NRC Research Press

ARTICLE

Beech bark disease: spatial patterns of thicket formation and disease spread in an aftermath forest in the northeastern United States

Lisa M. Giencke, Martin Dovčiak, Giorgos Mountrakis, Jonathan A. Cale, and Myron J. Mitchell

Abstract: Beech bark disease (BBD) has affected the composition, structure, and function of forests containing a significant proportion of American beech (*Fagus grandifolia* Ehrh.) across North America. BBD spread has been investigated at landscape and regional scales, but few studies have examined spatial patterns of disease severity and spread within stands where forest management mitigation measures can be implemented. We analyzed changes in forest composition between 1985 and 2009 and fine-scale spatial patterns of BBD between 2000 and 2009 in a ~2 ha northern hardwood stand in the Adirondack Mountains of New York using location and disease severity of beech trees. A bivariate point pattern analysis was implemented to examine spatial patterns of beech thicket formation and BBD spread to beech saplings. Abundance of beech saplings increased near highly diseased canopy beech trees and around dead beech and sugar maple (*Acer saccharum* Marsh.). Disease severity of beech saplings was highest in close proximity to highly cankered canopy beech trees. Thus, BBD leads to the formation of beech thickets, and thickets are often located where saplings are most likely to become infected, increasing the likelihood that secondary killing fronts will develop and lead to heavy BBD-induced mortality in aftermath northern hardwood forests of North America.

Key words: Adirondack Mountains, American beech, BBD, beech thickets, bivariate point pattern analysis.

Résumé : La maladie corticale du hêtre (MCH) a eu un impact sur la composition, la structure et la fonction des forêts composées d'une proportion importante de hêtre d'Amérique (*Fagus grandifolia* Ehrh.) partout en Amérique du Nord. La propagation de la MCH a été étudiée à l'échelle régionale et à l'échelle du paysage, mais peu d'études ont examiné le profil spatial de la propagation et de la sévérité de la maladie dans des peuplements où des pratiques d'aménagement visant à atténuer l'impact de la maladie peuvent être mis en œuvre. Nous avons analysé les changements dans la composition de la forêt entre 1985 et 2009 ainsi que la répartition spatiale à une échelle fine de la MCH entre 2000 et 2009 dans un peuplement de feuillus nordiques d'environ deux hectares situé dans les monts Adirondack, dans l'État de New York, en utilisant la position des hêtres et la sévérité de la maladie. Une analyse bidimensionnelle de semis de points a été utilisée pour étudier la structure spatiale de la formation des fourrés de hêtre et la propagation de la MCH sur les gaules de hêtre. L'abondance des gaules de hêtre a augmenté près des hêtres dans le couvert forestier qui étaient très affectés par la maladie et autour des hêtres et des érables à sucre (*Acer saccharum* Marshall) morts. La sévérité de la maladie sur les gaules de hêtre était la plus élevée à proximité des hêtres dans le couvert forestier qui étaient sévèrement chancrés. La MCH entraîne par conséquent la formation de fourrés de hêtre qui sont souvent situés là où les gaules sont les plus sujettes à devenir infectées, ce qui augmente la probabilité que des fronts de mortalité secondaires se développent et entraînent une mortalité élevée induite par la MCH dans les forêts de feuillus nordiques subséquentes en Amérique du Nord. [Traduit par la Rédaction]

Mots-clés : Adirondacks, hêtre d'Amérique, maladie corticale du hêtre, fourrés de hêtre, analyse bidimensionnelle de semis de points.

Introduction

American beech (*Fagus grandifolia* Ehrh.) is an important tree species with a wide range in eastern North America, extending from Nova Scotia and Wisconsin to northern Florida and eastern Texas (Tubbs and Houston 1990). At a landscape scale, beech is most abundant (i.e., highest basal area per hectare) in the Adirondack Mountains of New York, with smaller areas of high beech abundance scattered throughout its range (Morin et al. 2005). Beech regenerates from seeds and vegetative root sprouts (Tubbs and Houston 1990). As a shade-tolerant species, beech saplings are able to monopolize understory resources and recruit into small canopy gaps resulting from single-tree deaths (Canham 1988; Wagner et al. 2010). Because shade-tolerant tree species can persist below full canopies for many years, advance regeneration (e.g., seedlings and sprouts) is an important determinant of the composition of gap-capturing individuals and future forest canopy composition (McClure et al. 2000).

Beech bark disease (BBD) has been affecting American beech populations throughout northeastern North America since its establishment more than a century ago (Hewitt 1914; Twery and

Received 22 January 2014. Accepted 7 June 2014.

L.M. Giencke,* M. Dovčiak, J.A. Cale, and M.J. Mitchell. SUNY College of Environmental Science and Forestry, Department of Environmental and Forest Biology, 1 Forestry Drive, Syracuse, NY 13210, USA.
G. Mountrakis. SUNY College of Environmental Science and Forestry, Department of Environmental Resources Engineering, 1 Forestry Drive, Syracuse, NY 13210, USA.

Corresponding author: Lisa Giencke (e-mail: lisa.giencke@jonesctr.org).
*Present address: Joseph W. Jones Ecological Research Center, 3988 Jones Center Drive, Newton, GA 39870, USA.

Can. J. For. Res. **44**: 1042–1050 (2014) dx.doi.org/10.1139/cjfr-2014-0038

Patterson 1984; Garnas et al. 2011). Beech trees infested by the non-native beech scale *Cryptococcus fagisuga* Lind. (Houston et al. 1979), potentially in combination with physiological stress due to extreme temperatures and drought stress (Lonsdale 1980), become susceptible to infection by the causal agents of BBD. These fungal pathogens, *Neonectria faginata* (Lohman et al.) Castl. & Rossman and *N. ditissima* (Tul. & C. Tul.) Samuels & Rossman, kill bark tissue, which creates necrotic lesions (cankers) on the bark. BBD results in reduced growth and vigor (Gavin and Peart 1993); declining crown health (Jones and Raynal 1987); a weakened bole, which leads to stem breakage ("beech snap") and decreased resistance to windthrow (Houston 1994; Papaik et al. 2005); and eventual mortality (Houston 1994). BBD-induced mortality has altered forest composition, structure, and function across a large portion of the northern hardwood forests of the northeastern United States (Morin et al. 2007).

Shigo (1972) identified three phases of BBD: (*i*) advance front, characterized by the buildup of beech scale and near absence of fungal pathogens; (*ii*) killing front, characterized by high levels of beech scale and fungal pathogens and high beech mortality; and (*iii*) aftermath zone, characterized by widespread trunk deformities on surviving trees. Additional characteristics of aftermath forests include reduced beech scale infestation and *Neonectria* infection severity and reduced presence of overstory beech (Leak 2006; Cale et al. 2012).

BBD-induced mortality during the killing front can greatly influence forest dynamics in aftermath forests. Premature decline or mortality of large beech trees can increase total area of canopy gaps (Krasny and DiGregorio 2001). Depending on local conditions, beech density and basal area can decrease due to elevated mortality rates (Runkle 1990) or increase due to the formation of dense thickets of beech saplings that outpace the loss of canopy beech (Forrester et al. 2003). Beech thickets can preclude recruitment of co-occurring species (e.g., sugar maple, *Acer saccharum* Marsh.) through vigorous competition for light and below-ground resources or due to potential phytotoxic effects of beech leaf leachate (Hane et al. 2003). Such changes in forest composition can scale up to ecosystem-level processes by affecting nutrient cycling, litter decomposition, soil pH, exchangeable cations, and soil C:N ratios (Finzi et al. 1998; Lovett et al. 2010). Beech thickets can also decrease species richness and diversity of understory vegetation (Cale et al. 2013).

