with mean survivorship of 13% after 7 years, whereas group B (six sites) had 5% and group C (13 sites), with the lowest survival, had only 1% (Fig. 2).

Group A (highest survival) sites stood out as having seedlings with larger leaves and less initial damage. These sites also tended to be at lower elevations, more westerly aspects, steeper slopes, and deeper organic matter layer (Table 1). Group B had a lower average number of damage agents per seedling (Table 1). Group C (lowest survival) had seedlings with higher foliar P and Mg concentrations.

Short-term survival and damage agents

Sugar maple seedling survival for the first season (marking in spring to leaf-off in fall 2007) varied widely among sites, ranging

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Table 1. Summary of mean differences (SD in parentheses) between site groups for site and seedling measures that were important variables in survival and (or) logistic regression models of sugar maple survival at HBEF.

Variable importance			Site group		
First-season survival	Damage agents	Variable	A (3)	B (6)	C (13)
Site measures					
4	C, F	Elevation (m)	477 (65)	608 (92)	612 (112)
		Slope (%)	26.0 (7.8)	9.3 (5.6)	12.4 (7.3)
	C	Northness (N = 1)	−0.44 (0.43)	−0.21 (0.66)	−0.39 (0.58)
		Eastness (E = 1)	−0.78 (0.34)	0.33 (0.76)	0.43 (0.62)
5	F	Depth OM (cm)	4.48 (0.50)	3.54 (0.78)	3.45 (0.49)
		Soil Ca ($\mu g \cdot g^{-1}$)	103 (11)	140 (76)	77 (42)
		SM forest floor (%)	22.7 (7.1)	27.4 (9.3)	31.8 (21.2)
Seedling measures					
	F	Seedling density (m^2)	2.84 (0.98)	4.44 (1.92)	6.45 (4.83)
	C	June arbuscules (%)	26.8 (9.3)	19.0 (10.7)	14.4 (10.6)
		Seedling Ca ($\mu g \cdot g^{-1}$)	5392 (1488)	6132 (1355)	5840 (1376)
	C	Seedling P ($\mu g \cdot g^{-1}$)	3041 (418)	2897 (501)	3498 (455)
		Seedling Mg ($\mu g \cdot g^{-1}$)	2478 (73)	2137 (306)	2670 (410)
		Seedling Mn ($\mu g \cdot g^{-1}$)	694 (308)	702 (187)	864 (361)
3		Leaf area (cm^2)[a]	15.3 (4.5)	14.3 (4.3)	14.3 (4.3)
1		Initial leaf damage (%)	11.6 (14.7)	19.6 (19.8)	19.3 (18.7)
		Damage agents (no.)	3.2 (1.1)	2.7 (0.9)	3.1 (1.1)

Note: The number of sites included in each group is given in parentheses following the group letter. Variable importance for first-season survival is ranked by explanatory value. Note that site was also an important variable for first-season survival (rank 2). Variable importance for damage agents are coded caterpillar herbivory (C) and fungal infection (F). Site and seedling measures are described and summarized by site in Supplementary Tables S2 and S4. OM, organic matter; SM, sugar maple.

[a] The last three seedling variables were measured at the seedling scale and have much larger *N* (group A (281); group B (650); group C (1249)). Please refer to Supplementary material for complete details.

from 6% to 81%. In group A, survival was 74% compared with 33% and 20% in groups B and C, respectively (Fig. 2). In order of variable importance, the survival of seedlings over the first season was best explained by amount of leaf damage in spring 2007; next, and of about equal importance, were site, seedling leaf area, and elevation (Table 1; Supplementary Fig. S1). All of these variables were at least four times larger than the null importance value (Supplementary Fig. S1).

The majority of the leaf damage in the first season was fungal damage (*Rhizoctonia* vascular fungus) and caterpillar herbivory (mainly Geometridae). Fungal damage was more prevalent than caterpillar damage, with very few seedlings completely free of fungal infection (Table 2). Group B sites had a lower overall number of damage agents per seedling and a lower frequency of occurrence for all damage agents except *Rhizoctonia* vascular fungus (Table 2). Group A sites had lower percentage of damage on their leaves at the time of marking in spring 2007 (Table 1).

