

STAND-LEVEL PATTERNS AND ECOSYSTEM CONSEQUENCES OF BEACH BARK DISEASE

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Abstract

Synthesis of existing literature indicates that beech bark disease has direct and indirect effects on forest structure and function through the stand-level consequences of individual tree mortality. Tree-level factors known to influence disease severity include tree size, distance from pathogen source, topographical position, wind direction and speed, nitrogen concentration of bark tissue, and genetic resistance. When considering forested stands, tree-level factors must be combined with additional parameters to determine the effects of the disease on forest function. Additional stand-level controls on beech bark disease severity involve forest history, beech basal area, and forest composition. Aside from direct mortality attributed to disease, indirect mortality may arise from increased susceptibility of diseased trees to windthrow and ice storm damage. Combined direct and indirect mortality results in losses of larger American beech (*Fagus grandifolia* Ehrh.) stems, potentially increasing light availability for other tree species. However, large stem losses are balanced by prolific root sprouting in aftermath forests, which maintains dense stands of small beech stems that are effective resource competitors with economically valuable species. In addition to shifts in tree size classes, mortality also results in elevated amounts of coarse woody debris. Due to a paucity of baseline data from disease-free forests, it can be difficult to isolate the effects of beech bark disease relative to other forest processes in determining current forest structure and function. Research emphasis should be on monitoring key structural and functional attributes, such as coarse woody debris loads and nitrogen dynamics, in forests free of disease or those in the early stages of disease progression. Future research should also address the synergistic effects of beech bark disease and other major forest disturbances such as other introduced pathogens and windthrow.

Introduction

The ecological and biogeochemical characters of forested ecosystems are determined in large part by the dominant

tree species, which in many eastern forests includes the late-successional American beech. The gradual loss of this species due to the introduced insect-fungal disease complex, beech bark disease, is likely to have multiple spatiotemporal scale consequences for the structure and function of these forests. Invasions of nonnative pathogens, plant, animal, insect, and earthworm species can result in major changes in forest stand diversity and productivity, biogeochemical processes, availability of natural resources, aesthetic conditions, and human economies. One dramatic example of the effects of an exotic pest introduction on a native ecosystem is that of the introduced fungal pathogen, *Cryphonectria parasitica*, which resulted in the extirpation of the once dominant American chestnut (*Castanea dentata* (Marsh.) Borkh.) from forests of eastern North America in the early 1900s. The ecologically and economically important chestnut trees have largely been replaced by extant co-occurring species including several oak species, American beech, and eastern hemlock (Stephenson 1986). However, continued dominance of the latter two species is uncertain due to introduced pathogens. In an attempt to better evaluate the role of American beech in temperate forest ecosystems the objective of this paper is to review current scientific understanding of the effects of beech bark disease on those systems. This requires a synthetic approach that combines our knowledge of disease progression through stands and across the landscape with information on the composition, structure, and function of diseased stands. Consideration of the interactions between beech bark disease and other forest disturbances will provide a more complete framework in order to assess the role of beech bark disease in shaping future forest composition and function.

Literature Review

Disease Progression and Severity

The initiating insect of the disease, *Cryptococcus fagisuga* (Lind.) was first introduced into Halifax, Nova Scotia on nursery stock of European copper beech (Ehrlich 1934). In the following years the insect moved north, west, and southwards (Houston et al. 1979). It has been shown that those forests with a longer history of insect infestation also tend to exhibit more severe disease symptoms (Houston 1994; Latty et al. 2002). For example in one study beech trees were assigned to one of 4 classes of disease severity based on visual external defect of beech bark (Latty et al. 2002). Individuals with no indication

