

Spread of beech bark disease in the eastern United States and its relationship to regional forest composition

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Abstract: Beech bark disease (BBD) is an insect–fungus complex involving the beech scale insect (*Cryptococcus fagisuga* Lind.) and one of two canker fungi. Beech scale was introduced to Halifax, Nova Scotia around 1890, presumably with the fungus *Neonectria coccinea* var. *faginata* Lohm. The disease has subsequently spread through a large portion of the range of beech. We used historical maps of the extent of the advancing BBD front (defined by presence of scale insects) in North America to estimate its rate of spread as 14.7 ± 0.9 km/year. This estimate did not account for stochastic “jumps” by the scale insects to several disjunct locations; therefore, this rate is a conservative estimate. Comparison of the year of scale colonization with beech density did not suggest a relationship between the scale spread rate and beech density. Our analyses also indicated that BBD has invaded less than 30% of regions where beech is present, but it has invaded most of the regions where beech is a dominant component of stands. Despite regional increases in beech mortality following invasion, considerable amounts of live beech remain in invaded areas. Moreover, the volume of beech has increased in most areas, though generally at lower rates than that observed for associated tree species.

Résumé : La maladie corticale du hêtre est le résultat d’une association entre un insecte et un champignon impliquant la cochenille du hêtre (*Cryptococcus fagisuga* Lind.) et un ou deux champignons qui causent un chancre. La cochenille du hêtre a été introduite vers 1890 à Halifax, en Nouvelle-Écosse, vraisemblablement accompagnée du champignon *Neonectria coccinea* var. *faginata* Lohm. La maladie s’est par la suite répandue dans une grande partie de l’aire naturelle du hêtre. Nous avons utilisé de vieilles cartes qui retracent l’avance du front de la maladie corticale du hêtre (déterminé par la présence de la cochenille) en Amérique du Nord pour estimer son taux de progression à $14,7 \pm 0,9$ km/an. Cette estimation n’a pas tenu compte des « bonds » aléatoires de la cochenille vers plusieurs endroits isolés. Par conséquent, il s’agit d’une estimation conservatrice. Une comparaison entre l’année de la colonisation par la cochenille et la densité du hêtre n’a pas montré qu’il y avait une relation entre le taux de progression de la cochenille et la densité du hêtre. Nos analyses indiquent également que la maladie corticale du hêtre a envahi moins de 30 % des régions où le hêtre est présent mais elle a envahi la plupart des régions où le hêtre est une composante dominante des peuplements. Malgré des augmentations régionales de la mortalité du hêtre à la suite d’une invasion, des hêtres vivants sont toujours présents en grande quantité dans les zones qui ont été envahies. De plus, le volume de hêtre a augmenté dans la plupart des régions quoique généralement à un taux plus faible que ce qui a été observé chez les espèces qui y sont associées.

[Traduit par la Rédaction]

Introduction

Invasions by nonindigenous species are one of the most important threats to the stability and productivity of forest ecosystems around the world (Liebhold et al. 1995; Vitousek et al. 1996; Pimentel et al. 2000). Over the last century, forests of eastern North America have suffered effects by well-known disturbance agents such as chestnut blight, gypsy moth, hemlock woolly adelgid, and beech bark disease (BBD) (Mattson 1997). These biological invasions are known to result in a multitude of community level direct and indirect effects, including changes in plant species richness, community structure, vegetation dynamics, and plant–

animal interactions (Parker et al. 1999; Mack et al. 2000; Mooney and Cleland 2001). While there have been many attempts to measure the impacts of nonindigenous species in specific locations (e.g., Kegg 1973; Fosbroke and Hicks 1989; Davidson et al. 1999), few estimates exist of the impacts that these invasions have over large landscapes (cf. Pimentel 2002) despite the importance of evaluating the impacts of invaders across their entire range (Parker et al. 1999).

Beech bark disease, also known as beech scale *Neonectria* canker, is an insect–fungus complex involving the beech scale insect (*Cryptococcus fagisuga* Lind.) and the exotic canker fungus *Neonectria coccinea* var. *faginata* Lohm. or

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the native *Neonectria galligena* Bres. (Rossman and Samuels 1999). The disease kills or injures American beech (*Fagus grandifolia* Ehrh.) when these fungi invade bark altered by the feeding activity of the beech scale insects. Sometime around 1890 the beech scale was accidentally introduced to Halifax, Nova Scotia from Europe. Although Halifax is the only documented port of entry, there may have been other introductions in areas near Boston, Massachusetts, and New York City (Houston 1994). It has since spread continuously into the New England states, New York, Pennsylvania, and West Virginia (Manion 1991) and several discontinuous “jumps” have transported it into North Carolina, Tennessee, and Michigan. Three phases of BBD are generally recognized: (1) the “advancing front”, which corresponds to areas recently invaded by scale populations; (2) the “killing front”, which represents areas where fungal invasion has occurred (typically 3–5 years after the scale insects appear, but sometimes as long as 20 years) and tree mortality begins; and (3) the “aftermath forest”, which are areas where the disease is endemic (Shigo 1972; Houston 1994).

Neonectria fungi invade the inner living bark and cambium, which may ultimately lead to death, though trees may survive for decades (Mize and Lea 1979; Houston 1994). The disease is capable of killing trees as small as 10 cm DBH, but its effects are most intense in trees 25 cm DBH and larger (Mize and Lea 1979; Jones and Raynal 1987). In the aftermath zone, a second scale species, *Xylococcus betulae*, sometimes attacks beech resulting in stem deformation, or further infection by *Nectria* spp. While some trees survive infections for several decades, one effect of the accumulation of cankers is reduced growth (Gavin and Peart 1993; Gove and Houston 1996). The long-term effect of BBD on forest composition is not clear. It appears that in some stands, the advent of BBD results in significant decreases in the proportion of beech but in other stands, beech is able to persist because of its often prolific regeneration through sprouts and seedlings (Houston 1975; Twery and Patterson 1984; Runkle 1990; Houston 2001).

Although several studies have documented the impacts of BBD at specific sites (Mize and Lea 1979; Jones and Raynal 1987; Gavin and Peart 1993; Gove and Houston 1996), there have been no attempts to evaluate its regional impact as it has invaded North America. In this study, we quantified the historical rate of spread of the advancing BBD front and showed that its range expansion was characterized by continuous radial expansion, with occasionally disjunct, stochastic jumps in spread. We also used regionally sampled forest inventory data to show that BBD has not resulted in the elimination of beech from invaded areas, though regional rates of beech volume increase appeared slightly lower than those for other tree species associated with beech. Finally, we used our estimate of the rate of beech scale range expansion to predict its future distribution in North America, and to characterize how BBD may affect the composition of forests not yet invaded.