The best logistic regression model for predicting incidence of caterpillar herbivory included seedling P concentration, site elevation, June arbuscules, and northness (model: df = 4, –LL = 86.77, $\chi^2 = 173.5$, $p < 0.0001$) (Supplementary Table S5*a*). Caterpillar herbivory was more likely to occur on seedlings with higher average P concentration and fewer arbuscules in their roots and at sites that were more south-facing and lower in elevation. The best model for predicting fungal infection included elevation, pH of the organic horizon, and initial seedling density (model: df = 3; –LL = 45.53; $\chi^2 = 91.07$; $p < 0.0001$) (Supplementary Table S5*b*). Seedlings with fungal damage had a higher probability of occurring at sites lower in elevation with higher initial seedling densities and more acidic organic horizon.

Table 2. Frequency of damage agents on seedlings of sugar maple at HBEF at the time of marking in spring 2007.

	Site group			
Damage agent	A (281)	B (650)	C (1249)	All sites (2180)
Rhizoctonia	80.4a	86.0b	88.3b	86.6
Leaf spot	91.8b	82.0a	80.7a	82.5
All fungal	99.3a	97.9a	98.4a	98.4
Caterpillar	39.2b	29.1a	43.7b	38.8
Other invert	24.6c	6.2a	11.9b	11.8
All invert	50.5b	34.9a	51.9b	46.7
Mechanical	14.2a	26.0b	29.0b	26.2
Leaf gone	4.6a	8.8b	8.6b	8.1

Note: The number of seedlings included in each group is given in parentheses following the group letter. Site groups are based on significant difference in the survivorship curves between sites. Values are the percentage of seedlings with a given damage agent present. Percentages within a row are significantly different ($\alpha = 0.05$) by post hoc contingency tests when they are followed by a different letter.

Damage agents subsequent to first growing season

Using the full remarked set of seedlings from fall 2007 (2500 seedlings), damage agents appearing as the main cause of seedling demise could be assigned for 2127 seedlings. Seedling leaf size was clearly the most important predictor of first-winter survival; the importance value was not only 40 times greater than the null value, but also three times more important than the next best predictor (bud damage) (Supplementary Fig. S2).

Three principal causes of seedling mortality were observed during the first fall–winter interval: late fall stem herbivory by invertebrates, winter freeze damage to the stems or roots, and rodent tunneling (Table 3). These three causes did not differ in importance between the site groups (Supplementary Table S6), and winter freeze damage was the primary agent of winter damage. Group A sites lost a lower percentage of seedlings (32% compared with 51% and 58% at groups B and C, respectively) during the first winter (Table 3).

Growing season damage agents differed significantly between site groups and years (Figs. 3 and 4; Supplementary Table S6). Sites in group C (lowest survival) had a higher percentage of seedlings die from caterpillar herbivory (both winter and growing season) and from mechanical damage (Fig. 3). In 2008, group C had twice as many deaths from caterpillars as the other two site groups