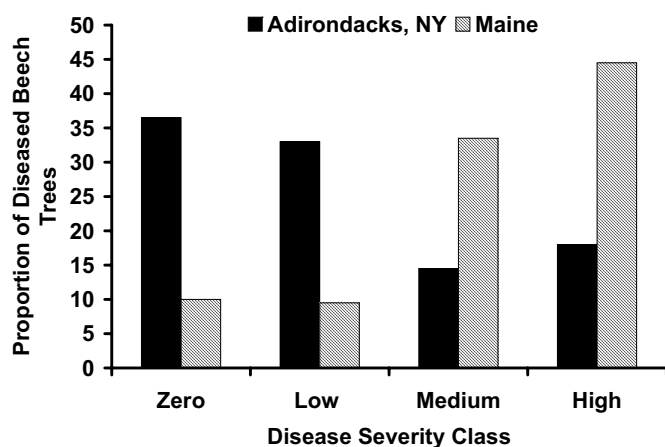


Figure 1.—Proportion of beech trees in four disease severity classes in New York and Maine. Source: Modified from Latty et al. 2003.

of bark defect attributable to disease were assigned to the Zero class and the High class consisted of trees with the most intense damage to outer bark and cambial tissues. The study was conducted in two regions, which had been affected by disease at different times. In northern Maine the insect first progressed through the area between 1945 and 1950, whereas in the western Adirondack region of New York the insect likely became established after 1960 (Houston et al. 1979). A higher proportion of Maine trees in the medium and high disease classes balanced by a lower proportion of undiseased and lightly diseased trees in New York likely reflect the longer residence time of the disease in Maine forests (Fig. 1).

In addition to the site of scale introduction, landscape dynamics of disease severity may also be related to beech basal area and topographical position (Ehrlich 1934, Houston et al. 1979, Griffin et al. 2003). At the landscape scale (hundreds of hectares) in the Catskill Mountains, NY, a significant positive relationship was established between disease severity level and beech basal area (Griffin et al. 2003). Moreover, when examined by 100 m elevation bands the middle elevation bands, 600-1,000 m, exhibited the highest levels of disease severity and the greatest beech abundance. Low (300-600 m) and high (1,000-1,300 m) elevation bands generally supported lower beech basal area and less severely diseased trees. Studies conducted within forest stands have also demonstrated a relationship between the intensity of infestation and topographical position with the lowest infestation rates reported from lower slope

positions (Houston et al. 1979). However infestation patterns were also influenced by the intensity with which the scale insect colonized the stem. Insect density is further influenced by annual weather patterns as greater fecundity is promoted by mild winter temperatures and dry fall conditions (Houston and Valentine 1988). The effect of topographical position on disease severity is thus likely related to beech basal area as well as other factors such as aspect, proximity to an inoculum source, and prevailing wind direction because the scale insect is wind dispersed.

The majority of the studies examining disease progression have been conducted at the stand-scale and it is at this scale that factors related to scale establishment have been most closely examined (e.g., Houston et al. 1979, Twery and Patterson 1984, Houston and Valentine 1988, Wargo 1988, Gavin and Peart 1993, Latty et al. 2003). In an English plantation, consistently high levels of disease infestation were measured on the north and northeast sides of a large tree that served as a source of inoculum (Houston et al. 1979). These patterns corresponded with the prevailing wind direction. Aside from wind and air temperature, insect dynamics are also related to forest characters like composition and land-use history. The dense shade cast by eastern hemlock (*Tsuga canadensis* Carr.) and the resulting moist conditions may favor high scale fecundity (Twery and Patterson 1984). A survey of stands in Massachusetts and New Hampshire demonstrated the highest beech mortality in hemlock dominated stands, 38.6%, as compared to only 13.6% mortality in beech dominated stands (Twery and Patterson 1984).