Within-stand spread of BBD is related to the dispersal mechanisms of the disease-related organisms. Early-instar nymphs of beech scale are able to crawl, but their movement on a given tree is negligible (Houston et al. 1979), and mature beech scale are sessile. The main mode of dispersal for beech scale appears to be passive transport of the first instar by wind (Wainhouse 1980), but birds and humans may act as long-distance dispersal vectors (Wieferich et al. 2011). *Neonectria* spores are transported by wind and water (Ehrlich 1934; Houston 1994). Management guidelines designed to slow the spread of BBD have called for the removal of heavily diseased trees that may act as an inoculum source (Houston 1975; Wainhouse 1980). However, an understanding of fine-scale disease heterogeneity within affected stands and mechanisms of disease spread and persistence in aftermath forests is generally lacking.

It is essential to understand spatial patterns of beech recruitment and disease spread and persistence in aftermath forest stands to mitigate the negative impacts of BBD on forest composition, structure, and function. Although spatially explicit studies of tree demography and recruitment can provide useful insights into tree population dynamics (Barot et al. 1999; Dovčiak et al. 2001), few studies have investigated spatiotemporal patterns of beech recruitment and disease spread relative to diseased mature trees. In our study, we examined how the abundance and disease severity of beech saplings varied spatially across a forest stand over more than a decade relative to diseased canopy beech trees. We used a spatially explicit approach to test two hypotheses: (1) beech recruitment occurs primarily around highly diseased beech and recently dead canopy trees, and (2) sapling disease severity is highest near highly diseased mature beech, which can act as an inoculum source and (or) as a source of seedlings and sprouts that are also susceptible to BBD.

Methods

Site description

This study was conducted in the Adirondack Mountains within Huntington Wildlife Forest (HWF; 43°59′N, 74°14′W; 450–820 m above sea level), a 6000 ha field station operated by the SUNY College of Environmental Science and Forestry in Newcomb, New York. Mean annual temperature in Newcomb from 1981 to 2010 was 4.8 °C, and mean annual precipitation was 108.7 cm (U.S. Department of Commerce 2011). The soil is a fine sandy loam derived from glacial till overlying gneiss bedrock (Somers 1986). Northern hardwood forests in this region are dominated by sugar maple, beech, and yellow birch (*Betula alleghaniensis* Britton; Braun 1950). Initially disparate outbreaks of BBD in New England and near New York City coalesced as BBD spread into the Adirondack Mountains by the mid-1960s (Houston 1994).

We surveyed forest compositional changes and tree recruitment patterns over 24 years and BBD spread over 9 years in a 140 × 140 m (2 ha) permanent study plot established in 1985 at HWF as part of the Integrated Forest Study (IFS), which investigated the effect of atmospheric deposition on nutrient cycling in forests across the United States (Johnson and Lindberg 1992; Mitchell et al. 1992). Elevation of the IFS plot ranges from 525 to 543 m above sea level. The site is located in a second-growth northern hardwood forest that regenerated following wildfire in the early 1900s (McGee et al. 2007) and is co-dominated by beech and sugar maple, with a smaller component of red maple (*Acer rubrum* L.), yellow birch, and a few individuals of several other tree species (Forrester et al. 2003). The IFS plot has been characterized as an aftermath forest by Forrester et al. (2003). With the exception of a few trees that were removed in 1988 to install a monitoring tower, no known disturbances (e.g., timber harvesting or natural disturbance events) have occurred at this site since the establishment of the IFS plot (M. Gooden, personal communication).

Data collection

All trees with a diameter at breast height (DBH; 1.4 m above the ground) ≥ 5 cm within the IFS plot were mapped in 1985. Newly recruited trees with DBH ≥ 5 cm were mapped in 2000 and again in 2009. Species identity, DBH, and status (live or dead) were recorded for every mapped tree in all survey periods. Beech trees were divided into three size classes following Ward et al. (1996): saplings (5–9.9 cm DBH), subcanopy trees (10–24.9 cm DBH), and canopy trees (>25 cm DBH). Due to the long-term nature of the study plot, we were not permitted to destructively sample vegetation to verify the origins (i.e., seedling vs. root sprout) of saplings in our study. Severity of both beech scale infestation and *Neonectria* infection was characterized in 2000 and 2009 by visually estimating the percentage of each stem (following Wainhouse 1980) covered by beech scale wax masses and *Neonectria* cankers, which included both raised and sunken cankers. Trees were placed into disease severity classes based on these estimates (modified from Forrester et al. 2003): none (0%), low (0.1%–9.9%), medium (10%–49.9%), and high (50%–100%).

Forest composition and beech mortality

We used tree importance values as an integrated metric to examine changes in forest composition over time following Forrester et al. (2003). We calculated relative density and relative basal area of an individual species by dividing its density and basal area by total plot tree density and basal area, respectively. We then calculated importance values by averaging relative density and relative basal area for each species.

Table 1. Density, basal area, and importance value of tree species[a] in the Huntington Wildlife Forest Integrated Forest Study plot in the Adirondack Mountains, New York, from 1985 to 2009.

	Density (trees·ha^{-1})			Basal area (m^2·ha^{-1})			Importance value (%)[b]		
	1985	2000	2009	1985	2000	2009	1985	2000	2009
Fagus grandifolia Ehrh.	351	411	759	8.6	8.6	9.5	41.8	48.4	58.2
Acer saccharum Marsh.	196	134	116	11.9	10.5	10.1	35.7	30.1	25.5
Acer rubrum L.	40	32	27	3.6	3.8	3.6	10.1	10.2	8.2
Betula alleghaniensis Britton	49	40	26	3.6	3.3	2.6	9.4	8.7	6.4
Other species[c]	14	18	18	1.1	0.6	0.4	3.0	2.5	1.7
Total	651	635	946	28.8	26.8	26.2	100	100	100

[a] Based on an inventory of all stems ≥5 cm DBH in each survey year.

[b] Calculated as ([density of an individual species / total density] + [basal area of an individual species / total basal area])/2.

[c] Includes *Abies balsamea* (L.) Mill. (balsam fir), *Acer pensylvanicum* L. (striped maple), *Fraxinus americana* L. (white ash), *Picea rubens* Sarg. (red spruce), *Populus grandidentata* Michx. (big-tooth aspen), *Populus tremuloides* Michx. (quaking aspen), *Prunus pensylvanica* L. f. (fire cherry), *Prunus serotina* Ehrh. (black cherry), and *Tsuga canadensis* (L.) Carr. (eastern hemlock).

We calculated mortality as

$$(1)\qquad M = [1 - (S/N_0)^{1/y}] \times 100$$

where M is mortality rate in percent per year, S is the number of trees that survived from the beginning to the end of the survey period, N_0 is the number of living trees at the beginning of the survey period, and y is the number of years between surveys (Runkle 1990; Forrester et al. 2003). Mortality rates were calculated for each beech size class and for all beech for both survey periods (1985–2000 and 2000–2009).

Spatial analyses

We used bivariate point pattern analysis following Bailey and Gatrell (1995) to examine dependencies in spatial locations of points in one dataset (type 1) versus a second dataset (type 2). We investigated the effect of BBD on beech recruitment by examining spatial relationships between beech saplings in 2009 (type 2 trees) and canopy beech trees that were categorized into different canker severity classes during the previous survey (in 2000; type 1 trees). We also analyzed spatial relationships between newly recruited beech saplings (type 2 trees) and canopy beech or sugar maple (the only other species with enough canopy individuals for analysis) that had died since the previous survey (type 1 trees). To examine the effects of diseased mature beech on the disease severity of beech recruits, we analyzed spatial patterns of beech saplings in different canker severity classes in 2009 (type 2 trees) relative to canopy and subcanopy beech that were highly diseased during the previous survey (in 2000; type 1 trees). For each analysis, we tested the null hypothesis of spatial independence of the two population types (e.g., highly diseased canopy beech (type 1 trees) and beech saplings (type 2 trees); Goreaud and Pélissier 2003). The observed number of type 2 trees that were less than or equal to distance h from type 1 trees was calculated using Ripley's cross-K-function:

