EFFECTS OF BEECH BARK DISEASE ON TREES AND ECOSYSTEMS

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Abstract

The beech bark disease complex has long been an extremely important exotic pest issue as it has spread throughout eastern North America since its introduction in 1890. This insect-fungal disease complex is continuing its expansion and reaching new areas such as the state of Michigan. As it does so, it has serious implications for the health of both individual trees and beech–containing ecosystems as whole. Numerous tree characteristics affect abundance of beech scale on individual trees, including tree age, diameter, area and texture of bark, bark chemical composition, other bark-dwelling organisms, tree genetics, side of tree bole examined, and crown health variables. Beech scale colonization is generally greater in favorable microsites. These microsites include such characteristics as large areas of rough bark, higher levels of bark nitrogen, favorable associations with bark-dwelling organisms, more shade, and low temperature fluctuations. The development of beech bark disease through its three stages of progression once beech scale is on trees in an area is affected by a number of factors such as tree age, size, vigor, and stress levels from other factors. Spread of beech bark disease through ecosystems is likely most strongly controlled by the spatial patterns of beech stands and beech trees within stands, although other agents such as wind and animals can play important roles as well. Research to date in Michigan supports the importance of contiguous forest stands in increasing the rate of beech bark disease spread. Beech bark disease has a wide array of effects on tree health, including notably greater levels of damage, poorer tree crown conditions, and reduced radial wood growth. Negative effects can occur even when the amount of beech scale present on the tree is relatively small. Further research directions are suggested.

Introduction

Beech bark disease is a complex composed of a scale insect and a fungal pathogen. This disease complex attacks both American beech (*Fagus grandifolia*) and European beech (*F. sylvatica*) (Houston 1994). The scale insect involved, *Cryptococcus fagisuga*, is not native to North America. It was introduced to Nova Scotia around 1890 on plantings of European beech and was discovered in the United States in 1929 (Hawboldt 1944). The fungi involved are three species of Nectria, two native (*N. ochroleuca* and *N. galligena*) and one introduced (*N. coccinea* var. *faginata*). Together, the beech scale and beech bark disease have gradually spread south and west from the initial point of scale introduction. The limits of the range at this time are Virginia, North Carolina, Tennessee, Ohio, Michigan, and Ontario (McCullough et al. 2001).

The state of Michigan is the most recent location where beech bark disease has been confirmed. This state also represents the western edge of its current range and somewhat different ecosystem conditions than the eastern areas where beech bark disease occurs. Beech scale was first discovered in Michigan in 2000 in both the Lower Peninsula (Mason County) and Upper Peninsula (Luce County). Given the extent of the infestation at the time of its discovery, beech scale was likely present in the state for at least 15 to 20 years prior to being noticed and confirmed. By 2004, the beech scale had spread to six counties in the Lower Peninsula and five counties in the Upper Peninsula. Beech bark disease is now found in at least three Lower Peninsula counties and five Upper Peninsula counties. This exotic pest complex has been the focus of much concern and study since its discovery in the leading-edge area of Michigan, just as it has been for many years in the more eastern areas of North America.

Beech Scale Distribution and Abundance on Individual Trees

Numerous tree characteristics affect abundance of the beech scale, including tree age, diameter of the tree at breast height (DBH), area of live bark, bark textural characteristics, bark nitrogen content, organisms colonizing the bark, tree genetics, the side of the tree bole examined, and crown health variables such as transparency and dieback.

Beech scale tends to first colonize those trees in a stand that have rougher bark (Houston et al. 1979a, Lonsdale 1983, Burns and Houston 1987). Such rough bark is often found on trees of larger diameter and on trees that are older. Young trees, on the other hand, tend to have fairly smooth bark. Larger diameter trees are also important to beech scale populations because they have a greater amount of bark surface area available for scales to colonize.