Methods

Estimation of spread

The historical rate of spread of beech scale was estimated

from maps depicting the distribution of the advancing disease front as defined by the presence of beech scale. The expansion of the beech scale's range in the USA and Canada from 1911 to 1990 was extracted from a published map (Houston et al. 1979; Houston 1994) that depicted the scale front in 1911, 1926, 1935, 1945, 1950, 1960, 1975, and 1990 (Fig. 1). Each boundary was digitized in vector format using a GIS. The boundary of beech scale distribution in the USA in 2003 was derived from county-level records compiled by the USDA Forest Service, Forest Health Protection (Newtown Square, Pennsylvania and Atlanta, Georgia). We also digitized the approximate scale boundary in Canada for 2003 based upon other descriptions (Natural Resources Canada 2000; Hopkin and Scarr 2003). Data from both Canada and the USA were not based upon systematic surveys, and therefore there may be slight inconsistencies among years and regions in how scale populations were detected. Although these error sources may affect estimates of spread over short periods, the effect should be negligible on spread estimated from many years of data. Nevertheless, the extent of beech scale in Canada in 2003 was excluded from our estimation of spread rates, because a single summary of the scale front in this area was not available. Furthermore, by 2003, the scale front appeared to be very close to or coincident with the northern extent of beech (Fig. 1) and range saturation could introduce bias into estimates of spread.

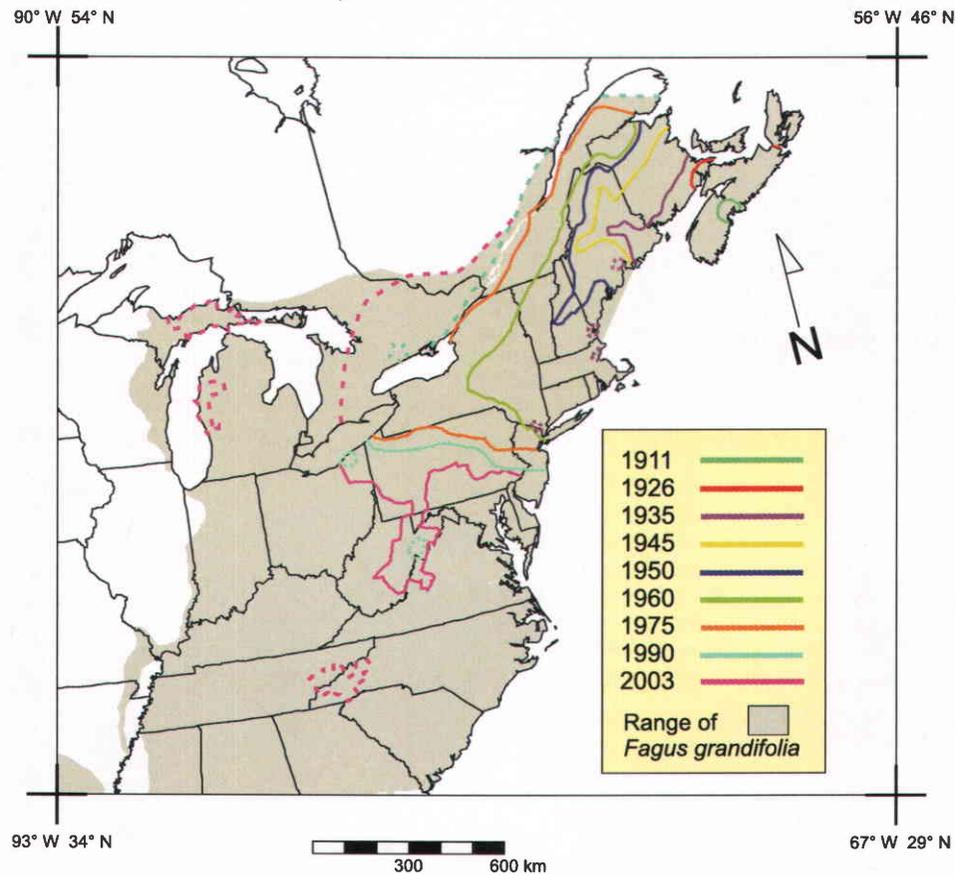
Historical boundaries of the scale extent were used to estimate the rate of spread of the advancing front using a method similar to that described by Tobin et al. (2007). A GIS was used to locate reference points at 20 km intervals along each boundary, and then the distance from each point to Halifax was measured. The median distance was then computed from all points on each boundary. We then used linear regression (PROC GLM, SAS Institute Inc. 2004) to estimate the linear model of these median distances as a function of the year that the boundary was recorded. The radial rate of spread was estimated by the slope of this linear model. The existence of geographically disjunct populations (identified here as areas that became infested when they were not spatially continuous with the main infested area) was evident in the historical spread of the beech scale (Fig. 1), but boundaries from these disjunct populations were not used to estimate the spread rate.

The estimated spread rate was applied to the 2003 scale insect distribution to generate a map representing predicted spread through 2025. These predictions of future spread were slightly conservative, because they assumed that there would not be any future “jumps” of the scale to form disjunct populations. The map of future spread was overlaid with USA county boundaries to generate predicted years of future (and past) scale establishment for each county.

Forest composition data

The USDA Forest Service has conducted surveys of overstory forest composition in the eastern USA as part of the Forest Inventory and Analysis (FIA) program since the 1940s (cf. www.fia.fs.fed.us). These surveys are conducted by sampling randomized plots in each state (typically one per 2428 ha) for overstory forest composition. These surveys have historically been collected approximately every 10 years in each state.

Fig. 1. Map of historical (1911–2003) spread of the beech scale in the USA and Canada. Boundaries of scale distributions from 1911 to 1990 are from Houston (1994). The scale boundary in the USA in 2003 is based upon county-level records assembled by USDA Forest Service Forest Health Protection. The 2003 boundary in Canada is based upon data published by Natural Resources Canada (2000) and Hopkin and Scarr (2003). Solid lines are boundaries that were used in estimation of spread rates, whereas dotted lines were not used, because they were either from disjunct populations or they were near the limits of the distribution of beech.



We used data from the most recent FIA surveys to characterize current forest composition in relation to historical and future BBD spread. These data were collected from 93 611 plots located in 37 states in the eastern USA (Hansen et al. 1992). The geographical distribution of beech basal area interpolated from forest inventory plots (Morin et al. 2005) was used to form county level estimates of beech density (1 km × 1 km basal area estimates were averaged by county). These estimates were then paired with either the year in which each county was first known to be invaded by BBD, or the year that it was predicted to become colonized by BBD. Predictions through 2025 were obtained by applying our estimate of the historical spread rate. This analysis provided a representation of the amount of beech in historically infested areas as well as information about the amount of beech in areas not yet affected.

These data were also used to investigate the role of beech density as a factor influencing the rate of BBD spread. We examined the correlation between beech density (basal area per hectare summarized by US county) and the difference between predicted (by applying the estimated spread rate) and observed year of scale colonization (derived from historical data in Fig. 1) using the Pearson's correlation coefficient (PROC CORR; SAS Institute Inc. 2004). Counties falling in disjunct BBD populations were not used in this analysis.