Patterns of beech mortality and disease infection have also been linked to the harvest history of the forest (Gavin and Peart 1993, Latty et al. 2003). In New Hampshire a comparison of the radial ring widths of infected and uninfected trees demonstrated that the earliest significant growth reduction from disease occurred in old-growth forests in 1949 but was not detected in nearby second-growth forests until 1965 (Gavin and Peart 1993). Assuming that the disease front reached the two forests at the same time, the effects of the disease were delayed in the second-growth stands. The old-growth stands in this study had both a greater abundance of hemlock and a higher density of large beech trees, which could account for the observed

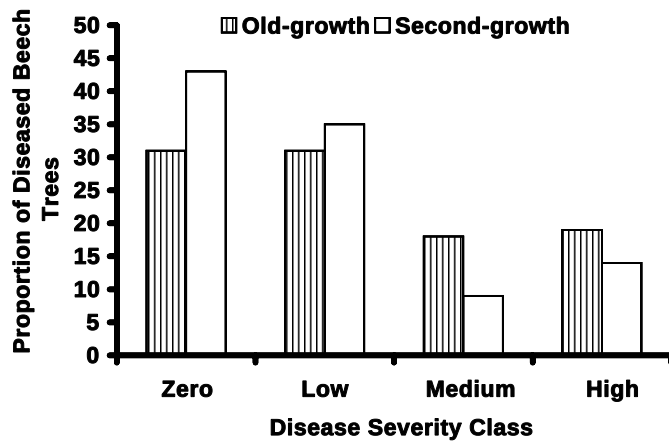


Figure 2.—Proportion of beech trees in four disease severity classes in old-growth and second-growth forests of Adirondack Park. Source: Modified from Latty et al. 2003.

patterns (Gavin and Peart 1993). A separate study examining the importance of forest history in determining disease severity patterns demonstrated that the concentration of total nitrogen (N) in beech bark may also influence severity symptoms (Latty et al. 2003). Amino nitrogen is a critical dietary component of sucking insects (Dadd and Mittler 1965) such as the beech scale, which feed by inserting their stylets into the bark parenchyma tissue (Wainhouse and Gate 1988). The acquisition of key amino acids, such as methionine, can influence insect growth and development (Mittler 1967, Dadd and Krieger 1968) and disease resistant trees have significantly lower amino N in their bark compared to diseased trees (Wargo 1988). In some Adirondack forests, old-growth beech trees have significantly higher total N in bark tissue than similarly sized second-growth trees (Latty et al. 2003). Overall the old-growth stands also have a higher proportion of moderately and severely diseased trees whereas the second-growth stands have a

higher proportion of undiseased and slightly diseased trees (Fig. 2).

Although differences in disease severity between old-growth and second-growth forests were detected, there were no significant differences in other potentially important factors such as beech basal area, hemlock basal area, and median beech tree size. Thus scale establishment may also be limited by the nitrogen concentrations in beech bark and thereby forest history may impact overall disease severity patterns.

Structure and Function of Aftermath Stands

One of the most commonly made observations of aftermath stands is the large number of small beech stems resulting from the greater loss of large beech stems and the prolific sprouting capabilities of beech (Forrester et al. 2003, Hane 2003, Latty 2001, Houston 1994). From 1985 to 2000 the smallest diameter class of beech trees, 5.0-9.9 cm, has increased from 123 to 173 stems/ha in Adirondack forests in NY (Forrester et al. 2003). Data from other Adirondack forests show that old-growth stands have higher beech densities in the smaller size classes than do second-growth forests (Fig. 3A) and that this pattern does not hold when all canopy trees are considered (Fig 3B). A pattern that may be attributable to the more moderately and severely diseased trees in the old-growth stands (Fig. 2). Similar results have been reported from New Hampshire where the number of small beech saplings (< 10 cm) has increased 5-fold since 1965 and small beech stem densities may reach as high as 3500 stems/ha (Hane 2003). In addition to the preponderance of small live stems, standing dead beech stems make up the majority of overall standing dead stem density, 30%, and basal area, 27% (Latty 2001). In some