Another important bark characteristic besides texture and area is the bark's chemical composition. Those beech trees that are more susceptible to scale have higher concentrations of individual amino acids and higher levels of total amino nitrogen than do trees that tend to show resistance to scale colonization (Wargo 1988). Bark chemistry is inter-related with other tree characteristics such as DBH and location in the environment. Larger trees have higher levels of amino nitrogen in their bark than do smaller trees (Wargo 1988). Those trees that are found in undisturbed old-growth areas also tend to have higher levels of nitrogen in their bark than do trees of similar size located in second-growth stands found on areas previously disturbed (Latty et al. 2003). Trees with higher bark nitrogen concentrations not only have higher beech scale populations, but may also show increased severity of beech bark disease symptoms (Latty et al. 2003).

Many organisms in addition to beech scales may colonize a tree's bark. These other colonizers commonly include flora such as lichens, algae, and fungi, and fauna such as a variety of insects. The way in which beech scales are impacted by the presence of these other organisms is very variable. For instance, presence of the common crustose lichen *Lecanora conizaeoides* on trees in southern England increases survival of scale crawlers and leads to higher scale population build-up (Houston et al. 1979a). Algae colonizing beech bark also can protect scale crawlers, inducing increased scale population levels (Wainhouse and Gate 1988). On the other hand, in Nova Scotian forests the presence of the crustose lichen Graphis scripta has a negative effect on beech scale populations, greatly depressing scale colonization of trees and decreasing subsequent population growth on those trees (Houston 1983). In England, the presence of the fungus *Ascodichaena rugosa* on beech trees has been found to prevent scale establishment and population growth; further negative effects for scales may occur due to reduced presence of the scale-benefiting *L. conizaeoides* lichen when the *A. rugosa* fungus is densely present (Butin 1977, Houston et al. 1979a). Unlike some of the microflora colonizing bark, insects on the bark of beech trees have relatively little effect on beech scale populations. There are no insects that are known to parasitize beech scales. The most common predators on beech scales are generalist beetles in the family *Coccinellidae* and a specialized fly genus in the family *Cecidomyidae*. None of these predators are usually seen when scale populations are light. On trees with moderate to heavy scale populations, the various predators may build up higher levels. While heavy predation has occasionally been observed on individual trees, the insects often have relatively little effect on scale population levels overall in beech stands (Wainhouse and Gate 1988, Mayer and Allen 1983).

Like colonizers on tree bark, a tree's genetic make-up can have either beneficial or detrimental effects on beech scale populations. Approximately 1% of beech trees in the eastern portions of Canada and the United States have been found to be resistant to beech scale and beech bark disease (Houston 1983, Houston and Houston 2000). Resistant trees typically carry lower scale densities than do surrounding, susceptible trees.

Density of scales on susceptible trees differs for sides of the tree bole facing different compass directions. Survival of colonizing scales is affected by variation in microclimatic conditions on the different sides of the bole (Ehrlich 1934, Houston et al. 1979b, Wainhouse and Gate 1988, Cohen 2002). In general, greater temperature fluctuations and increased levels of solar radiation place scales under greater environmental pressure on the south- and west-facing sides of the tree than on the north- and east-facing sides (Ehrlich 1934, Andresen et al. 2001). For those trees located at edges of stands, the sides of the boles facing open areas will have fewer scales because of the increased sunlight on these surfaces (Ehrlich 1934, Houston et al. 1979a). In Michigan, for stands with only low amounts of beech scale present or for stands containing relatively few beech trees, the north- and east-facing sides of beech boles have greater abundances of beech scale than the south- and west-facing sides of the boles (Figs. 1 and 2). In those stands where there is a high abundance of beech scale or where beech trees are very common, south- and west-facing sides of tree boles have a greater abundance of beech scale than the north- or east-facing sides (Fig. 3). The shift in directional preference of scales between stands with low and high beech scale levels is likely due to the fact that scales first tend to occur in the more moderated microclimates of the north- and east-facing sides of the bole, but as scale populations increase on these sides the bark begins to be killed and eventually a