$$(2)\qquad \hat{K}_{ij}(h) = \frac{R}{n_1 \cdot n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} I_h(d_{ij})$$

where R is the area of the study region, n_1 and n_2 are the number of type 1 and type 2 trees, respectively, and I is a counter variable that equals 1 if the distance between the ith type 1 tree and the jth type 2 tree (d_{ij}) is less than distance h and 0 otherwise (Bailey and Gatrell 1995, p. 120). Distances h ranged in 1 m increments from 0 to 20 m, slightly larger than stand neighborhood scale (cf. Dovčiak et al. 2001). We calculated Ripley's cross-L-function, a square root transformation of the cross-K-function, to linearize the function, stabilize the variance, and give an expected value of 0 at all distances h (Bailey and Gatrell 1995, p. 94):

$$(3)\qquad \hat{L}(h) = \sqrt{\frac{\hat{K}(h)}{\pi}} - h$$

To test the null hypothesis of spatial independence, we simulated 1000 Monte Carlo randomizations in which the overall spatial patterns of type 1 and type 2 trees were preserved. During each simulation, all type 2 trees were randomly shifted by the same distance using a toroidal edge correction around type 1 trees, whose spatial locations were held constant (Bailey and Gatrell 1995, p. 121). $\hat{L}(h)$ values were calculated for each randomization, and the upper and lower 2.5% of the results of the Monte Carlo randomizations were removed to create the upper and lower confidence envelopes for the null hypothesis. When the observed pattern fell within the upper and lower confidence envelopes, type 1 and type 2 trees were considered to be distributed independently of one another; otherwise, the two types of trees were positively associated when the observed pattern was above the upper envelope and negatively associated when the observed pattern was below the lower envelope. All data analyses were performed in R version 3.0.2 (R Core Team 2013).

Results

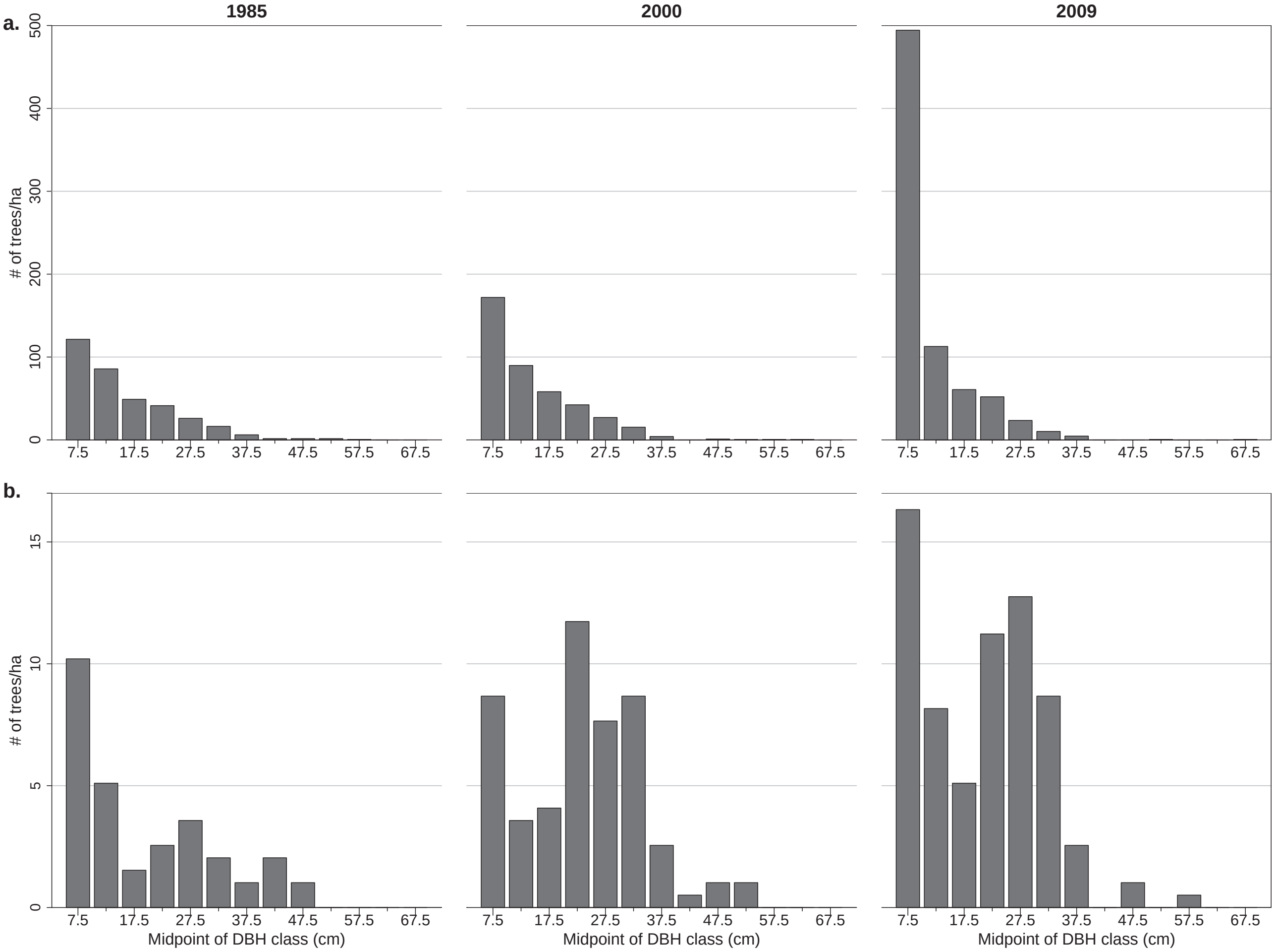
Forest composition and beech mortality

Between 1985 and 2009, the study plot became increasingly dominated by beech, the only tree species that increased in density, basal area, or importance value during this period (Table 1). Beech density increased primarily due to increased sapling recruitment between 2000 and 2009 (Fig. 1*a*); beech comprised 89% and 98% of all recruitment in 2000 and 2009, respectively (data not shown). The presence of saplings also contributed to an increase in beech basal area between 1985 and 2009 (Table 1), despite an increase in the number of dead trees (Fig. 1*b*) and mortality of 76% of canopy beech trees that were alive in 1985. The largest beech trees had DBH of 55.4, 63.0, and 65.3 cm in 1985, 2000, and 2009, respectively.

The density of sugar maple declined rapidly from 1985 to 2000 (Table 1; Fig. 2*a*), largely due to mortality of saplings and small subcanopy trees (Fig. 2*b*). Decreased density of red maple and yellow birch (Table 1) was due to a reduction in the number of stems of all sizes (data not shown). With the exception of red maple, a short- to medium-lived species (Walters and Yawney 1990), it is unlikely that any substantial mortality of the four most common species (i.e., those with importance value >5%; Table 1) at this ca. 100-year-old site was due to age.

Mortality rates of all size classes and for all beech increased from 1985–2000 to 2000–2009. Mortality of saplings increased from 0.5% to 1.1% per year. Subcanopy mortality increased from 0.8% to 1.6% per year, and mortality of canopy trees increased from 3.3% to 7.8% per year. The overall mortality rate of beech doubled,

Fig. 1. Frequency distribution of the density of (*a*) living and (*b*) dead beech in 5 cm DBH size classes for each survey period.



rising from 1.0% per year from 1985–2000 to 2.0% per year from 2000–2009.

Beech bark disease severity

Beech scale infestation was generally low in 2000 and 2009, which is characteristic of aftermath forests (Leak 2006; Cale et al. 2012). Saplings were split evenly between the no and low beech scale severity classes in 2000, while the majority of subcanopy (71%) and canopy trees (57%) were in the low scale severity class (Table 2). In 2009, the majority of trees in all size classes (>98%) were characterized as having low scale abundance.