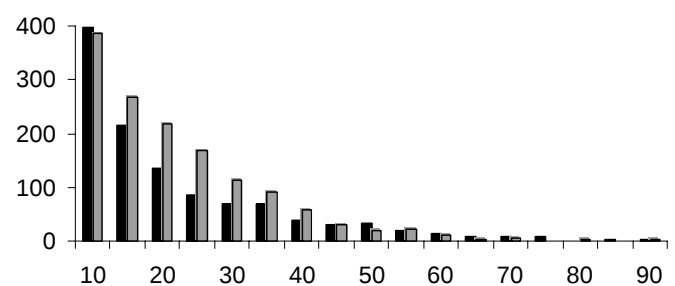
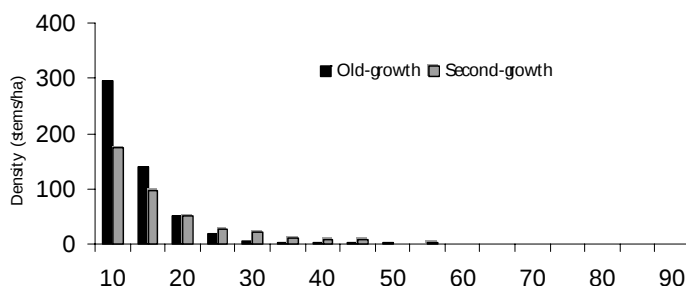


Figure 3.—Canopy stem density per size class for (A) beech trees only and (B) all canopy trees. Source: Modified from Latty 2001.

stands a 99% increase in dead beech biomass has been observed over a 15 year period (Forrester et al. 2003). A high proportion of downed woody beech debris in Adirondack forests is attributable to disease-induced death, an average of 64% in old-growth stands and 75% in maturing stands (McGee 2000).

Structural changes in aftermath forests are accompanied by changes in tree species composition. Eastern hemlock and sugar maple (*Acer saccharum* Marsh.) are in many cases co-dominant with beech and their interactions with declining beech are the focus of many studies (Twery and Patterson 1984, Runkle 1990, DiGregorio et al. 1999, Hane 2003). Comparisons of importance values of the major tree species in plots with and without beech mortality in New England demonstrated that hemlock benefited most from disease-induced mortality (Twery and Patterson 1984). Temporal analysis of stands in New York state showed increases in hemlock and sugar maple basal area concomitant with declining beech basal area (Runkle 1990). The latter study also noted increases in red maple (*A. rubrum* L.) and red oak (*Quercus rubra* L.) over the same time interval. Much emphasis has been placed on sugar maple response to beech death owing to its ability to respond to gap openings in conjunction with its tolerance of shady forest understory conditions (Canham 1988). Twenty year radial growth patterns of sugar maples growing in distinct gaps compared with those growing in the closed canopy demonstrated growth increases in subcanopy trees coincident with the onset of beech bark disease in the stands (DiGregorio et al. 1999). Similar radial growth increases were not observed in canopy trees. However, subcanopy maples have also been shown to exhibit some of the highest mortality in diseased northern hardwood stands (Forrester et al. 2003). Thus small diameter sugar maples may be able to take advantage of higher understory light conditions resulting from beech death but not in all situations. Sugar maple survival in the smaller size classes in diseased stands is also related to the outcome of competition with advance regeneration of beech. An experimental study in New Hampshire demonstrated that sugar maple seedling survival was consistently higher in plots from which advance beech generation was removed than in control plots where beech saplings ranged from 2000 to 3500 stems/ha (Hane 2003). Sugar maple response to canopy beech death is therefore strongly influenced not only by canopy size class but also the overall species composition of the subcanopy layer.