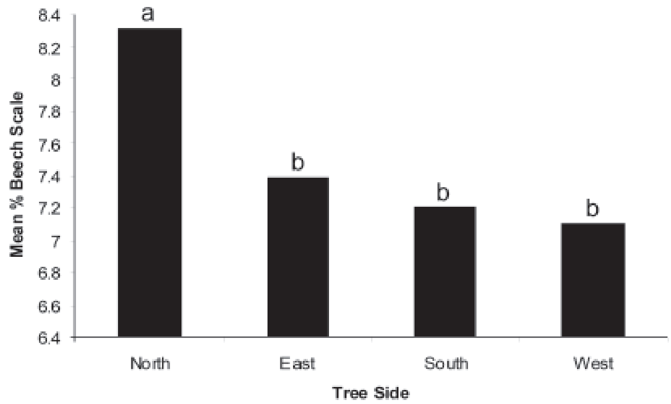

Figure 1.–Mean percent beech scale on different aspects of beech trees in low beech scale intensity stands. Different letters indicate mean values that are significantly different among tree sides.

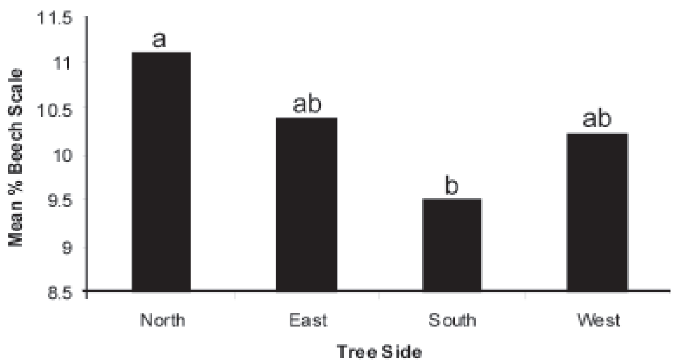

Figure 2.–Mean percent beech scale on different aspects of beech trees in low beech density stands. Different letters indicate mean values that are significantly different among tree sides.

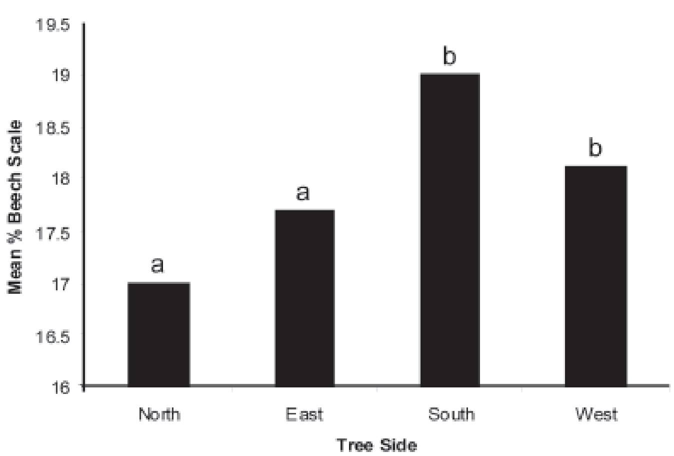

Figure 3.–Mean percent beech scale on different aspects of beech trees in high beech density stands. Different letters indicate mean values that are significantly different among tree sides.

lack of live bark on north- and east-facing sides results. Therefore, by the time scale populations are high, most insects are found on the greater area of live bark that is available on the south- and west-facing sides of the bole. The shift in directional preference of scales that is seen between stands with low and high abundances of beech trees is likely due to a similar phenomenon. When beech trees occur at low density, there also tends to be a lower abundance of beech scales present so most scales can colonize the more favorable north- and east-facing sides of the boles, but when beech trees are common so too are the scales after a time, and once again bark death will force the scales to the less favorable south- and west-facing sides of the bole over time.

Tree crown conditions can also affect beech scale populations on trees, in part due to microclimatic effects. Trees with below-normal amounts of foliage have high crown transparency ratings. Low amounts of foliage mean potentially sunnier, hotter conditions on the tree bole below. Additionally, the tree is less able to photosynthesize, possibly reducing the food quality and/or quantity available to the scales. High levels of dieback on branches in the upper and outer crown may affect scale populations for much the same reasons, although it is likely that the effects are more severe than those resulting from simply thinning foliage. As well, trees with high crown dieback may often have a much smaller area of live bark available on them, which makes them less attractive to future settlement of scale crawlers.