The majority of saplings (77%) in 2000 had no signs of fungal infection, whereas the majority of subcanopy trees (54%) were in the low canker severity class, and almost half of canopy trees (48%) were highly cankered (Table 2). Canker severity increased for saplings and subcanopy trees between 2000 and 2009: the majority of saplings (86%) had low canker severity in 2009, while subcanopy trees were divided between the low and medium canker severity classes (Table 2). The majority of canopy trees in 2009 were in the medium canker severity class; canopy trees in the high canker severity class dropped to 35% in 2009 due to mortality of highly cankered canopy trees between 2000 and 2009 (Table 2).

Beech recruitment relative to diseased and dead canopy trees

Beech recruitment was clustered around highly diseased beech and recently dead canopy trees. The degree of clustering of beech saplings around canopy beech increased with disease severity of canopy beech. Beech saplings were distributed independently relative to canopy beech in the low and medium canker severity classes across most spatial scales (Figs. 3*a* and 3*b*) but were positively associated with highly cankered canopy beech at a fine scale (<5 m; Fig. 3*c*). Additionally, beech sapling recruitment became increasingly positively associated with dead canopy beech (Fig. 4) and sugar maple (Fig. 5) between 2000 and 2009.

Beech sapling health relative to highly diseased canopy beech

Highly diseased mature beech (e.g., canopy and subcanopy trees) may act as an inoculum source or produce root sprouts or seedlings susceptible to BBD. Unlike canker-free saplings, which were negatively associated with highly diseased mature beech throughout most of the stand neighborhood scale (Fig. 6*a*), those with low canker severity were largely distributed independently relative to highly diseased mature beech (Fig. 6*b*), and saplings with medium disease severity were positively associated with highly diseased mature beech at all distances analyzed (Fig. 6*c*). Few highly cankered beech saplings were present. Similar spatial patterns were present for beech saplings relative to mature beech in the high beech scale severity class (Fig. 7).

Discussion

Although beech thickets have been observed to occur in stands affected by BBD (Houston 1975; Farrar and Ostrofsky 2006; Cale et al. 2013), we used a spatially explicit approach to show for the first time the link between beech thicket formation and heavily diseased and dead trees in aftermath forests. Root sprouting has

Fig. 2. Frequency distribution of the density of (*a*) living and (*b*) dead sugar maple in 5 cm DBH size classes for each survey period.

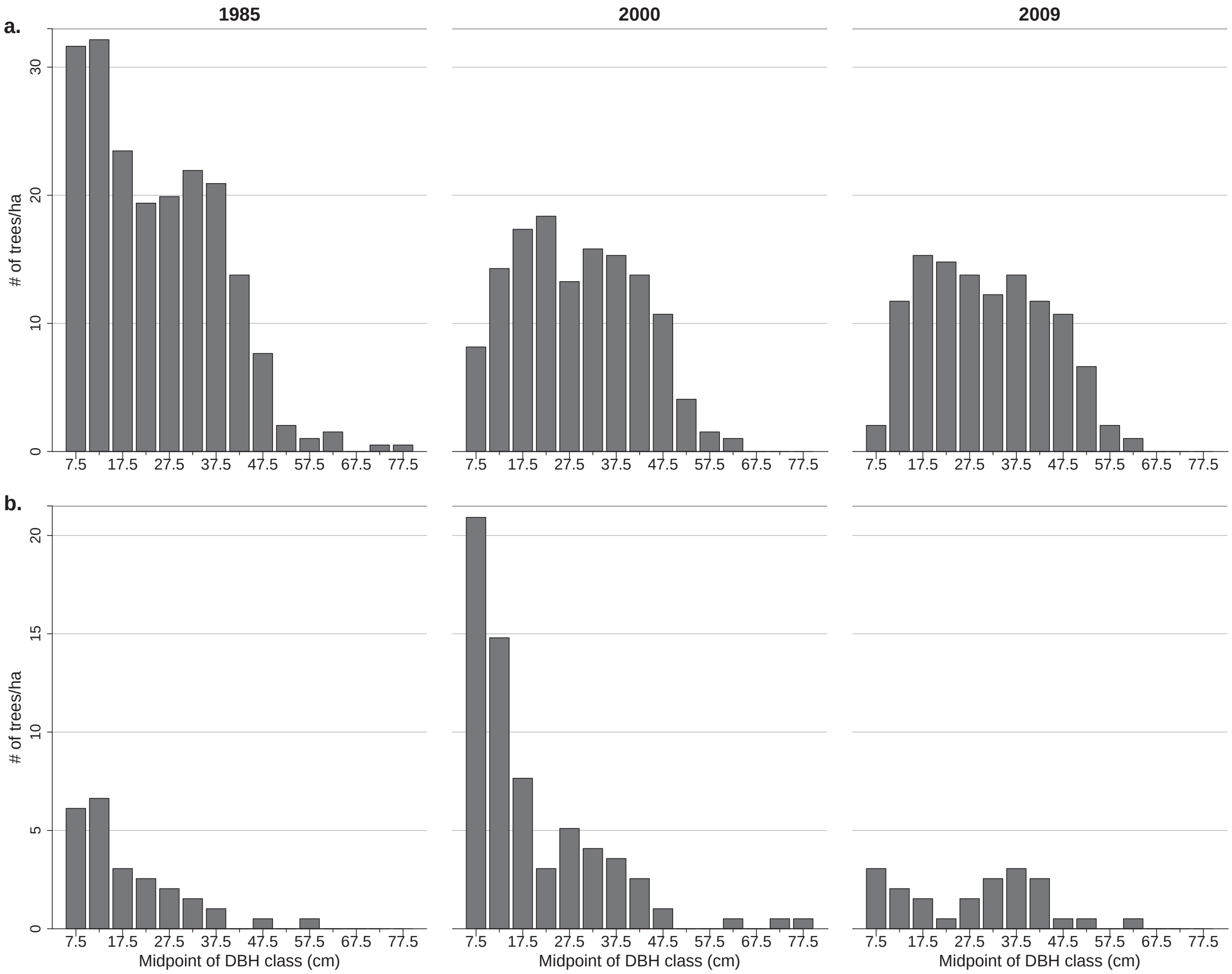


Table 2. Number of beech trees and percentage of trees in each combination of beech scale and fungal cankering severity classes by tree size class and year.

		Canker severity class							
		2000				2009			
Tree size class	Beech scale severity class	None	Low	Medium	High	None	Low	Medium	High
Sapling	No. of trees	337				969			
	None	46.4	2.7	0.3	0.0	0.8	0.6	0.0	0.0
	Low	30.7	15.7	2.1	0.9	6.1	85.7	6.5	0.3
	Medium	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
	High	0.0	0.3	0.0	0.6	0.0	0.0	0.0	0.0
Subcanopy	No. of trees	373				442			
	None	4.4	3.0	0.3	0.5	0.0	0.0	0.0	0.0
	Low	16.7	44.5	6.6	3.3	0.9	44.4	44.0	8.8
	Medium	0.3	4.6	5.2	2.7	0.0	0.0	1.6	0.2
	High	0.0	1.9	1.4	4.6	0.0	0.0	0.0	0.0
Canopy	No. of trees	96				77			
	None	1.1	1.1	1.1	4.3	0.0	0.0	0.0	0.0
	Low	1.1	16.0	18.1	22.3	0.0	11.7	51.9	35.1
	Medium	0.0	5.3	6.4	7.4	0.0	0.0	1.3	0.0
	High	0.0	0.0	2.1	13.8	0.0	0.0	0.0	0.0

often been suggested as the main mechanism behind the formation of beech thickets in BBD-affected forest stands (Houston 1975), but MacKenzie (2005) found that trees affected by BBD produced fewer sprouts than unaffected trees. Further, Jones and Raynal (1986) concluded that root sprouts are unlikely to account for significant outward spread from a parent tree. Though we did not determine origins of the saplings in our study, clustering of saplings at 3–4 m from highly diseased or dead trees is greater

Fig. 3. Spatial locations (left) and cross-L-functions (right) of beech saplings in 2009 (+; regardless of canker severity class) relative to canopy beech (•) from (*a*) low, (*b*) medium, and (*c*) high canker severity classes in 2000 (too few uncankered canopy beech ($n = 2$) were present to be analyzed). Canker severity classes are as follows: none (0%), low (0.1–9.9%), medium (10–49.9%), and high (50%–100%; see Methods, Data collection for details). In the cross L-function graphs, dashed lines represent upper and lower confidence envelopes for spatial independence of canopy beech and beech saplings; solid lines represent the observed data.