The most recent FIA data were also used to estimate the percentage of beech basal area that was dead in each county. A county was excluded from the analysis if it had <10 beech stems at least 12.7 cm DBH, because meaningful estimates of percent beech mortality could not be obtained in counties that contained too little beech. We examined the correlation between these estimates of percent standing beech that was dead and the year the county was first infested or predicted to become infested using the Pearson's correlation coefficient (PROC CORR; SAS Institute Inc. 2004). Because standard FIA surveys did not measure dead beech that had fallen, these estimates likely represented only a fraction of beech killed by BBD. Nevertheless, these data did provide relative measures of the accumulation of standing dead beech in aftermath stands.

We used historical FIA surveys from eastern US states to examine changes in tree species composition following the invasion of BBD. Since FIA plot data collected prior to the 1980s are not available electronically, we used tables from previously published reports (Appendix A) that provided estimates of the relative volume of tree species for each state. By extracting volumes of beech from successive surveys, we were able to characterize temporal trends in beech relative volume. To elucidate the effect of BBD on these trends, we also estimated similar time series of the relative volume for

sugar maple, *Acer saccharum* Marsh., and eastern hemlock, *Tsuga canadensis* (L.) Carr. These species tend to be closely associated with beech and therefore provide an approximation of volume trends for non-host species likely to occur in stands affected by BBD. While basal area would have been more suitable than volume as a measure of relative dominance, tables with basal areas were not provided in published reports.

To determine the effect of BBD on the proportion of beech relative to sugar maple and eastern hemlock, we used a Friedman test (Hollander and Wolfe 1973) in R (R Development Core Team 2004). This nonparametric statistic can be used when data arise from an unreplicated block design. Although abundance of beech, eastern hemlock, and sugar maple were derived from statewide FIA plots, the summary data we analyzed represent only single observations by state for a specific time period. We tested the effect of BBD invasion status (i.e., before, during, or after invasion) on the proportion of beech using individual states as blocks.

Results and discussion

Estimation of spread

A map of historical beech scale spread is shown in Fig. 1. Short-range, continuous spread can be attributed to the dispersal of scale insects from infested stands, and this form of dispersal may largely be responsible for the spatially continuous range expansion that has dominated its spread (Fig. 1). However, historical spread of beech scale has also been characterized by the formation of 10 populations that were geographically disjunct from the expanding population front (Fig. 1; Table 1). The formation of these isolated populations provides evidence of a long-range form of dispersal. These less frequent, long-distance dispersal events are probably the result of accidental movement of infested material by humans.

Skellam (1951) proposed a simple model for the spread of an invading species. This model incorporated random (diffusive) dispersal with exponential population growth to demonstrate that spread proceeds at a constant radial rate. While some invading organisms spread at constant radial velocities as predicted by this model (Levin 1989; Andow et al. 1990), other species exhibit rates of spread that continuously change through time (Shigesada and Kawasaki 1997; Weber 1998). This type of spread can be caused when short-range, continuous dispersal is coupled with less frequent long-range dispersal. This “stratified dispersal” results in a pattern of spread characterized by the formation of isolated colonies ahead of the advancing front, which grow and ultimately coalesce with the rest of the population (Shigesada and Kawasaki 1997; Hastings et al. 2005). Stratified dispersal has been documented in several alien species, such as the gypsy moth in North America (Liebhold et al. 1992; Sharov and Liebhold 1998).

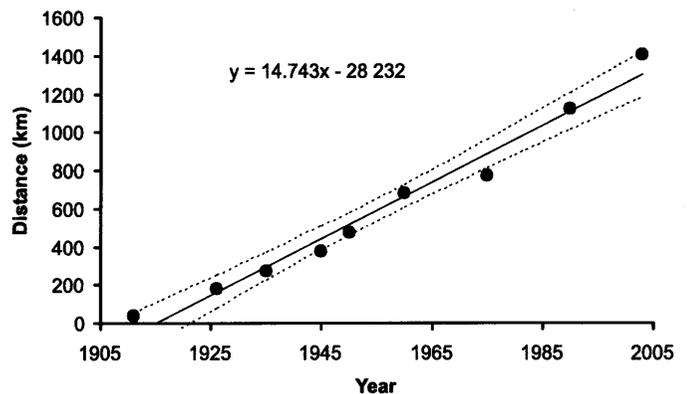
Spread of beech scale thus appears to be an example of stratified dispersal and discontinuous range expansion (Shigesada and Kawasaki 1997; Hastings et al. 2005). However, because the formation of disjunct populations was relatively rare ($n = 10$ from 1911 to 2003, Table 1) and a result of a stochastic process, we based our predictions of future spread on an expectation of constant radial expansion that equals

Table 1. Characteristics of disjunct beech scale populations.

Year of first detection	Location	Distance from scale front (km)*
1935	Maine	32
1935	Maine, New Hampshire	227
1935	Massachusetts	301
1935	New York, New Jersey	597
1990	West Virginia	344
1990	Ontario	283
1999	North Carolina, Tennessee	733
2001	Ohio	57
2001	Michigan	402
2001	Michigan	510

*Distance from scale front is the nearest location of the continuous scale front in the year of first detection.

Fig. 2. Historical spread of beech bark disease (BBD) (1911–2003) documented by plots of year of survey versus distance of the scale front from the initial site of disease establishment (Halifax). Each observation represents the median distance (from Halifax) of points along the boundary at a given survey record. Disjunct populations were not included when forming medians. The solid line represents the linear regression model, and the dotted line is the 95% estimation interval.



the historical radial rate of spread. Our estimate (\pm SE) of this historical spread rate (excluding disjunct populations) was 14.7 (0.89) km/year ($R^2 = 0.975$; Fig. 2). This rate was applied to the current range to create a predicted future range map of the advancing BBD front (as defined by the presence of the beech scale insect) through 2025 (Fig. 3).

It is possible to incorporate long-distance “jumps” into models of spread (e.g., Morales et al. 2004), but given that only 10 “jumps” have occurred over a ca. 100 year period, we did not have enough data to parameterize a more complex model that included such discontinuous dispersal events. Moreover, these 10 discontinuous populations constitute a relatively small amount of the current area generally infested by the beech scale, although radial spread from these disjunct populations will increase their importance over time. Therefore we adopted the more parsimonious approach of modeling continuous spread only.

Another possible limitation of our spread predictions was that landscape heterogeneity was not considered. While the distribution of beech is highly discontinuous across North America, there is no evidence that this heterogeneity af-

Fig. 3. Spread of the beech scale through 2025 predicted using a radial rate of 14.7 km/year estimated from historical data.