Changes in forest functioning such as nitrogen cycling could accompany the disease-induced changes in forest composition reported in some studies (Twery and Patterson 1984, Runkle 1990). Tree species composition has the potential to influence soil properties through many pathways including species-specific effects on litter quality and mass (Finzi and others 1998, Ferrari 1999). No direct measurements of soil nitrogen transformation rates in diseased and disease-free stands have been reported. However, recent attention has been focused on the use of foliar tissue chemistry as a potential indicator of the nitrogen status of the soil (Aber and others 1998, Ollinger et al 2002). Limited sampling of bark tissue has revealed no significant variation in nitrogen concentrations of bark collected from diseased beech trees of New York and Maine compared with bark from disease-free trees of Michigan (Latty et al. 2003). The disease-induced loss of large beech trees could also result in decreased biomass of beech foliage that could alter forest nutrient cycling. In one study, the high mortality of large beech stems was countered by advance regeneration of beech resulting in no change in beech foliar biomass over a 15 year period and the overall lignin content of leaf litter remained virtually unchanged (Forrester et al. 2003). More research is necessary to elucidate the consequences of beech bark disease on forest function, particularly nutrient cycling. This will likely require a better understanding of the competitive outcome between small diameter beech and sugar maple, species with distinct litter chemistries, on soils with differing fertility.

Interactions with other Forest Disturbances

Beech bark disease weakens beech trees causing them to be more susceptible to other disturbances such as windthrow and ice storms (Houston et al. 1979, Canham et al. 2001, Rhoads et al. 2002). In southeastern forests without beech bark disease, intermediate sized beech trees have a high resistance to windthrow leading to relatively stable beech populations (Batista et al. 1998). However northeastern beech trees exhibit some of the highest susceptibility to windthrow compared to co-dominant species such as sugar maple (Canham et al. 2001). Modeling studies have determined that susceptibility to windthrow is nearly identical for beech and sugar maple in disease-free stands in Michigan but susceptibility of beech more than doubles in diseased stands in New York with little change in sugar maple

susceptibility (Papaik unpublished). Long-term model runs indicate that yellow birch (*Betula alleghaniensis* Britt.) and hemlock basal area could increase in these stands from diseased regions (Papaik unpublished). Other studies from the Northeast have revealed that severely diseased beech trees show signs of heavier ice damage compared to other dominant tree species (Rhoads et al. 2002). Both windthrow and ice damage could result in increases in beech abundance in smaller size classes because physical injury promotes root sprouting (Jones and Raynal 1988). However, it is likely that the maturing beech stands will eventually succumb to disease.

Novel disturbances such as chronic elevated nitrogen deposition and other introduced tree pathogens have the potential to interact with beech bark disease. Eastern forests with a dominant beech component receive some of the highest loads of atmospheric N in the United States. The nitrogen content of foliage and bolewood has been demonstrated to increase following fertilization with ¹⁵N-labelled nitrate (Nadelhoffer et al. 1995, Magill et al. 1996). Given the importance of nitrogen in the diet of sucking insects, those forests receiving high N loads, especially early in disease progression where bark quality limits scale establishment more than bark quantity, could experience accelerated disease progression through the stand. Beech bark disease interaction s with other human accelerated disturbances include the introduction of exotic pathogens, which could result in potential changes to forest composition. For example in northeastern forests harboring both beech bark disease and gypsy moths, gap area increased from 19.7 to 31.9% over a 6 year period (Krasny and DiGregorio 2001). The additional light available to the understory could potentially result in either higher beech stem densities or greater sugar maple density. To distinguish which alternative is more likely in a give forest type requires more studies of the competitive interactions of the two species on different substrates.