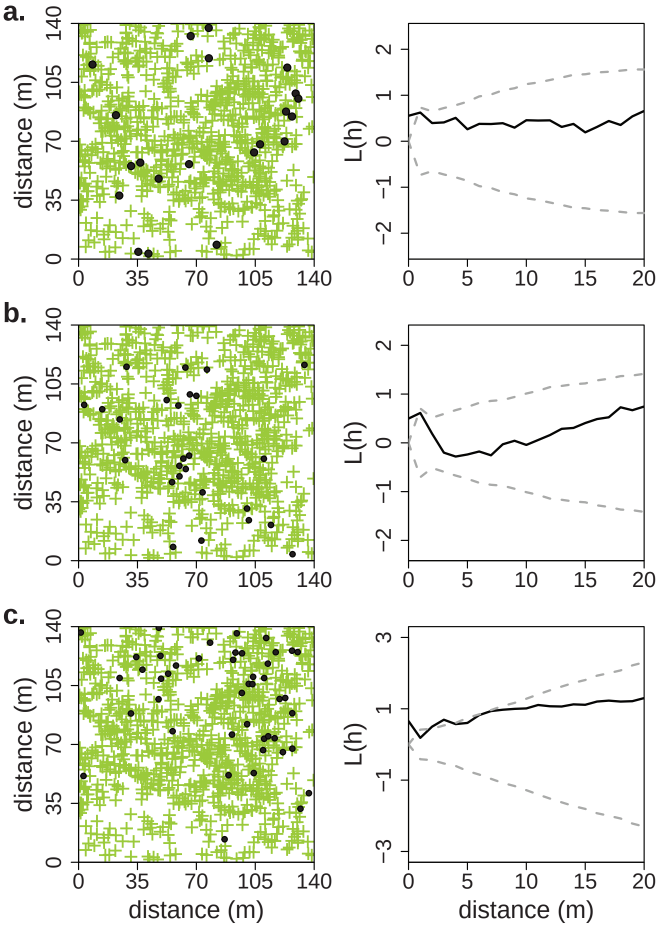


Fig. 4. Spatial locations (left) and cross-L-functions (right) of newly recruited beech saplings (+) in (*a*) 2000 and (*b*) 2009 relative to canopy beech that died since the previous survey year (•). In the cross-L-function graphs, dashed lines represent upper and lower confidence envelopes for spatial independence of beech saplings and dead canopy beech; solid lines represent the observed data.

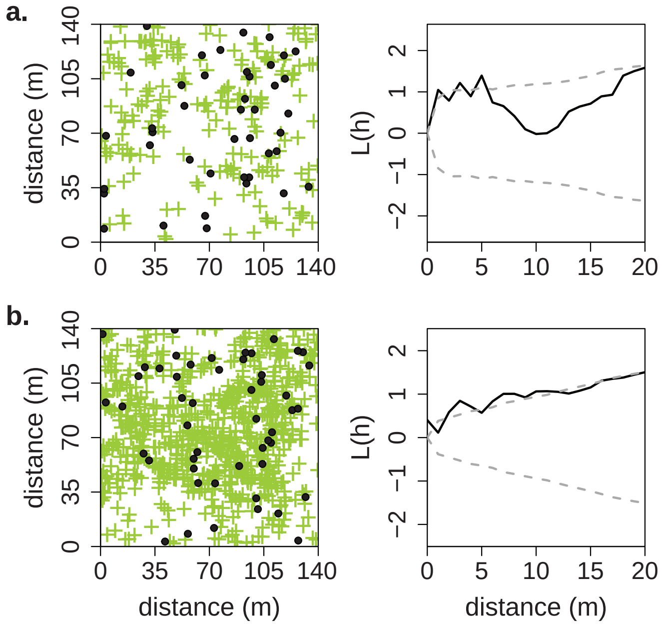
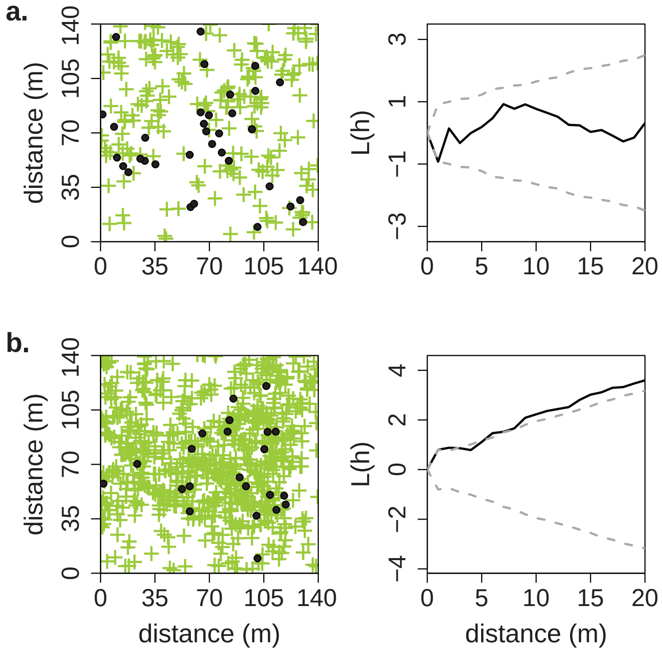


Fig. 5. Spatial locations (left) and cross-L-functions (right) of newly recruited beech saplings (+) in (*a*) 2000 and (*b*) 2009 relative to canopy sugar maple that died since the previous survey year (•). In the cross-L-function graphs, dashed lines represent upper and lower confidence envelopes for spatial independence of beech saplings and dead canopy sugar maple; solid lines represent the observed data.



than the distance at which sprout density is highest (i.e., 1–2 m), beyond which sprout density decays exponentially (Jones and Raynal 1986). This result suggests that saplings of seed origin may be responsible, at least in part, for beech thicket formation at our site.

A combination of additional factors supports the idea that seedlings may at least partially contribute to thicket formation. Contrary to early predictions of a decline in seed production due to BBD-induced mortality of large beech trees, beechnut production has increased over time at HWF, despite few >40 cm DBH trees remaining (McNulty and Masters 2005). Beechnuts are a highly valuable food source for wildlife (e.g., rodents, bears, and blue jays; Tubbs and Houston 1990), and seed predation by these animals reduces seed supply. However, Garneau et al. (2012) estimated production of beechnuts at HWF in fall 2008 at >500 000·ha^{-1}, and a profusion of beech seedlings (with cotyledons still present) was observed during our 2009 survey (L.M. Giencke, personal observation). Caching of beechnuts by blue jays has been observed (Johnson and Adkisson 1985) and may be responsible for some fine-scale clustering of saplings; however, the spatial dependence between two groups of individuals (e.g., saplings and mature trees) could differ from the spatial pattern of each group in isolation (Bailey and Gatrell 1995).

Regardless of the origin of beech recruits (from seeds or sprouts), a likely cause for their clustering in the vicinity of dead and highly

Fig. 6. Spatial locations (left) and cross-L-functions (right) of canopy and subcanopy beech in the high canker severity class in 2000 (•) relative to beech saplings in 2009 (+) from (*a*) none, (*b*) low, and (*c*) medium canker severity classes (too few highly cankered beech saplings (n = 3) were present to be analyzed). In the cross-L-function graphs, dashed lines represent upper and lower confidence envelopes for spatial independence of beech saplings and canopy and subcanopy trees; solid lines represent the observed data.