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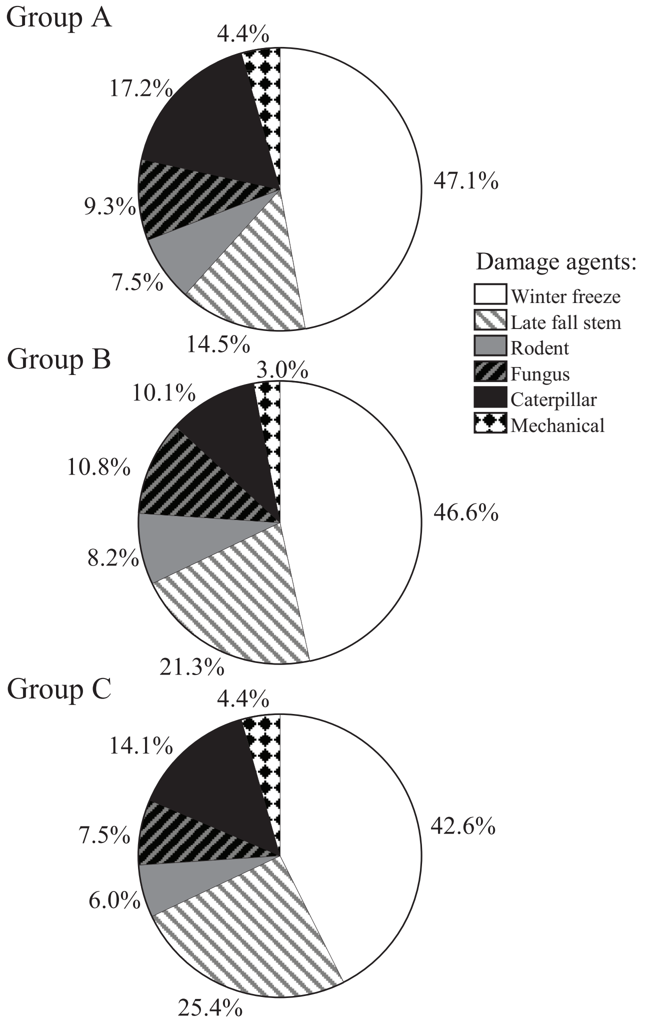
Table 3. Summary of damage agents that accounted for 4% or more of deaths at two or more site groups for sugar maple seedlings at HBEF marked in fall 2007 through fall 2013.

		Site group			
Year	Damage agent	A (227)	B (564)	C (1336)	All sites (2127)
Winter, 1st year		**32.15**	**50.75**	**57.58**	**51.71**
2007	Late fall herbivory	11.45	15.60	18.94	17.25
2008	Winter freeze	18.94	30.54	34.22	30.28
2008	Rodent tunneling	1.76	4.61	4.42	4.18
Growing season, 2nd year		**7.05**	**13.83**	**15.79**	**14.33**
2008	Caterpillar herbivory	5.73	5.67	10.55	5.59
2008	Fungal infection	1.32	8.16	5.24	8.74
Winter, 2nd year		**10.57**	**10.81**	**11.67**	**11.33**
2008	Late fall herbivory	1.76	4.96	5.01	4.65
2009	Winter freeze	8.81	5.85	6.66	6.68

Note: The number of seedlings included in each group is given in parentheses following the group letter. Values are the percentage of all deaths occurring within this site group during this time period by mortality agent. Values in bold are the sum of the percentage of deaths for that time period. Note that seedling numbers were low enough at all sites by the third year that no sites had mortality agents that accounted for 4% or more of the total.

Fig. 3. Comparison of frequencies for six main causes of sugar maple seedling damage over 6 years (first fall to seventh fall) at three groups of sites. Sites were divided into three groups (A–C) based on differences in survivorship, with group A having the highest survival and group C having the lowest survival. The six damage agents are shown in the legend.



(Table 3). Growing season damage agents accounted for fewer seedling deaths (46.7%) at sites in group A than at the other sites, but this difference was not significant (Fig. 3; Supplementary Table S6). As in the first season, fungal infection and caterpillar herbivory were the most important causes of growing season damage for the next six growing seasons (Fig. 4). In 2008, sites in group B had more deaths related to fungal damage than to caterpillar damage, while the reverse was true at most of the sites (Table 3) and this pattern can also be seen for all years (Fig. 4).