Disease Development and Subsequent Spread through the Ecosystem

Beech scale is always present in forest stands before beech bark disease occurs. This first stage of the problem, with only the scales present, is referred to as the advancing front (Shigo 1972). As beech scale spreads south and west across the United States from its initial point of introduction, it reaches many stands where beech bark disease has not yet occurred. In the second stage, called the killing front, beech scales build up to high populations on susceptible trees and *Nectria* fungi are present along with the scales. The first *Nectria* to infect trees is typically the native *N. galligena* that is found throughout the eastern United States on non-beech hosts. Later, the exotic *N. coccinea* var. *faginata*, which is spreading across the country in the wake of beech scale, tends to replace *N. galligena*. Together the scale and *Nectria* form the beech bark disease complex that leads to tree infection and the beginning of tree death in the stand (Shigo 1964, Houston 1994).

There are a number of factors that contribute to subsequent mortality patterns once stands enter the killing front stage. Those beech trees that are older and have larger DBH tend to be the first trees in a given stand to die of beech bark disease (Ehrlich 1934, Houston 1975, Miller-Weeks 1983, Houston 1994). Tree that are of low vigor preceding the advent of beech bark disease in an area also are understandably among the first to succumb to the disease (Mize and Lea 1979). Lack of adequate moisture during the growing season is one important type of stress that has been shown to increase susceptibility to beech bark disease (Lonsdale 1983, Lonsdale and Sherriff 1983). Other types of prior stress that lead to significant tree wounds such as broken crowns or extensive areas of decay are also contributing factors in disease development in individual trees (Mize and Lea 1979, Gavin and Peart 1993).

On the other hand, lack of association with conspecifics tends to be protective for beech trees. Trees that are found in stands with only a low beech component or trees that occur individually in areas that are fairly isolated from contiguous stands high in beech are more likely to avoid severe scale build-up and disease exposure and are therefore more likely to survive beech bark disease outbreaks that may be affecting surrounding area.

For those stands where beech scale and *Nectria* fungi do occur at high levels, the stands move over time from the killing front stage to a final stage of development referred to as the aftermath forest. In this stage, the stand is generally left with smaller-stemmed beech trees along with maples and other associates, since beech bark disease typically kills 50% of the overstory beech trees when it invades an area for the first time (McCullough et al. 2001). An additional 25% of the trees are usually infected with *Nectria* although they are not yet dead (Houston et al. 1979a). These trees are of low vigor, however, and grow slowly. Studies in Maine, where beech forests have been exposed to beech bark disease for over 60 years, have found that nearly all large diameter beech trees are dead (Miller-Weeks 1983).

Whether a given stand is likely to become infected and experience this three-stage mortality process is due to a number of factors. A key factor in determining infestation potential is the proximity of a stand to areas of local scale infestation and the spatial patterns of surrounding beech. The main stage of dispersal for the scale insect is the crawler stage, a time when the insects are very tiny and mobile before they settle on a life-long feeding spot. Whether beech stands are continuous or geographically separated and the density of beech trees throughout those stands affect how readily beech scales can spread. Approximately 99% of crawlers disperse no further than 10 m from their tree of birth, making tree and stand proximity a vital characteristic in determining movement patterns across the landscape (Wainhouse 1980). The remaining 1% of crawlers is picked up by wind and carried much larger distances. On the whole, spread in North America has been occurring at a rate of 6 –16 km per year (Houston et al. 1979a, LaChance 1983, Towers 1983). While not much is known regarding the assistance of other animals in the spread of beech scale, it is likely that mammals such as bears and squirrels, in addition to birds and other organisms, play a role in transport of scales over both short and long distances as well (Ehrlich 1934). Humans also affect infestation patterns by moving scales inadvertently on ornamental trees, logs, firewood, and vehicles (McCullough et al. 2001).