Conclusion

Investigations of the role of beech bark disease in shaping the patterns and processes of temperate forests have become increasingly important as the disease continues to spread west and southward. To fully evaluate the ecosystem changes caused by beech bark disease requires quantitative data that describes forest parameters prior to

the onset of disease. The challenge is determining which quantitative data is most useful to establish reference conditions, management priorities, and restoration goals. Baseline data collected from a disease-free forest in Ohio were selected for their propensity to be influenced by disease presence and included species composition, mortality and growth rates, canopy replacement, coarse woody debris dynamics, and understory replacement (Forrester and Runkle 2000). Given the role of N dynamics in the patterns of scale establishment and the sensitivity of nutrient cycling to changes in species composition it may be prudent to consider nitrogen dynamics in future baseline studies as well. From a forest management perspective it would be useful to have better measures of the impacts of beech bark disease on forest productivity thereby adding quantification of net primary productivity to the growing list of measured baseline parameters. It is unlikely that one list of measurements will suit every need or be doable by all interested parties. However, if an organized beech bark disease monitoring system were put into place it is critical that data needs are discussed, defined, and refined by interested parties with complementary overarching goals.

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References

- Aber, J., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, I. Fernandez. 1998. **Nitrogen saturation in temperate forest ecosystems.** *Bioscience* 48, 921-933.
- Batista, W.B., W.J. Platt, and R.E. Macchiavelli. 1998. **Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest.** *Ecology* 79, 38-53.
- Canham, C.D. 1988. **Growth and canopy architecture of shade-tolerant trees: response to canopy gaps.** *Ecology* 69, 786-795.
- Canham, C.D., M.J. Papaik, and E.F. Latty. 2001. **Interspecific variation in susceptibility to**

- windthrow as a function of tree size and storm severity for northern temperate tree species. Canadian Journal of Forest Research 31, 1-10.
- Dadd, R.H., and T.E. Mittler. 1965. **Studies on the artificial feeding of the aphid *Myzus persicae* (Sluzer). III. Some major nutritional requirements.** Journal of Insect Physiology 11, 717-43.
- Dadd R.H., and D.L. Krieger. 1968. **Dietary amino acid requirements of the aphid *Myzus persicae*.** Journal of Insect Physiology 14, 741-764.
- DiGregorio, L.M., M.E. Krasny, and T.J. Fahey. 1999. **Radial growth trends of sugar maple (*Acer saccharum*) in an Allegheny northern hardwood forest affected by beech bark disease.** Journal of the Torrey Botanical Society 126, 245-254.
- Ehrlich, J. 1934. **The beech bark disease, a *Nectria* disease of *Fagus*, following *Cryptococcus fagi* (Baer.).** Canadian Journal of Forest Research 10, 593-692.
- Ferrari, J.B. 1999. **Fine-scale patterns of leaf litterfall and nitrogen cycling in an old-growth forest.** Canadian Journal of Forest Research 29:291-302.
- Finzi, A.C., van Breeman, N., and C.D. Canham. 1998. **Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen.** Ecological Applications 8(2):440-446.
- Forrester, J.A., and J.R. Runkle. 2000. **Mortality and replacement patterns of an old-growth *Acer-Fagus* woods in the Holden Arboretum, Northeastern Ohio.** The American Midland Naturalist 144, 227-242.
- Forester, J.A., G.G. McGee, and M.J. Mitchell. 2003. **Effects of beech bark disease on aboveground biomass and species composition in a mature hardwood forest, 1985-2000.** Journal of the Torrey Botanical Society 130, 70-78.
- Gavin, D.G., and D.R. Peart. 1993. **Effects of beech bark disease on the growth of American beech (*Fagus grandifolia*).** Canadian Journal of Forest Research 23, 1566-1575.
- Griffin, J.M., G.M. Lovett, M.A. Arthur, and K.C. Weathers. 2003. **The distribution and severity of beech bark disease in the Catskill Mountain, N.Y.** Canadian Journal of Forest Research 33, 1754-1760.
- Hane, E.N. 2003. **Indirect effects of beech bark disease on sugar maple seedling survival.** Canadian Journal of Forest Research 33, 807-813.
- Houston, D.R. 1994. **Major new tree epidemics: beech bark disease.** Annual Review of Phytopathology 32, 75-87.
- Houston, D.R., and H.T. Valentine. 1988. **Beech bark disease: the temporal pattern of cankering in aftermath forests of Maine.** Canadian Journal of Forest Research 18, 38-42.
- Houston, D.R., E.J. Parker, and D. Lonsdale. 1979. **Beech bark disease: patterns of spread and development of the initiating agent *Cryptococcus fagisuga*.** Canadian Journal of Forest Research 9, 336-344.
- Jones, R.H., and D.J. Raynal. 1988. **Root sprouting in American beech (*Fagus grandifolia*): Effect of root injury, root exposure, and season.** Forest Ecology and Management 25, 79-90.
- Krasny, M.E., and L.M. DiGregorio. 2001. **Gap dynamics in Allegheny northern hardwood forests in the presence of beech bark disease and gypsy moth disturbances.** Forest Ecology and Management 144, 265-274.
- Latty, E.F. 2001. **Interactions between land-use history, nitrogen cycling, and beech bark disease in northern hardwood forests.** Ph.D. diss., Cornell University, Ithaca, NY.
- Latty, E.F., C.D. Canham, and P.L. Marks. 2003. **Beech bark disease in northern hardwood forests: the importance of nitrogen dynamics and forest history for disease incidence.** Canadian Journal of Forest Research 33, 257-268.
- Magill, A.H., M.R. Downs, K.J. Nadelhoffer, R.A. Hallet, and J.D. Aber. 1996. **Forest ecosystem**