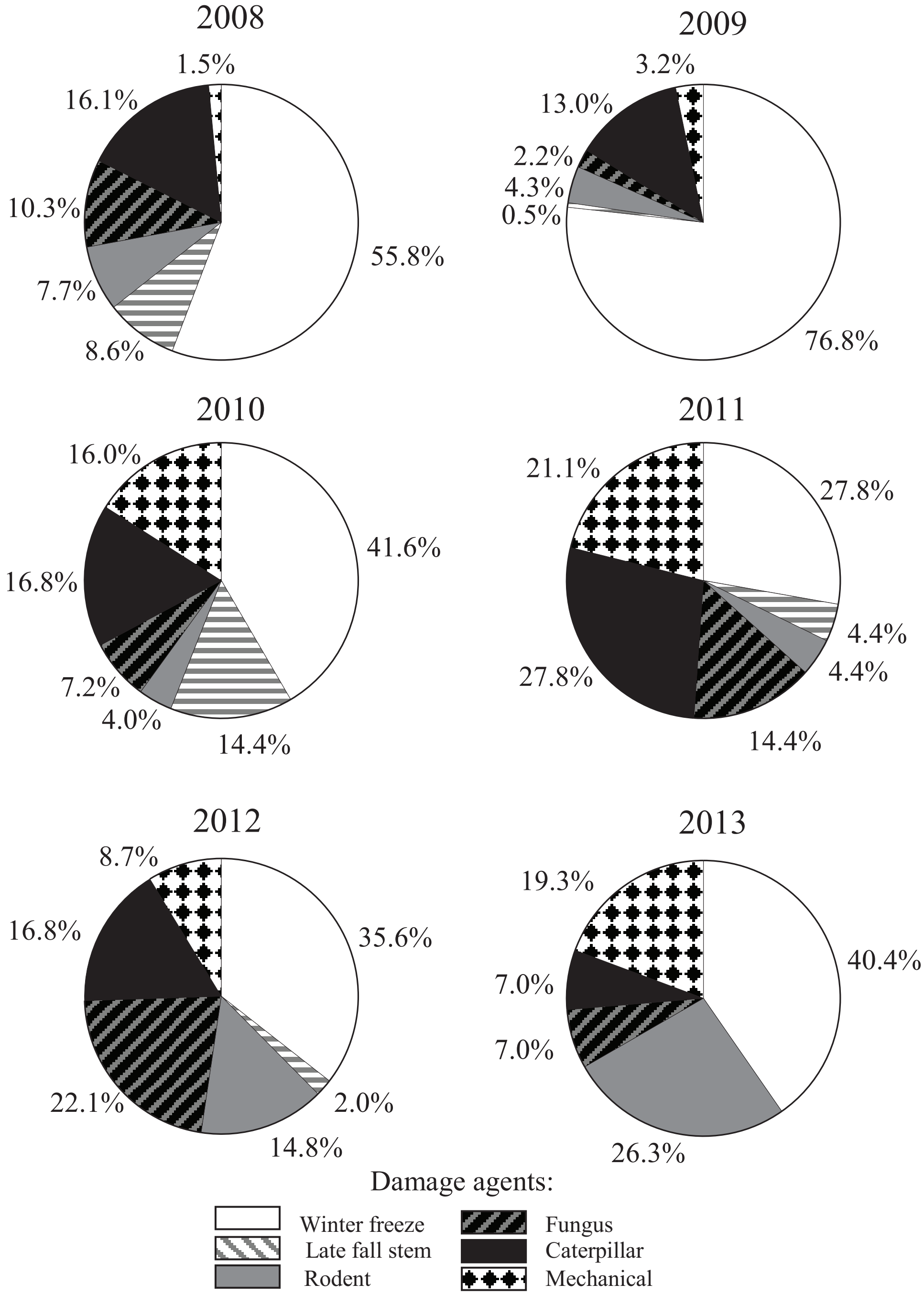
Between years, winter freeze damage varied most dramatically in importance, from a low of 27.8% of deaths in 2011 to a high of 76.8% of deaths in 2009 (Fig. 4). Winter freeze damage was the most important mortality agent for all years except 2011. In 2011, caterpillar herbivory related deaths were particularly high, whereas winter freeze damage was particularly low (Fig. 4). Late fall stem herbivory peaked in 2007 (Table 3) and 2010 (Fig. 4). Rodent tunneling was highest in the winter of 2012–2013 (26.3%). Fungal damage was greatest in 2007 (Table 2) and 2012 (Fig. 4). Mechanical damage was noticeably greater in 2011 and 2013 (Fig. 4).