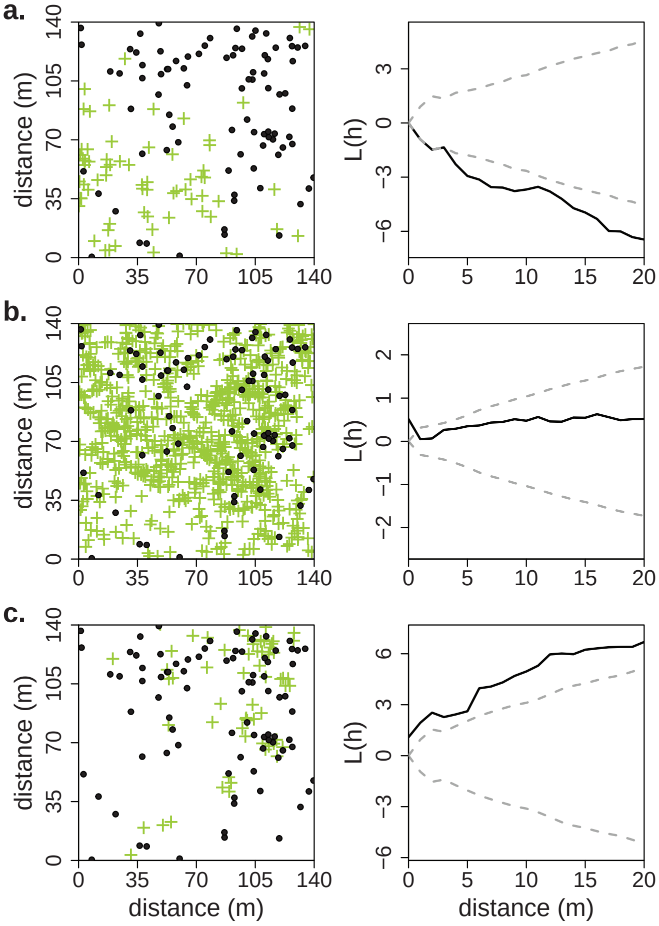
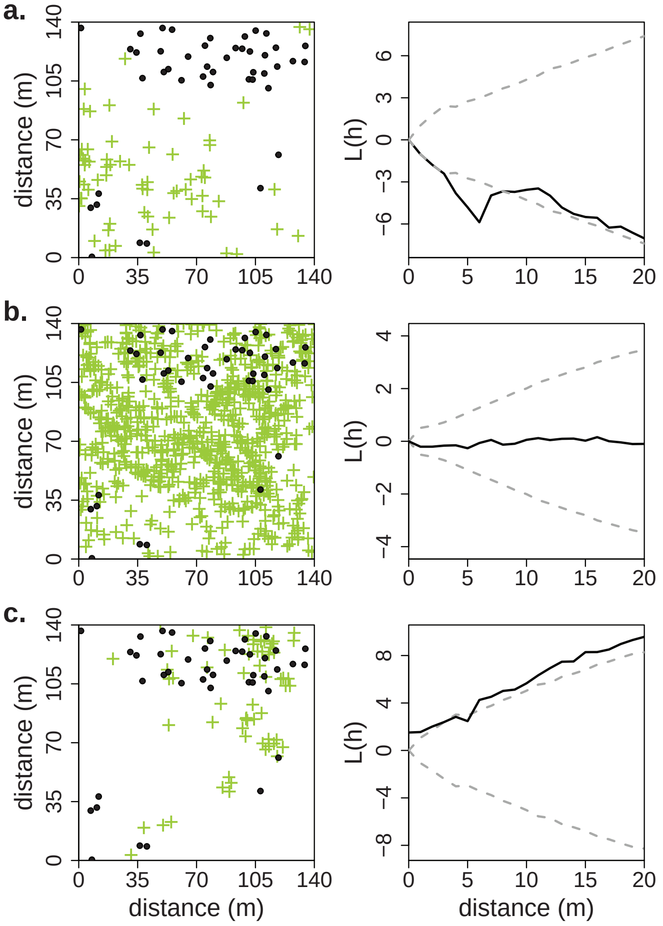


Fig. 7. Spatial locations (left) and cross-L-functions (right) of canopy and subcanopy beech in the high beech scale severity class in 2000 (•) relative to beech saplings in 2009 (+) from (*a*) none, (*b*) low, and (*c*) medium canker severity classes (too few highly cankered beech saplings (n = 3) were present to be analyzed). In the cross-L-function graphs, dashed lines represent 95% confidence envelopes for spatial independence of beech saplings and canopy and subcanopy trees; solid lines represent the observed data.



diseased beech trees is that BBD-induced decline in beech crown health (Jones and Raynal 1987) allowed greater light penetration and early gap-phase recruitment of advance regeneration beech around diseased and dead beech trees (cf. Runkle 1981; Wagner et al. 2010). Thus, BBD appeared to act as an agent of forest change by affecting canopy beech decline and eventual mortality, as well as forest development (recruitment) processes in canopy gaps and around diseased trees (cf. Castello et al. 1995). The additional clustering of beech saplings near dead canopy sugar maple is more consistent with gap-phase recruitment of beech from seeds rather than from sprouts given the greater dispersal ability of beechnuts compared with beech sprouts (Jones and Raynal 1986; Wagner et al. 2010).

The positive spatial association between beech saplings and highly cankered canopy beech and dead beech and sugar maple indicates that trees of all species will be replaced by beech in this stand (i.e., self-replacement and directional replacement sensu Runkle 1981) as beech thickets tend to preclude regeneration of other species (Hane 2003; Nyland et al. 2006). This outcome is likely highly dependent on initial forest conditions, including beech abundance and vigor, and species composition of advance regeneration. Previous work at our study site reported no advance regeneration (stems with DBH 1.4–4.9 cm) of sugar maple in 2000 compared with >3000 stems·ha^{-1} of advance beech regeneration (Forrester et al. 2003). In contrast to increased beech dominance at our study site in the Adirondack Mountains, where beech basal area is very high (Morin et al. 2005), beech may be replaced by species such as sugar maple or eastern hemlock (*Tsuga canadensis* (L.) Carr.) in aftermath forests (including stands in New York state and in western Massachusetts) where beech basal area is lower (Twery and Patterson 1984; Runkle 1990; Lovett et al. 2010). In addition to BBD, forest composition (especially sugar maple abundance) in northern hardwood forests can be influenced by factors such as deer browse and sugar maple decline caused by acid deposition (Horsley et al. 2000; Duchesne et al. 2002; Lovett and Mitchell 2004).

Our results suggest that the within-stand spread of BBD to beech saplings is related to their proximity to highly diseased canopy and subcanopy trees. Houston et al. (1979) found that beech scale abundance on individual trees within a young beech plantation declined with distance from their source population on a large relic beech tree. Conversely, Garnas et al. (2012) found little evidence for spatial aggregation of diseased trees when examining nearest infected neighbor distances at local, meso, and landscape scales. They concluded that BBD-affected areas are fully saturated with beech scale and *Neonectria* and that their dispersal may play an insignificant role in the spread of BBD. However, unlike the current study, Garnas et al. (2012) did not investigate spatial aggregation by tree size or fungal infection severity, nor did they include a temporal component, all of which were important components in the spread of BBD in this study.

Beech trees vary in susceptibility to BBD, with a small fraction of trees (<2%) apparently resistant to the disease (Houston 1994; MacKenzie 2005). Our results suggest an even more conservative estimate of resistance to BBD as only 8 of 1488 beech trees (all saplings and ~0.5% of all beech) were free of both beech scale and fungal cankering in 2009. Given the scarcity of unaffected trees, we were unable to assess their spatial patterns within the stand, but partial genetic resistance to BBD may be an additional explanation of the clustering of diseased beech saplings near diseased canopy trees (which likely produce genetically more susceptible root sprouts and seedlings). Because highly diseased individuals tended to be more abundant at slightly higher elevations in our study (L.M. Giencke, unpublished data), it is also possible that trees were predisposed to disease by an environmental factor that co-varied with elevation (such as moisture or nutrient availability; Houston et al. 1979).