In Michigan, where the scale and disease are at their leading western population edge, patterns of spread are being recorded by a monitoring and impact analysis system set up to study this exotic complex. The monitoring system is currently composed of over 200 beech stands (Fig. 4). Information from this system, together with other field data, has been used to generate

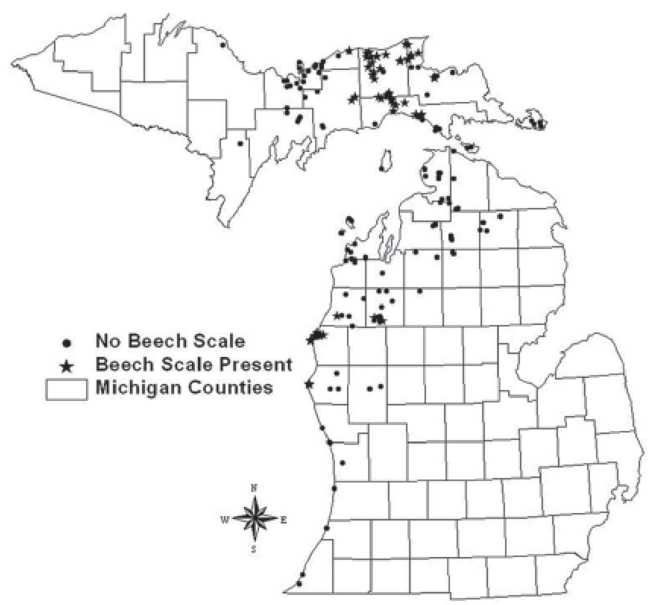

Figure 4.–Map location of plots in the Michigan Beech Bark Disease Monitoring and impact Analysis System.

figures that map changes over time in locations of the advancing front and killing front in this state (Figs. 5 and 6). These figures make readily apparent the much greater rapidity of spread for the advancing front in the Upper Peninsula at this time as compared to the Lower Peninsula. This difference is thought to be attributable to the much more contiguous nature of Upper Peninsula beech stands as compared to the highly fragmented nature of forest stands in the Lower Peninsula.

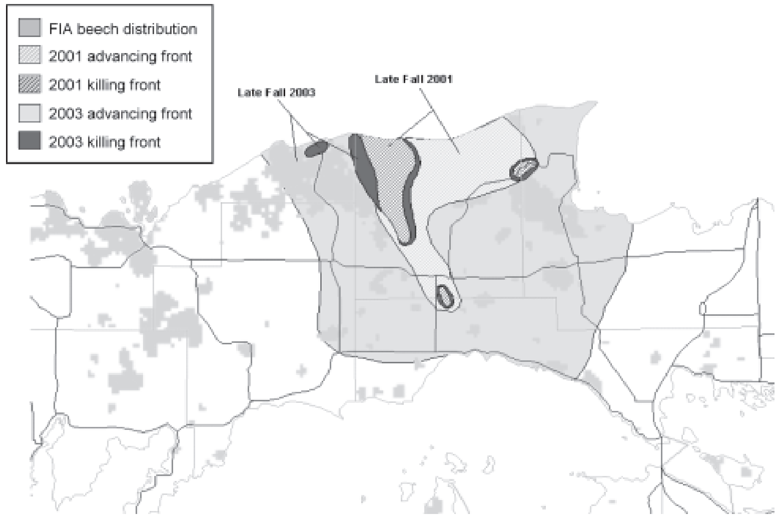

Figure 5. –Map showing beech distribution and the spread of beech bark disease in the Upper Peninsula of Michigan between 2001 and 2003.