Discussion

Our findings suggest that regeneration potential of sugar maple is determined primarily by biotic factors, namely seedling size and prevalence of fungi and caterpillars, and secondarily by abiotic site factors such as elevation and aspect through their effects on seedling growth and damage agent abundance and severity. As expected, seedling mortality was very high during the first growing season, and this early mortality was strongly influenced by the size of seedlings and the prevalence of the key damage agents pathogenic fungi and caterpillar herbivory at the time of initial census. These key factors interacted in complex ways across the 22 sites to influence long-term (7 year) survivorship.

In particular, the importance of site conditions to seedling survivorship was best described by the classification of the 22 sites into three distinctive groups based on their survivorship curves. Group A sites are evidently optimal for sugar maple regeneration; seedlings are bigger and healthier, and hence damage agents such as fungi and insects do not inflict as much damage as elsewhere. On both group B and C sites, where survivorship is much lower, seedling growth is suppressed, but on group B sites, survivorship is significantly higher than on group C sites because the key damage agents are less abundant. Group C sites, with the lowest survivorship and high prevalence of the damage agents, appear to represent the dominant scenario for sugar maple across the HBEF. Study of additional cohorts will be needed to confirm that these observations, based on one large cohort, apply across multiple cohorts. Moreover, the mechanistic interactions between site conditions and damage agents must be better understood to predict

Fig. 4. Comparison of frequency for six main causes of sugar maple seedling damage between years (first fall to seventh fall). The six damage agents are shown in the legend. Late fall stem herbivory was not assessed for 2013 as this takes place in spring 2014. Winter freeze damage refers to the winter preceding the growing season (e.g., for 2008, the winter damage occurred in the winter from December 2007 to March 2008).



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future patterns of sugar maple survival across the complex landscape, as emphasized for other plant species by van der Putten et al (2010).

Survival patterns

Our data are for a cohort born after a notable mast year. Hett (1971), working with a series of plots in Wisconsin, found that the probability of dying was higher in years with high seed input and suggested that density-dependent mortality was important for sugar maple. However, neither Gardescu (2003) nor Hane (2003) found evidence for density-dependent mortality in sugar maple seedlings. In our study, there was some suggestion of density-dependent mortality in the first season, with initial seedling density being an important predictor of fungal damage (Supplementary Table S5*b*). Our cohort only had 29% survival from June to leaf-off. In comparison, Gardescu (2003) had 94% and 89% survival from two separate mast year cohorts (1985 and 1990, respectively) each at a different site. Some important differences between the studies include the absence of *Rhizoctonia* as a mortality agent in Gardescu (2003), differences in base cation status of the sites, with Gardescu (2003) on more base cation rich soils, and climatic differences between our study years. In other words, the manifestation of density-dependent mortality in sugar maple appears to be context dependent.

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Many studies have considered first-year survival of sugar maple seedlings (summary in Gardescu 2003; values ranging from 11% to 94% survival). In our study, seedling survival averaged 26%, with a range of 17% to 61% survival between site groups. Other studies of sugar maple seedlings using plots at HBEF have found values for survival similar to ours (Forcier 1973; Hane 2003). Forcier's plots covering watershed 6 (adjacent to our plots 7, 11, 19, and 22) had 58% survival from the first June to the following June and 32% survival after 3 years (Forcier 1973). In Hane's (2003) study, seedling survival in control plots was 6% after 4 years and 1% after 6 years. Forcier's data from the late 1960s is very close to the survival values on our best locations (group A survival: 61% from June to June; 39% after 3 years), while Hane's (2003) more recent data from 1997 and 1999 cohorts are close to our numbers for the more widespread poor regeneration sites (group C survival: 4% after 4 years; 1% after 6 years). Since Forcier's (1973) early study, it seems likely that regeneration of sugar maple at Hubbard Brook has been impacted by both the primary effects of base cation leaching (Juice et al. 2006) and secondary effects of beech bark disease (Hane 2003).