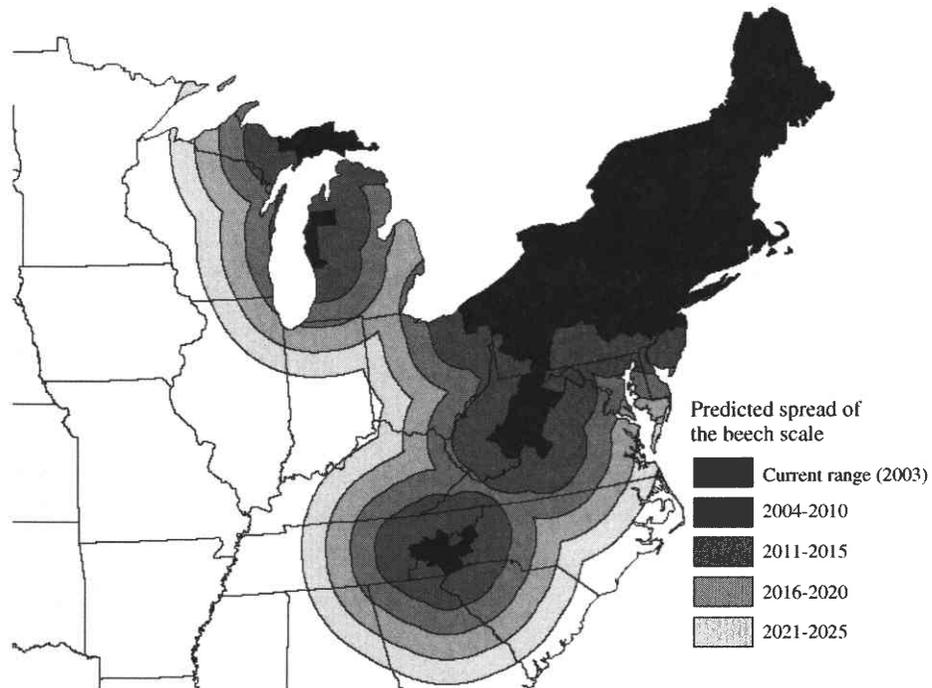


Fig. 4. Map of beech basal area (m^2/ha) interpolated from Forest Inventory and Analysis data (reprinted with permission from Morin et al. 2005).

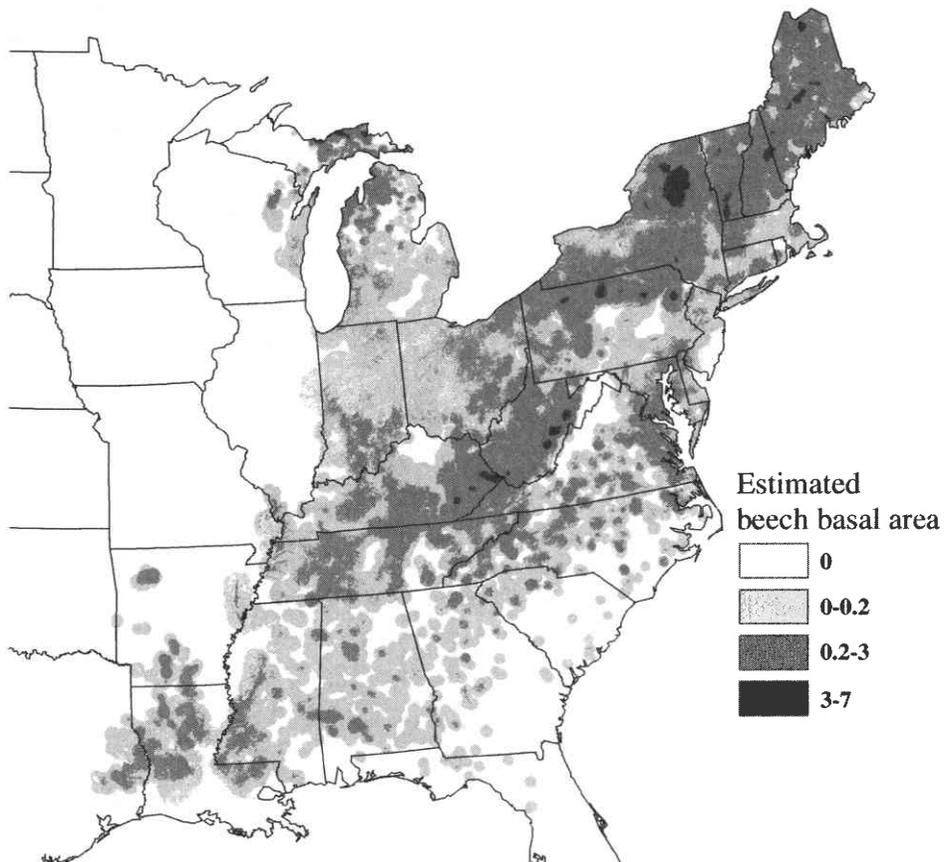


Fig. 5. Plot of average (from interpolated map, Fig. 4) beech basal area per hectare for those counties that are or may become infested in relation to past and future spread of beech scale with a quadratic model fit to the data.