Effects of Beech Bark Disease on Tree Health

Trees that are infected with beech bark disease score lower on a number of measures of general health than do uninfected trees on average. Individual beech trees with scale and beech bark disease have more damage present on them, such as conks, seams, cracks, open wounds, and decayed areas, than do uninfected trees (Thompson 2003). Additionally, the extent of the surface area affected by damage is greater when the trees have beech bark disease. Those trees that are infected also tend to have higher crown transparency ratings, indicative of below-normal amounts of foliage in the crown (Thompson 2003). They generally have higher levels of dieback in the upper and outer crown as well (Thompson 2003). Together, these two crown health measures indicate that trees with beech bark disease have less photosynthetic material available and are likely less able to produce the quantities of food needed to maintain normal tree health and growth.

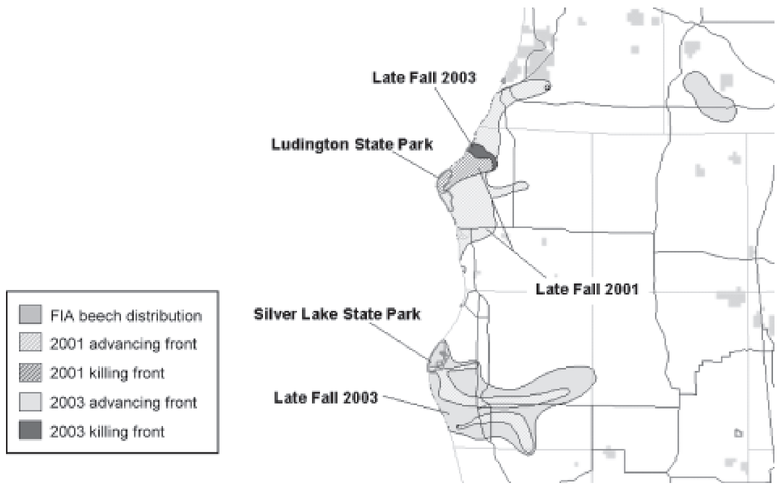

Figure 6.–Map showing beech distribution and the spread of beech bark disease in the Lower Peninsula of Michigan between 2001 and 2003.

Studies on the radial growth of beech trees in New York and New Hampshire have in fact indicated that trees infected with beech bark disease show reductions in tree growth of 20 – 40% compared to uninfected trees (Mize and Lea 1979, Gavin and Peart 1993). These reductions in growth tended to increase with increasing severity of beech bark disease. In particular, levels of internal defects, or cankers in the xylem, due to beech bark disease were most strongly correlated with growth reductions, having more predictive power in relation to growth reductions than did external defects such as raised lesions, blocky bark, fissures, or dead bark areas (Gavin and Peart 1993). Growth reductions were also found to be higher on older trees and trees located in old-growth areas—both conditions that are typically associated with higher scale populations.

Studies in Michigan have similarly found significant reductions in radial growth for trees affected by beech bark disease as compared to those trees that are disease-free (Yocum 2002) (Fig. 7). Across both the Upper and Lower Peninsulas of Michigan, the radial growth of trees infected with beech bark disease was reduced by 19%

compared to healthy trees from 1997 to 2001 (Fig. 8). In fact, just a small amount of scale coverage was enough to be significantly damaging to growth; once scale coverage on the bole was at any level above the lowest category, it made no significant difference to further growth reductions whether tree boles were covered by low or high amounts of scale (Fig. 9). These growth reductions were not attributable to site factors since the stands with and without beech bark disease in this study overlapped each other in terms of site and stand variables such as landform type, site index, and age of stand.

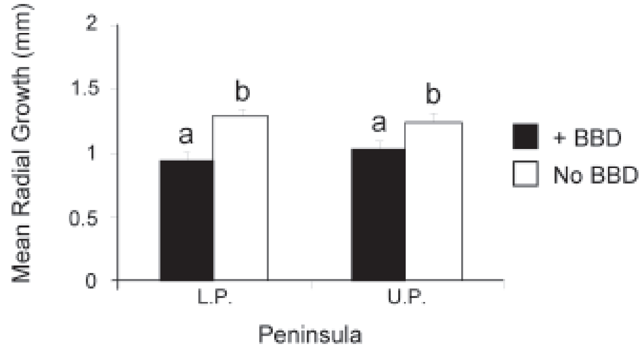

Figure 7.–Mean radial growth (mm) of beech trees in northern hardwood stands in the Lower Peninsula (L.P.) and Upper Peninsula (U.P.) of Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different among tree sides.