Survivorship and elevation

Across the elevation range of our survey in the HBEF (350–800 m; Supplementary Table S2), sugar maple approaches its upper elevation limit in the White Mountains of New Hampshire (Bormann et al. 1970); hence, climatic stressors were expected to result in decreasing seedling survival with increasing elevation. For the large 2007 cohort, this was indeed the case for first-year survivorship (Table 1) and agrees with Forcier (1973), but the mechanisms of declining survivorship at higher elevations appear to be complex. Warmer temperatures at lower elevation would favor faster growth due to earlier germination and a longer growing season, but additional interactions related to damage agents also intervene, with both fungus and caterpillar damage higher at lower elevations (Supplementary Tables S4 and S5).

Colonization by beneficial AMF, as indicated by the frequency of arbuscules in seedling roots (Table 2), decreased significantly with increasing elevation and was also significantly lower on more northerly slopes, suggesting a soil temperature control. Initiation of AMF early in the growing season may be important as early-season carbon gain is critical to sugar maple seedling performance at its northern range limits where 80% of carbon gains occur within 15 days of leaf emergence (Kwit et al. 2010). Moreover, early formation of AMF may help protect against fungal pathogens (Jung et al. 2012) such as the *Rhizoctonia* root rot fungus that is a principal mortality agent in these sites (this study; Cleavitt et al. 2011).

Although the warmer and wetter climate predicted for the coming decades (Hayhoe et al. 2007) could conceivably facilitate sugar maple expansion to higher elevations, and some limited evidence of such an expansion has been reported for Vermont's Green Mountains (Beckage et al. 2008), a variety of constraints on seedling establishment must be overcome to facilitate such a trend at the HBEF. First, both Forcier (1973) and Cleavitt et al. (2011) observed that seed production by sugar maple is reduced at higher elevations in the south-facing experimental watersheds. Second, the generally lower base status of soils at higher elevations also could limit seedling establishment by effects on growth or AMF colonization (Juice et al. 2006). Third, first-season survival was significantly lower at higher elevation sites.

Survivorship and soil Ca

Based on earlier studies of the effects of soil Ca availability on sugar maple regeneration at the HBEF (Juice et al. 2006; Cleavitt et al. 2011) and elsewhere (Moore et al. 2012), we expected early survivorship to vary with soil Ca status, which exhibited a ninefold range across the study sites (Supplementary Table S2). Indeed, seedling Ca on nearly half of the sites (Supplementary Table S4) was below the critical threshold (5500 $\mu g \cdot g^{-1}$) for sugar maple seedlings given by Hallett et al. (2006). Although soil Ca was positively related to sugar maple abundance and initial seedling densities (Supplementary Table S3), by itself, Ca status was not a significant predictor of first-year mortality (Table 1).

Thus, although Ca availability and soil Ca depletion by acid deposition clearly play a role in sugar maple regeneration, a variety of intervening factors can complicate the landscape-level controls. For example, comparison of previous studies based on a Ca-addition experiment at HBEF (Juice et al. 2006; Cleavitt et al. 2011) indicated a diminishing effect on regeneration and AMF colonization as the levels of Ca and the pH in surface soils declined several years after the addition. The range of Ca availability across our landscape sites did not reach the high levels in the early years of the experimental Ca additions here (Juice et al. 2006) or elsewhere (Long et al. 1997), based on seedling and soil Ca status. Therefore, despite the wide range in soil Ca captured by our 22 sites, the natural soil Ca levels are probably still limiting maple regeneration.