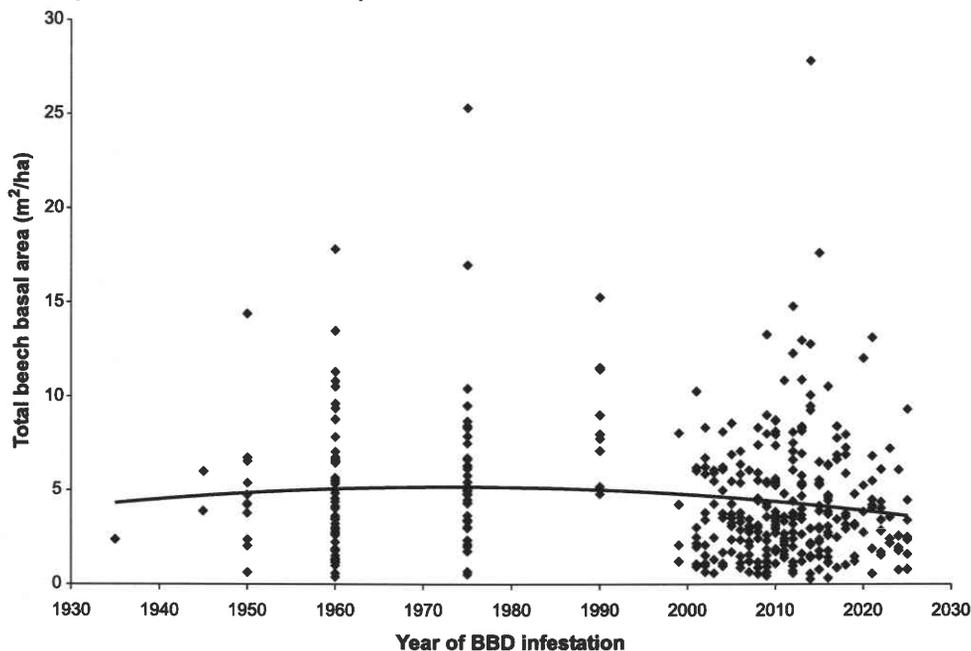
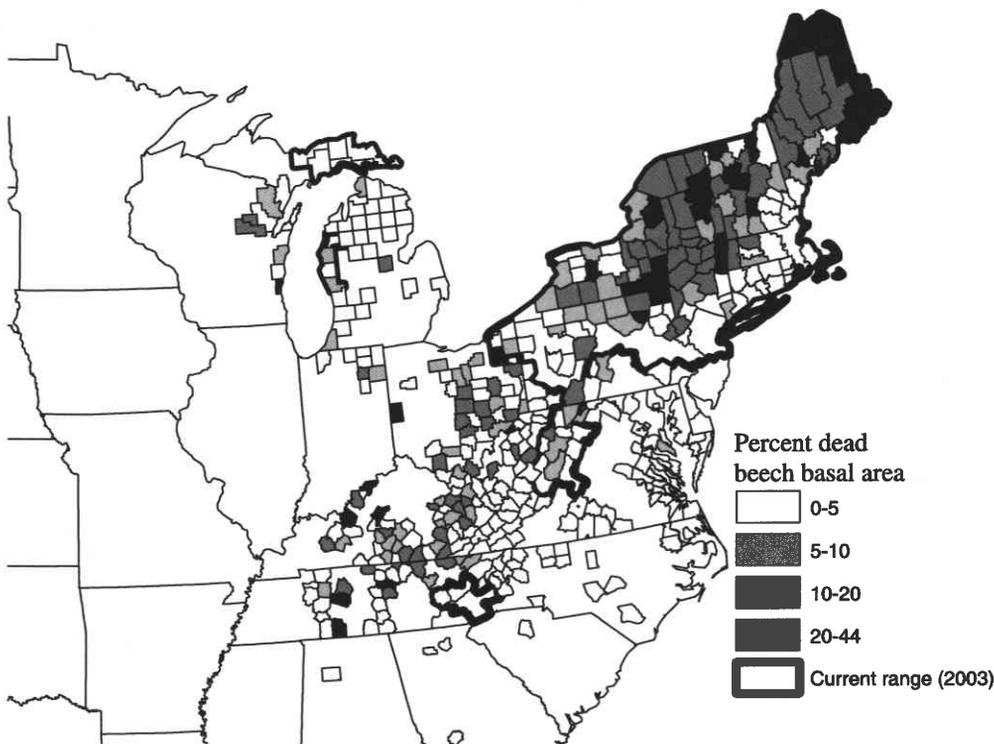


Fig. 6. Map of percentage of standing beech basal area that was dead (estimates are only provided from counties with at least 10 beech stems >12.7 cm in diameter per Forest Inventory and Analysis plot) by county.



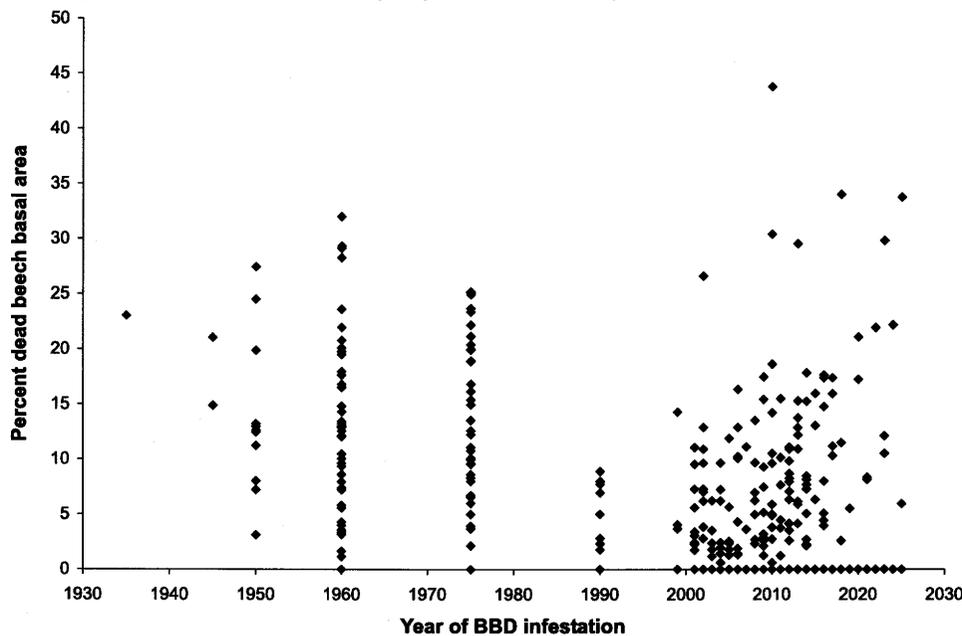
fectured spread rate (see below). Natural barriers (e.g., the Great Lakes or large expanses of farmland) do exist across the landscape of the northern US that could impede the spread of beech scale, but evidence that such features function as barriers is currently lacking. In fact, observations of the spread of the gypsy moth over the same area (i.e., from

Michigan to Wisconsin) has not indicated that the Great Lakes has impeded its spread (Tobin et al. 2007).

Forest composition data

The geographical distribution of beech basal area interpolated from forest inventory plots (cf. Morin et al. 2005) is

Fig. 7. Plot of average percentage of standing dead beech basal area (estimates are only provided from counties with at least 10 beech stems >12.7 cm in diameter per Forest Inventory and Analysis plot) in relation to past and future spread of beech scale.



shown in Fig. 4. In areas where BBD has already been established for many years, this map may under-represent the beech component that existed prior to initial invasion. The greatest concentration of beech in the USA is in the Adirondack Mountains of northern New York State; however, other areas of elevated beech abundance occur in northern New England (Maine, New Hampshire, Vermont), northern Pennsylvania, and the central Appalachian mountains (West Virginia and eastern Kentucky). The range of beech also includes a large area throughout the southern USA where the species exists at relatively low levels. Visual comparison of the distribution of beech (Fig. 4) with the current distribution of BBD (Fig. 1) suggests that the disease has already invaded most of the areas with the greatest host abundance. Prior work indicated that while >50% of the total beech basal area in the USA occurs in the area where BBD is already present, the disease currently occurs in <30% of the potential BBD host range (Morin et al. 2005). We also recognize that both beech and BBD exist throughout much of eastern Canada (Fig. 1), but we did not have forest inventory data from Canada to include in our analyses.