Past management strategies for BBD-affected forests involved the removal of highly diseased beech trees to slow the within-stand spread of the disease (Houston 1975; Wainhouse 1980) and to increase the overall health of beech trees in a stand (Leak 2006); our results support these practices, regardless of the mechanism that allows for saplings to become more highly diseased in the presence of highly diseased mature beech. However, our study also suggests that additional management measures may be required to limit the development of beech thickets where heavily diseased trees have been removed (for example, by different types of thinning; e.g., Sprugel et al. 2009), especially where the saplings comprising the thickets are also highly susceptible to BBD. Given the additional effort needed to control beech thicket development, silvicultural management of BBD may be applicable only in relatively small forest stands. Furthermore, although our dataset has a relatively extensive temporal component, it is more limited spatially. Thus, we recommend that similar long-term intensive sampling and analytical efforts are carried out across the geographic extent of BBD to determine whether such management strategies may be appropriate more broadly (e.g., for forests with a different stand structure or history).

Conclusion

The presence of beech thickets in BBD-affected forests has long been observed (Houston 1975; Farrar and Ostrofsky 2006; Cale et al. 2013), but evidence explicitly linking BBD to thicket formation has been lacking. In this study, we provide such evidence by showing that beech thickets form in canopy gaps surrounding heavily diseased beech and dead beech (and dead sugar maple where present) in an aftermath forest. Not only do beech thickets have the ability to alter species composition, structure, and overall forest dynamics through competition for light and other resources, but our results suggest that they provide an important and extensive new substrate to which BBD can spread from older diseased trees. Through this mechanism, it seems likely that secondary killing fronts of younger beech can develop even within aftermath forests. Indeed, beech mortality rates doubled throughout the duration of our study. Thus, as during the killing front, forest managers should again be concerned with heavy future BBD-induced mortality in northern hardwoods forests.

Acknowledgements

We thank M. Lee Davis, Joelle N. Chille Cale, and Anthony S. Vicente for assistance with fieldwork. This work was supported by a Zabel scholarship to Lisa M. Giencke and SUNY ESF funding to Martin Dovčiak. We would like to thank the staff of the Adirondack Ecological Center for logistical support and advice. Elizabeth P. Cox provided research support. Additionally, we thank L. Katherine Kirkman and three anonymous reviewers for helpful comments on the manuscript. The initial data came from the Integrated Forest Study, which was funded by the Electric Power Research Institute and the Empire State Electric Energy Research Corporation.

References

Bailey, T.C., and Gatrell, A.C. 1995. Interactive spatial data analysis. Longman, London, UK.

Barot, S., Gignoux, J., and Menaut, J.-C. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. Ecology, **80**: 1987–2005. doi:10.1890/0012-9658(1999)080[1987:DOASPT]2.0.CO;2.

Braun, E.L. 1950. Deciduous forests of eastern North American. Hafner Publishing Company, New York.

Cale, J.A., Letkowski, S.K., Teale, S.A., and Castello, J.D. 2012. Beech bark disease: an evaluation of the predisposition hypothesis in an aftermath forest. For. Pathol. **42**: 52–56. doi:10.1111/j.1439-0329.2011.00722.x.

Cale, J.A., McNulty, S.A., Teale, S.A., and Castello, J.D. 2013. The impact of beech thickets on biodiversity. Biol. Invasions, **15**: 699–706. doi:10.1007/s10530-012-0319-5.

Canham, C.D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology, **69**: 786–795. doi:10.2307/1941027.

Castello, J.D., Leopold, D.J., and Smallidge, P.J. 1995. Pathogens, patterns, and processes in forest ecosystems. BioScience, **45**: 16–24. doi:10.2307/1312531.

Dovčiak, M., Frelich, L.E., and Reich, P.B. 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. J. Ecol. **89**: 280–291. doi:10.1046/j.1365-2745.2001.00545.x.

Duchesne, L., Ouimet, R., and Houle, D. 2002. Basal area growth of sugar maple in relation to acid deposition, stand health, and soil nutrients. J. Environ. Qual. **31**: 1676–1683. doi:10.2134/jeq2002.1676.

Ehrlich, J. 1934. The beech bark disease. A *Nectria* disease of *Fagus*, following *Cryptoccus fagi* (Baer.). Can. J. Res. **10**: 593–692. doi:10.1139/cjr34-070.

Farrar, A., and Ostrofsky, W.D. 2006. Dynamics of American beech regeneration 10 years following harvesting in a beech bark disease-affected stand in Maine. North. J. Appl. For. **23**: 192–196.

Finzi, A.C., Canham, C.D., and Van Breeman, N. 1998. Canopy tree-soil interactions within temperate forests: species effects on pH and cations. Ecol. Appl. **8**: 447–454. doi:10.1890/1051-0761(1998)008[0447:CTSIWT]2.0.CO;2.

Forrester, J.A., McGee, G.G., and Mitchell, M.J. 2003. Effects of beech bark disease on aboveground biomass and species composition in a mature northern hardwood forest, 1985 to 2000. J. Torrey Bot. Soc. **130**: 70–78. doi:10.2307/3557531.

Garnas, J.R., Ayers, M.P., Liebhold, A.M., and Evans, C. 2011. Subcontinental impacts of an invasive tree disease on forest structure and dynamics. J. Ecol. **99**: 532–541. doi:10.1111/j.1365-2745.2010.01791.x.

Garnas, J.R., Houston, D.R., Twery, M.J., Ayres, M.P., and Evans, C. 2012. Inferring controls on the epidemiology of beech bark disease from spatial patterning of disease organisms. Agric. For. Entomol. **15**: 146–156. doi:10.1111/j.1461-9563.2012.00595.x.

Garneau, D.E., Lawler, M.E., Rumpf, A.S., Weyburne, E.S., Cuppernull, T.M., and Boe, A.G. 2012. Potential effects of beech bark disease on small mammals and invertebrates in northeastern US forests. Northeast. Nat. **19**: 391–410. doi:10.1656/045.019.0303.

Gavin, D.G., and Peart, D.R. 1993. Effects of beech bark disease on the growth of American beech (*Fagus grandifolia*). Can. J. For. Res. **23**(8): 1566–1575. doi:10.1139/x93-197.

Goreaud, F., and Pélissier, R. 2003. Avoiding misinterpretation of biotic interactions with the intertype K_{12}-function: population independence vs. random labeling hypotheses. J. Veg. Sci. **14**: 681–692. doi:10.1111/j.1654-1103.2003.tb02200.x.

Hane, E.N. 2003. Indirect effects of beech bark disease on sugar maple seedling survival. Can. J. For. Res. **33**(5): 807–813. doi:10.1139/x03-008.

Hane, E.N., Hamburg, S.P., Barber, A.L., and Plaut, J.A. 2003. Phytotoxicity of American beech leaf leachate to sugar maple seedlings in a greenhouse experiment. Can. J. For. Res. **33**(5): 814–821. doi:10.1139/x03-028.

Hewitt, C.G. 1914. Note on the occurrence of the felted beech coccus *Cryptococcus fagi* (Baerens) Dougl. in Nova Scotia. Can. Entomol. **14**: 15–16. doi:10.4039/Ent4615-1.

Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A., and Thomas, J.H. 2000. Factors associated with the decline disease of sugar maple on the Alleghany Plateau. Can. J. For. Res. **30**(9): 1365–1378. doi:10.1139/x00-057.

Houston, D.R. 1975. Beech bark disease: the aftermath forests are structured for new outbreak. J. For. **73**: 660–663.

Houston, D.R. 1994. Major new tree disease epidemics: beech bark disease. Annu. Rev. Phytopathol. **32**: 75–87. doi:10.1146/annurev.py.32.090194.000451.