Variation in damage agents

Across the three site types, classified by long-term survivorship, group A (high survivorship) was marked by relatively lower disease incidence and severity of the principal fungal damage agents (Fig. 4). The most prominent difference between groups B and C in the later years was the high incidence of caterpillar herbivory in the lowest survivorship class, group C. The factors controlling caterpillar abundance across the HBEF landscape are complex, including especially vegetation chemistry (e.g., foliar N) and early-season weather (Stange et al. 2011). In our logistic regression model for first-season caterpillar herbivory, caterpillars were more likely to be active at lower elevation, south-facing sites that tend to be warmer. Caterpillar herbivory was also more likely to occur on seedlings with higher average P concentration and fewer arbuscules in their roots, which suggests that AMF–plant–herbivore interactions (Koricheva et al. 2009) may be important for sugar maple seedlings. The importance of site for determining prevalence of specific damage agents agrees with the findings of Gardescu (2003), who had two main study sites that differed in importance of mortality agents. Caterpillar and slug herbivory dominated on one site and damage by pear thrips (*Taeniothrips inconsequens* (Uzel)) dominated on the second site. Pear thrips were only seen to kill seedlings at our sites in early spring of 2007 (Supplementary Table S1).

Overall, winter injury was the most common cause of seedling mortality after the first growing season (Fig. 4). Winter survival of tree seedlings is generally associated with carbon reserves (Canham et al. 1999); seedlings with a shorter growth period and less leaf area would be expected to fix less carbon and hence be disadvantaged over winter, and this was likely the case for seedlings that simply failed to break bud in the following spring. However, visual observations suggested that much of the winter injury involved freeze damage (Supplementary Table S1), including mechanical injury as indicated by stem shredding and bursting. The winter of 2008–2009 had the highest frequency of freeze damage and was exceptional in terms of (*i*) the number of soil freeze–thaw events ($N = 5$) as indicated by weekly soil frost measurements, (*ii*) low mean daily minimum air temperature (eighth coldest of the 47 winters in the HBEF data set), and (*iii*) high frequency of rain on snow events ($N = 18$) (Hubbard Brook website: http://www.hubbardbrook.org/data/).

Other important agents of seedling damage also exhibited some spatial and especially temporal variation (Fig. 4). In particular, late-fall stem herbivory by unidentified invertebrates was commonly observed in most sites during two study years (2008 and 2010). Rodent tunneling and perhaps winter foraging on seedling roots by Southern red-backed voles (*Myodes gapperi* Vigors, 1830) was also a significant cause of seedling mortality in 2012 and 2013. Voles have been shown to cause severe overwinter mortality of tree seedlings in Poland, with the autumn population levels of

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voles predictive of the amount of damage and a preference for certain tree genera including *Acer* (Borowski 2007). Mechanical damage was notably higher in 2011 due to flooding from hurricane Irene and in 2013 when HBEF experienced a severe windstorm on 2 June resulting in many downed trees and branches.

Implications

Sugar maple is a shade-tolerant species that employs a "seedling bank" strategy (Marks and Gardescu 1998) to maximize the chance of successful recruitment in gaps formed by overstory mortality. Currently, conditions for sugar maple regeneration are generally unfavorable across much of the HBEF as evidenced by depleted density and extent of the seedling bank and sapling layer (Juice et al. 2006; Van Doorn et al. 2011) and by the very low survivorship of seedlings in the 2007 cohort across most of the sites that we surveyed (Fig. 2). Initial seedling growth, mycorrhizal colonization, damage by pathogenic fungi and caterpillars, and winter injury had overriding effects on long-term seedling survival.

Models designed to predict sugar maple regeneration patterns will need to include the influence of site variables not only on seedling growth, but also on their primary damage agents. Because of the primary importance of biotic variables found here, simple models based on site characteristics or climate variables alone will likely fail to predict sugar maple regeneration accurately (e.g., Graignic et al. 2014). Detailed studies of the relationship between biotic and abiotic factors and their effects on multiple cohorts of sugar maple will be needed to improve predictions based on simple climatic envelopes of range expansion for this valuable species in the 21st century and beyond.

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