While beech bark disease presence and severity is very important in terms of affecting beech tree radial growth, it is well to remember that numerous other factors also play a role in affecting annual wood growth in addition. These factors include stress due to the presence of other insects or diseases, inadequate nutrient supplies or nutrient imbalances, competition, available light levels, and weather conditions during the year (Fritts 1958, Liebhold et al. 1994, Abrams et al. 1998, Tardif et al. 2001, Krasny and DiGregorio 2001, Sheppard et al. 2002). Of these additional factors, the most important in terms of affecting annual radial growth are the precipitation levels and average temperatures to which beech trees are exposed in a given year (Fritts 1958, Tardif et al. 2001). In general, wetter and warmer conditions lead to better growth, and even trees affected by beech bark disease will experience less severe growth reductions when weather conditions are favorable.

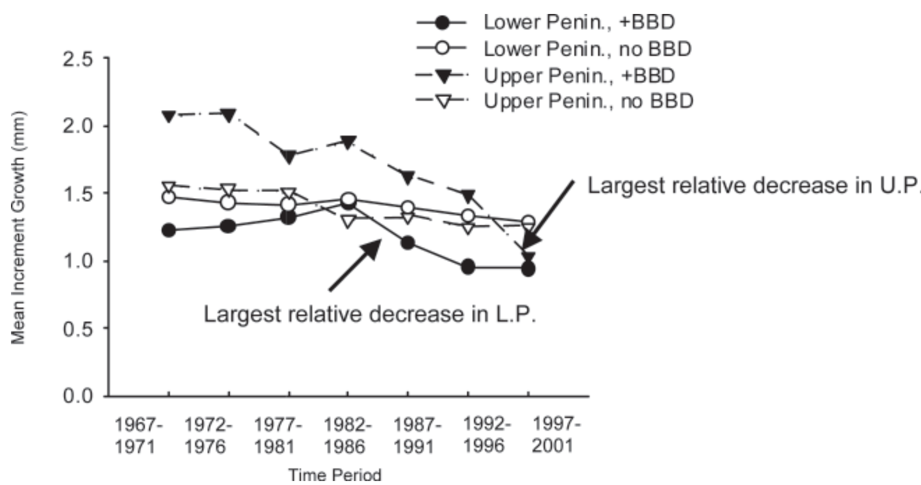

Figure 8.–Mean increment growth (mm) of beech trees in the Lower Peninsula (L.P.) and Upper Peninsula (U.P.) of Michigan with and without beech bark disease (BBD) present. Arrows point to the largest relative decrease within each Peninsula. Circles indicate northern hardwood stands in the L.P. and squares indicate northern hardwood stands in the U.P.

Knowledge Gaps

Despite the research that has been done on beech scale and beech bark disease over many years, there is still a great deal that is unknown about this exotic pest complex. On a basic level, better means of identifying and quantifying *Nectria* populations are sorely needed. Competitive and other interactions of the three *Nectria* species involved in this disease are not understood. Population dynamics of both the scale and the pathogens must be further elucidated, especially in terms of the effects of abiotic environmental factors and landscape

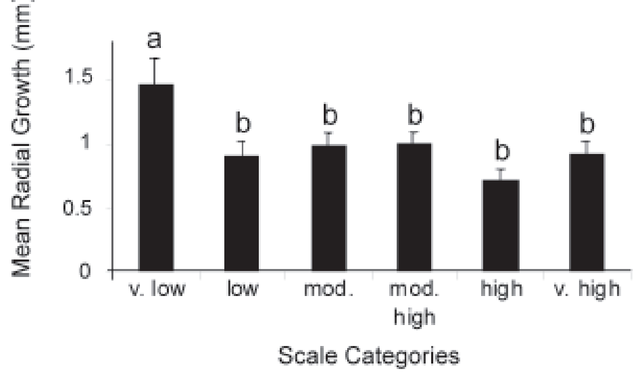

Figure 9.–Mean radial growth (mm) of beech trees in northern hardwood stands with different beech scale ratings. Bars indicate standard errors. Different letters indicate mean values that are significantly different among tree sides.

variables on these organisms. Finally, while we have begun to understand dispersal mechanisms and patterns for both the scale and *Nectria*, further work is needed in this area to clarify many issues.