- response of four years of chronic nitrate and sulfate additions at Bear Brook watershed, Maine, USA.** *Forest Ecology and Management* 84, 29-37.
- 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.** *Canadian Journal of Forest Research* 30, 1453-1462.
- Mittler, T.E. 1967. **Effect on aphid feeding of dietary methionine.** *Nature* 214, 386-387.
- Nadelhoffer, K.J., M.R. Downs, B. Fry, J.D. Aber, A.H. Magill, and J.M. Melillo. 1995. **The fate of ^{15}N -labelled nitrate additions to a northern hardwood forest in eastern Maine, USA.** *Oecologia* 103, 292-301.
- Ollinger, S.V., M.L. Smith, M.E. Martin, R.A. Hallet, C.L. Goodale, and J.D. Aber. 2002. **Regional variation in foliar chemistry and N cycling among forests of diverse history and composition.** *Ecology* 83, 339-355.
- Rhoads, A.G., S.P. Hamburg, T.J. Fahey, T.G. Siccama, E.N. Hane, J. Battles, C. Cogbill, J. Randall, and G. Wilson. 2002. **Effects of an intense ice storm on the structure of a northern hardwood forest.** *Canadian Journal of Forest Research* 32, 1763-1775.
- Runkle, J.R. 1990. **Eight years in an old *Tsuga Canadensis* woods affected by beech bark disease.** *Bulletin of the Torrey Botanical Club* 117, 409-419.
- Stephenson, S.L. 1986. **Changes in a former chestnut-dominated forests after a half century of succession.** *American Midland Naturalist* 116, 173-179.
- Twery, M.J., and W.A. Patterson. 1984. **Variations in beech bark disease and its effects on species composition and structure of northern hardwood forest stands in central New England.** *Canadian Journal of Forest Research* 14, 565-574.
- Wainhouse, D., and I.G. Gate. 1988. **The beech scale.** In: A.A. Berryman (Ed.), *Dynamics of forest insect populations*. Plenum Press, New York, NY, USA, pp. 67-85.
- Wargo, P.M. 1988. **Amino nitrogen and phenolic constituents of bark of American beech, *Fagus grandifolia*, and infestation by beech scale, *Cryptococcus fagisuga*.** *European Journal of Forest Pathology* 18, 279-290.

Evans, Celia A., Lucas, Jennifer A. and Twery, Mark J. 2005. **Beech Bark Disease: Proceedings of the Beech Bark Disease Symposium.** Gen. Tech. Rep. NE-331. Newtown Square PA, US. Department of Agriculture Forest Service, Northern Research Station. 149 p.

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