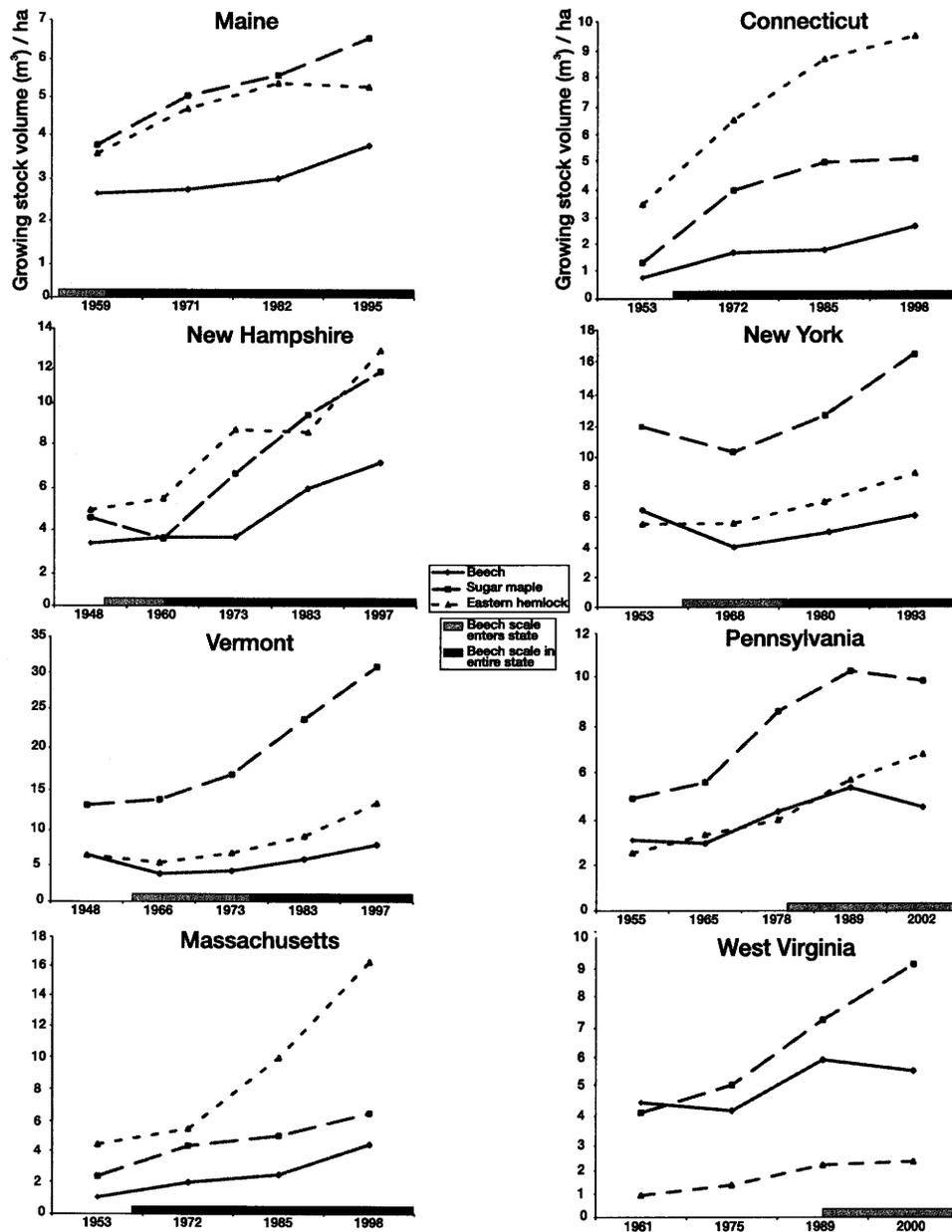
The relationship between year of historical or predicted BBD infestation and the basal area per hectare of beech is shown in Fig. 5. There was considerable variation in beech basal area, but the generally concave trend over time characterized the historical spread of BBD into areas of increasing beech density, followed by the future spread into areas of decreasing beech abundance. Because these estimates of beech density are derived from recent inventory data, they do not precisely represent conditions that existed when BBD first invaded these areas. However, they do demonstrate that in the aftermath forests, beech has persisted and remains generally abundant despite the presence of the disease. This result is in general agreement with previous studies that have documented the persistence of beech in specific stands in the aftermath of BBD invasion (Houston 1975; Twery and Patterson 1984; Griffin et al. 2003).

The difference, on a county level, between the predicted (based upon our estimates of spread rate) and observed date of scale colonization was not significantly correlated with beech density (basal area per hectare, $\rho = -0.05$, $df = 189$, $P = 0.53$). Thus, we had no evidence that beech density affects the rate of spread. Intuitively, one might expect that greater levels of beech would result in greater rates of scale population growth, and this would promote spread. However it is possible that rates of scale spread are more strongly influenced by dispersal than population growth thereby explaining the lack of a relationship between beech density and spread of beech scale.

The geographical distribution of standing dead beech is shown in Fig. 6. While the proportion of standing dead beech was generally higher within the range of BBD, there were several areas outside the range of the disease with relatively high levels of mortality. Comparison of current standing dead beech with historical and future spread (Fig. 7) indicated a significant negative association between proportional beech mortality and the timing of disease colonization (basal area per hectare, $\rho = -0.37$, $df = 407$, $P = 0.01$). Of course, the number of standing dead trees underestimates the cumulative effects of BBD, since trees affected by the disease often break (“beech snap”), topple, and (or) decay in place. Nevertheless, these data confirm the prediction of McGee (2000) in that BBD leads to regional increases in loading of standing coarse woody debris. Thus, the disease may play an important role in generating coarse woody debris that influences landscape scale wildlife habitat characteristics.

While it was not possible to reconstruct precise regional trends in beech abundance during the time course of historical invasion by BBD, inference of these trends could be derived from historical reports of beech volume reported by state in periodic forest inventories (Fig. 8). In a large number of northern hardwood stands, beech is closely associated with sugar maple and eastern hemlock (Eyre 1980). Histori-

Fig. 8. Estimated (from historical Forest Inventory and Analysis reports) volumes of beech, sugar maple, and eastern hemlock between 1940 and the present for eight selected states and years of beech scale entry into and infestation of entire state based on map in Houston (1994).



cal inventories over the last 50 years indicate that volumes of all three species have generally increased, a reflection of the maturation of second-growth forests following harvesting or agricultural abandonment 100 years ago or more (Appendix A). In most states, the invasion of BBD appears to have been associated with a slight decrease in the relative abundance (measured by volume) of beech compared with sugar maple and eastern hemlock (Fig. 8), though decline in the proportion of beech relative to hemlock and sugar maple was only marginally significant between, during, and after invasion by BBD (Friedman $\chi^2 = 4.8$, $df = 2$, $P = 0.09$). Only in New York and Vermont (and possibly Pennsylvania) has there been an actual decrease in total beech volume associated with the invasion. In several states (New York, New Hampshire, Connecticut, and Maine),

there appears to be an acceleration in beech volume accumulation 10–20 years after the original invasion. Other factors that could have an effect on changes in beech volume are herbicide applications and silvicultural activities including salvage and selective harvesting, but it is doubtful that these activities would have occurred over large enough areas to affect regional and state level estimates of beech density.