Houston, D.R., Parker, E.J., and Lonsdale, D. 1979. Beech bark disease: patterns of spread and development of the initiating agent *Cryptococcus fagisuga*. Can. J. For. Res. **9**(3): 336–344. doi:10.1139/x79-057.

Johnson, D.W., and Lindberg, S.E. (*Editors*). 1992. Atmospheric deposition and forest nutrient cycling. Springer, New York.

Johnson, W.C., and Adkisson, C.S. 1985. Dispersal of beech nuts by blue jays in fragmented landscapes. Am. Midl. Nat. **113**: 319–324. doi:10.2307/2425577.

Jones, R.H., and Raynal, D.J. 1986. Spatial distribution and development of root sprouts in *Fagus grandifolia* (Fagaceae). Am. J. Bot. **73**: 1723–1731. doi:10.2307/2444238.

Jones, R.H., and Raynal, D.J. 1987. Root sprouting in American beech: production, survival, and the effect of parent tree vigor. Can. J. For. Res. **17**(6): 539–544. doi:10.1139/x87-090.

Krasny, M.E., and DiGregorio, L.M. 2001. Gap dynamics in Alleghany northern hardwood forests in the presence of beech bark disease and gypsy moth disturbances. For. Ecol. Manage. **144**: 265–274. doi:10.1016/S0378-1127(00)00391-1.

Leak, W.B. 2006. Fifty-year impacts of the beech bark disease in the Bartlett Experimental Forest, New Hampshire. North. J. Appl. For. **23**: 141–143.

Lonsdale, D. 1980. *Nectria coccinea* infection of beech bark: variations in disease in relation to predisposing factors. Ann. For. Sci. **37**: 307–317. doi:10.1051/forest:19800406.

Lovett, G.M., and Mitchell, M.J. 2004. Sugar maple and nitrogen cycling in the forests of eastern North America. Front. Ecol. Environ. **2**: 81–88. doi:10.1890/1540-9295(2004)002[0081:SMANCI]2.0.CO;2.

Lovett, G.M., Arthur, M.A., Weathers, K.C., and Griffin, J.M. 2010. Long-term changes in forest carbon and nitrogen cycling caused by an introduced pest/pathogen complex. Ecosystems, **13**: 1188–1200. doi:10.1007/s10021-010-9381-y.

MacKenzie, M. 2005. Survival of the fittest: beech bark disease-resistant trees will leave more offspring. *In* Beech Bark Disease: Proceedings of the Beech Bark Disease Symposium, Saranac Lake, New York, 16–18 June 2004. *Edited by* C.A. Evans, J.A. Lucas, and M.J. Twery. USDA Forest Service, Northeastern Research Station, Gen. Tech. Rep. NE-331. pp. 65–67.

McClure, J.W., Lee, T.D., and Leak, W.B. 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. For. Ecol. Manage. **127**: 181–189. doi:10.1016/S0378-1127(99)00129-2.

McGee, G.G., Mitchell, M.J., Leopold, D.J., and Raynal, D.J. 2007. Relationships among forest age, composition and elemental dynamics of Adirondack northern hardwood forests. J. Torrey Bot. Soc. **134**: 253–268. doi:10.3159/1095-5674(2007)134[253:RAFACA]2.0.CO;2.

McNulty, S.A., and Masters, R.D. 2005. Changes to the Adirondack forest: implications of beech bark disease on forest structure and seed production. *In* Beech Bark Disease: Proceedings of the Beech Bark Disease Symposium, Saranac Lake, New York, 16–18 June 2004. *Edited by* C.A. Evans, J.A. Lucas, and M.J. Twery. USDA Forest Service, Northeastern Research Station, Gen. Tech. Rep. NE-331. pp. 52–57.

Mitchell, M.J, Burke, M.K., and Shepard, J.P. 1992. Seasonal and spatial patterns of S, Ca, and N dynamics of a northern hardwood forest ecosystem. Biogeochemistry, **17**: 165–189. doi:10.1007/BF00004040.

Morin, R.S., Liebhold, A.M., Luzader, E.R., Lister, A.J., Gottschalk, K.W., and Twardus, D.B. 2005. Mapping host-species abundance of three major exotic forest pests. USDA Forest Service, Northeastern Research Station, Res. Pap. NE-726.

Morin, R.S., Liebhold, A.M., Tobin, P.C., Gottschalk, K.W., and Luzader, E.R. 2007. Spread of beech bark disease in the eastern United States and its relation to regional forest composition. Can. J. For. Res. **37**(4): 726–736. doi:10.1139/X06-281.

Nyland, R.D., Beshant, A.L., Bohn, K.K., and Verostek, J.M. 2006. Interference to hardwood regeneration in northeastern North America: ecological characteristics of American beech, striped maple, and hobblebush. North. J. Appl. For. **23**: 53–61.

Papaik, M.J, Canham, C.D., Latty, E.F., and Woods, K.D. 2005. Effects of an introduced pathogen on resistance to natural disturbance: beech bark disease and windthrow. Can. J. For. Res. **35**(8): 1832–1843. doi:10.1139/x05-116.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. Available from http://www.R-project.org/.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology, **62**: 1041–1051. doi:10.2307/1937003.

Runkle, J.R. 1990. Eight years change in an old *Tsuga canadensis* woods affected by beech bark disease. J. Torrey Bot. Soc. **117**: 409–414. doi:10.2307/2996838.

Shigo, A.L. 1972. The beech bark disease today in the northeastern U.S. J. For. **70**: 286–289.

Somers, R.C. 1986. Soil classification, genesis, morphology and variability of soils found in the central Adirondack region of New York. Ph.D. dissertation, State University of New York College of Environmental Science and Forestry, Syracuse, N.Y.

Sprugel, D.G., Rauscher, K.G., Gersonde, R., Dovčiak, M., Lutz, J.A., and Halpern, C.B. 2009. Spatially explicit modeling of overstory manipulations in young forests: effects on stand structure and light. Ecol. Model. **220**: 3565–3575. doi:10.1016/j.ecolmodel.2009.07.029.

Tubbs, C.H., and Houston, D.R. 1990. *Fagus grandifolia* Ehrh., American beech. *In* Silvics of North America Volume 2: Hardwoods. *Edited by* R.M. Burns and B.H. Honkala. USDA Forest Service, Agric. Handbook 654. pp. 325–332.

Twery, M.J., and Patterson, W.A., III. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood forest stands in central New England. Can. J. For. Res. **14**(4): 565–574. doi:10.1139/x84-104.

U.S. Department of Commerce. 2011. 1981–2010 U.S. climate normals [online]. Available from http://www.ncdc.noaa.gov/land-based-station-data/climate-normals/1981-2010-normals-data [accessed 4 December 2013].

Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R.D., and Sagheb-Talebi, K. 2010. Beech regeneration research: from ecological to silvicultural aspects. For. Ecol. Manage. **259**: 2172–2182. doi:10.1016/j.foreco.2010.02.029.

Wainhouse, D. 1980. Dispersal of first instar larvae of the felted beech scale, *Cryptococcus fagisuga*. J. Appl. Ecol. **17**: 523–532. doi:10.2307/2402634.

Walters, R.S., and Yawney, H.W. 1990. *Acer rubrum* L., red maple. *In* Silvics of North America Volume 2: Hardwoods. *Edited by* R.M. Burns, and B.H. Honkala. USDA Forest Service, Agric. Handbook 654. pp. 60–69.

Ward, J.S., Parker, G.R., and Ferrandino, F.J. 1996. Long-term spatial dynamics in a deciduous old-growth forest. For. Ecol. Manage. **83**: 189–202. doi:10.1016/0378-1127(96)03722-X.

Wieferich, D.J., McCullough, D.G., Hayes, D.B., and Schwalm, N.J. 2011. Distribution of American beech (*Fagus grandifolia*) and beech scale (*Cryptococcus fagisuga* Lind.) in Michigan from 2005 to 2009. North J. Appl. For. **28**: 173–179.