These results are in general agreement with previous observations of the progression of BBD at specific forest stands. Houston (1994) recognized two phases of the disease invasion. In the first, high rates of infections often cause moderate to high levels of mortality in large diameter trees. This phase is illustrated by McIntosh (1972) who demonstrated considerable decreases in the beech component of

old growth stands following the first phase of BBD invasion. During the second phase, low-level infections of smaller diameter trees cause reduced growth, low vigor, and deformation, but they do not cause high levels of mortality. However, most studies confirm that beech persists in infected stands (Gavin and Peart 1993; Griffin et al. 2003). Eastern hemlock has been shown to increase in relative dominance because of the loss of beech to the disease (Twery and Patterson 1984; Runkle 1990; Le Guerrier et al. 2003). Lovett and Mitchell (2004) suggest that the disease could result in regional increases in sugar maple dominance as well. Shifts to a smaller size structure of the beech resource or shifts in species composition resulting in lower dominance of beech have the potential to decrease beech nut production and affect nutrient cycling in the forest system (Lovett et al. 2006).

Conclusions

Over the next 50 years, it is likely that BBD will continue to expand its range in the USA. However, these predictions of spread are conservative since they do not consider the role of long-range, stochastic movement. Maps of the historical spread of the beech scale insect indicate that the disease sometimes spreads through the formation of isolated colonies ahead of the expanding population front. Ten isolated colonies have formed ahead of the advancing front in various portions of North America during the last 20 years. If this pattern of stratified dispersal continues, spread can be expected to exceed levels that we predicted. Analyses of current forest inventory data suggest that BBD has already invaded most of the areas with relatively high densities of beech. However, the disease has yet to invade the bulk of the range of beech, where the species occurs at low densities. Invasion by BBD may have caused a slight but temporary regional decrease in the relative dominance of beech, but the disease has not eliminated the species. In areas where the disease has been present for 50 or more years, beech persists regionally as either a major or minor forest component.

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References

- Andow, D.A., Kareiva, P.M., Levin, S.A., and Okubo, A. 1990. Spread of invading organisms. *Landscape Ecol.* **4**: 177–188. doi:10.1007/BF00132860.
- Davidson, C.B., Gottschalk, K.W., and Johnson, J.E. 1999. Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. *For. Sci.* **45**: 74–84.
- Eyre, F.H. 1980. Forest cover types of the United States and Canada. Society of American Foresters, Washington, D.C.
- Fosbroke, D.E., and Hicks, R.R., Jr. 1989. Tree mortality following gypsy moth defoliation in southwestern Pennsylvania. *In* Proceedings of the 7th Central Hardwood Forest Conference, 5–8 March 1989, Carbondale, Indiana. *Edited by* George Rink and Carl A. Budelsky. USDA For. Serv. Gen. Tech. Rep. NC-132. pp. 74–80.
- 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**: 1566–1575.
- Gove, J.H., and Houston, D.R. 1996. Monitoring the growth of American beech affected by beech bark disease in Maine using the Kalman filter. *Environ. Ecol. Stat.* **3**: 167–187. doi:10.1007/BF02427860.
- Griffin, J.M., Lovett, G.M., Arthur, M.A., and Weathers, K.C. 2003. The distribution and severity of beech bark disease in the Catskill Mountains, N.Y. *Can. J. For. Res.* **33**: 1754–1760.
- Hansen, M.H., Frieswyk, T., Glover, J.F., and Kelly, J.F. 1992. The eastwide forest inventory data base: database description and user's manual. USDA For. Serv. Gen. Tech. Rep. NC-151.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmen-dorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C., and Thomson, D. 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecol. Lett.* **8**: 91–101. doi:10.1111/j.1461-0248.2004.00687.x.
- Hollander, M., and Wolfe, D.A. 1973. Nonparametric statistical methods. John Wiley, New York.
- Hopkin, A.A., and Scarr, T. 2003. Status of important forest pests in Ontario in 2003 [online]. Available from www.glf.forestry.ca/foresthealth/pdf/status_of_pests_in_ontario_2003_colour.pdf [cited 11 August 2006].
- Houston, D.R. 1975. Beech bark disease: the aftermath forests are structured for a 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. 2001. Effect of harvesting regime on beech root sprouts and seedlings in a north-central Maine forest long affected by beech bark disease. USDA For. Serv. Res. Pap. NE-717.
- 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**: 336–344.
- Jones, R.H., and Raynal, D.J. 1987. Root sprouting in American beech: production, survival, and the effect of parent vigor. *Can. J. For. Res.* **17**: 539–544.
- Kegg, J.D. 1973. Oak mortality caused by repeated gypsy moth defoliations in New Jersey. *J. Econ. Entomol.* **66**: 639–641.
- Le Guerrier, C., Marceau, D.J., Bouchard, A., and Brisson, J. 2003. A modelling approach to assess the long-term impact of beech bark disease in northern hardwood forest. *Can. J. For. Res.* **33**: 2416–2425. doi:10.1139/x03-170.
- Levin, S.A. 1989. Analysis of risk for invasions and control programs. *In* Biological invasions: a global perspective. Wiley, Chichester, UK. pp. 425–435.
- Liebholt, A.M., Halverson, J.A., and Elmes, G.A. 1992. Gypsy moth invasion in North America: a quantitative analysis. *J. Biogeogr.* **19**: 513–520. doi:10.2307/2845770.
- Liebholt, A.M., Macdonald, W.L., Bergdahl, D., and Mastro, V.C. 1995. Invasion by exotic pests: a threat to forest ecosystems. *For. Sci. Monogr.* **30**.
- 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.
- Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., and Fitzugh, R.D. 2006. Forest ecosystem responses to exotic pests and pathogens in Eastern North America. *Bioscience*, **56**: 395–405. doi:10.1641/0006-3568(2006)056[0395:FERTEP]2.0.CO;2.

- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**: 689–710. doi:10.2307/2641039.
- Manion, P.D. 1991. Fungi as agents of tree disease: canker diseases. *In* Tree disease concepts. 2nd ed. Prentice Hall Career & Technology, Upper Saddle River, N.J. pp. 182–208.
- Mattson, W.J. 1997. Exotic insects in North American forests — ecological systems forever altered. *In* Proceedings of Exotic Pests of Eastern Forests, 8–10 April 1997, Nashville, Tenn. Edited by Kerry O. Britton. USDA For. Serv. and Tennessee Exotic Pest Plant Council, Nashville, Tenn. pp. 187–193.
- McGee, G.G. 2000. The contribution of beech bark disease-induced mortality to coarse woody debris loads in northern hardwood stands of Adirondack Park, New York, U.S.A. *Can. J. For. Res.* **30**: 1453–1462. doi:10.1139/cjfr-30-9-1453.
- McIntosh, R.P. 1972. Forests of the Catskill Mountains, New York. *Ecol. Monogr.* **42**: 143–162. doi:10.2307/1942261.
- Mize, C.W., and Lea, R.V. 1979. The effect of beech bark disease on the growth and survival of beech in northern hardwoods. *Eur. J. For. Pathol.* **9**: 243–248.
- Mooney, H.A., and Cleland, E.E. 2001. The evolutionary impact of invasive species. *Proc. Natl. Acad. Sci. U.S.A.* **98**: 5446–5451. doi:10.1073/pnas.091093398. PMID:11344292.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E., and Fryxell, J.M. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**: 2436–2445.
- Morin, R.S., Liebhold, A.M., Gottschalk, K.W., and Luzader, E. 2005. Mapping host-species abundance of three major exotic forest pests. USDA For. Serv. Res. Pap. NE-726.
- Natural Resources Canada. 2000. State of Eastern Ontario's forests, forest area disturbed by tree diseases [online]. Available from sof.eomf.on.ca/Ecosystem_Condition_and_Productivity/Biotic/Indicators/Disease/Area/i_forest_area_affected_by_disease_e.htm [cited 11 August 2006].
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., and Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, **1**: 3–19. doi:10.1023/A:1010034312781.
- Pimentel, D. (Editor). 2002. Biological invasions. Economic and environmental costs of alien plant, animal, and microbe species. CRC Press, Boca Raton, Fla.
- Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience*, **50**: 53–65. doi:10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2.
- R Development Core Team. 2004. Available from www.r-project.org [cited 8 August 2005].
- Rossmann, A.Y., and Samuels, G.J. 1999. Genera of Bionectriaceae, Hypocreaceae and Nectriaceae (Hypocreales, Ascomycetes). *Stud. Mycol.* **42**: 158–160.
- Runkle, J.R. 1990. Eight years change in an old *Tsuga canadensis* woods affected by beech bark disease. *Bull. Torrey Bot. Club*, **177**: 409–419.
- SAS Institute Inc. 2004. SAS OnlineDoc®. Version 9.1.2. SAS Institute Inc. Cary, N.C.
- Sharov, A.A., and Liebhold, A.M. 1998. Model of slowing the spread of the gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecol. Appl.* **8**: 1170–1179. doi:10.2307/2640970.
- Shigesada, N., and Kawasaki, K. 1997. Biological invasions: Theory and practice. Oxford University Press, New York.
- Shigo, A.L. 1972. The beech bark disease today in the northeastern U.S. *J. For.* **54**: 286–289.
- Skellam, J.G. 1951. Random dispersal in random populations. *Biometrika*, **38**: 196–218. PMID:14848123.
- Tobin, P.C., Liebhold, A.M., and Roberts, E.A. 2007. Comparison of methods for estimating the spread of a non-indigenous species. *J. Biogeogr.* **34**: 305–312.
- Twery, M.J., and Patterson, W.A. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. *Can. J. For. Res.* **14**: 565–574.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., and Westbrooks, R. 1996. Biological invasions as global environmental change. *Am. Sci.* **84**: 468–478.
- Weber, E. 1998. The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *J. Biogeogr.* **25**: 147–154. doi:10.1046/j.1365-2699.1998.251119.x.

Appendix A. Historical Forest Inventory and Analysis report references

References

- Alerich, C.L. 1993. Forest statistics for Pennsylvania — 1978 and 1989. USDA For. Serv. Resour. Bull. NE-126.
- Alerich, C.L. 2000. Forest statistics for Connecticut: 1985 and 1998. USDA For. Serv. Res. Bull. NE-147.
- Alerich, C.L. 2000. Forest statistics for Massachusetts: 1985 and 1998. USDA For. Serv. Res. Bull. NE-148.
- Alerich, C.L., and Drake, D.A. 1995. Forest statistics for New York — 1980 and 1993. USDA For. Serv. Res. Bull. NE-132.
- Armstrong, G.R., and Bjorkbom, J.C. 1956. The timber resources of New York. USDA For. Serv.
- Bones, J.T. 1978. The forest resources of West Virginia. USDA For. Serv. Res. Bull. NE-56.
- Considine, T.J., Jr., and Frieswyk, T.S. 1982. Forest statistics for New York, 1980. USDA For. Serv. Res. Bull. NE-71.
- Dickson, D.R., and McAfee, C.L. 1988. Forest statistics for Connecticut — 1972 and 1985. USDA For. Serv. Res. Bull. NE-105.
- Dickson, D.R., and McAfee, C.L. 1988. Forest statistics for Massachusetts — 1972 and 1985. USDA For. Serv. Res. Bull. NE-106.
- DiGiovanni, D.M. 1990. Forest statistics for West Virginia — 1975 and 1989. USDA For. Serv. Res. Bull. NE-114.
- Ferguson, R.H. 1958. The timber resources of Pennsylvania. USDA For. Serv.
- Ferguson, R.H. 1964. The timber resources of West Virginia. USDA For. Serv. Res. Bull. NE-2.
- Ferguson, R.H. 1968. The timber resources of Pennsylvania. USDA For. Serv. Res. Bull. NE-8.
- Ferguson, R.H., and Howard, M.C. 1956. The timber resource in Massachusetts. USDA For. Serv.
- Ferguson, R.H., and Kingsley, N.P. 1972. The timber resources of Maine. USDA For. Serv. Res. Bull. NE-26.
- Ferguson, R.H., and Longwood, F.R. 1960. The timber resources of Maine. USDA For. Serv.
- Ferguson, R.H., and Mayer, C.E. 1970. The timber resources of New York. USDA For. Serv. Res. Bull. NE-20.
- Frieswyk, T.S., and Malley, A.M. 1985. Forest statistics for New Hampshire, 1973 and 1983. USDA For. Serv. Res. Bull. NE-88.
- Frieswyk, T.S., and Malley, A.M. 1985. Forest statistics for Vermont, 1973 and 1983. USDA For. Serv. Res. Bull. NE-87.

- Frieswyk, T., and Widmann, R. 2000. Forest statistics for New Hampshire, 1983 and 1997. USDA For. Serv. Res. Bull. NE-146.
- Frieswyk, T., and Widmann, R. 2000. Forest statistics for Vermont, 1983 and 1997. USDA For. Serv. Res. Bull. NE-145.
- Griffith, D.M., and Alerich, C.L. 1996. Forest statistics for Maine, 1995. USDA For. Serv. Res. Bull. NE-135.
- Griffith, D.M., and Widmann, R.H. 2003. Forest statistics for West Virginia: 1989 and 2000. USDA For. Serv. Res. Bull. NE-157.
- Griswold, N.B., and Ferguson, R.H. 1957. The timber resources of Connecticut. USDA For. Serv.
- Kingsley, N.P. 1976. The forest resources of New Hampshire. USDA For. Serv. Res. Bull. NE-43.
- Kingsley, N.P. 1977. The forest resources of Vermont. USDA For. Serv. Res. Bull. NE-46.
- Kingsley, N.P., and Barnard, J.E. 1968. The timber resources of Vermont. USDA For. Serv. Res. Bull. NE-12.
- McWilliams, W.H., Alerich, C.A., Devlin, D.A., Lister, A.J., Lister, T.A., Sterner, S.L., and Westfall, J.A. 2004. Annual inventory report for Pennsylvania's forests: results from the first three years. USDA For. Serv. Res. Bull. NE-159.
- US Department of Agriculture. Forest Service. 1954. The forest resources of New Hampshire. USDA For. Serv. For. Res. Rep. 8.