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References

Abrams, M.D., Ruffner, G.M., Morgan, T.A. 1998. **Tree-ring response to drought across species and contrasting sites in the ridge and valley of central Pennsylvania.** For. Sci. 44, 550-558.

Andresen, J.A., McCullough, D.G., Potter, B.E., Koller, N., Bauer, L.S., Lusch, D.P., Ramm, C.W. 2001. **Effects of winter temperatures on gypsy moth egg masses in the Great Lakes region.** Agric. For. Meteorol. 110, 85-100.

Burns, B.S., Houston, D.R. 1987. **Managing beech bark disease: evaluating defects and reducing losses.** North. J. Appl. For. 4, 28-33.

Butin, H. 1977. **Taxonomy and morphology of *Ascodichaena rugosa* gen. et. sp. nov.** Trans. Br. Mycol. Soc. 69, 249-254.

Cohen, J.I. 2002. **Directional Effects of American Beech (*Fagus grandifolia*) Bole on the Exotic Beech Scale (*Cryptococcus fagi*).** Undergraduate honors thesis, University of Michigan, Ann Arbor, Michigan.

Ehrlich, J. 1934. **The beech bark disease, a *Nectria* disease of *Fagus*, following *Cryptococcus fagi* (Baer.).** Can. J. Res. 10, 593-692.

Fritts, H.C. 1958. **An analysis of radial growth of beech in a central Ohio forest during 1954-1958.** Ecology 39, 705-720.

Gavin, D.G., Peart, D.R. 1993. **Effect of beech bark disease on the growth of American beech (*Fagus grandifolia*).** Can. J. For. Res. 23, 1566-1575.

Hawboldt, L.S. 1944. **History of spread of beech scale, *Cryptococcus fagi* (Baerensprung), an insect introduced to the Maritime provinces.** Acadian Naturalist 1, 137-146.

Houston, D.B., Houston, D.R. 2000. **Allozyme genetic diversity among *Fagus grandifolia* trees resistant or susceptible to beech bark disease in natural populations.** Can. J. For. Res. 30, 778-789.

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

Houston, D.R. 1983. **American beech resistance to *Cryptococcus fagisuga*.** In: Houston, D., Wainhouse, D. (Eds.), Proceedings of IUFRO Beech Bark Disease Working Party Conference. USDA For. Serv. Gen. Tech. Rep. WO-37, pp. 38-42.

Houston, D.R. 1994. **Major new tree epidemics: beech bark disease.** Ann. Rev. Phytopathol. 32, 75-87.

Houston, D.R., Parker, E.J., Lonsdale, D. 1979a. **Beech bark disease: patterns of spread and development of the initiating agent *Cryptococcus fagisuga*.** Can. J. For. Res. 9, 336-344.

Houston, D.R., Parker, E.J., Perrin, R., Lang, K.J. 1979b. **Beech bark disease: a comparison of the disease in North America, Great Britain, France, and Germany.** Eur. J. For. Pathol. 9, 199-211.

Krasny, M.E., DiGregorio, L.M. 2001. **Gap dynamics in Allegheny northern hardwood forests in the presence of beech bark disease and gypsy moth disturbances.** For. Ecol. Manag. 144, 265-274.

LaChance, D. 1983. **Status of beech bark disease in the province of Quebec.** In: Houston, D., Wainhouse, D. (Eds.), Proceedings of IUFRO Beech Bark Disease Working Party Conference. USDA For. Serv. Gen. Tech. Rep. WO-37, pp. 18-20.

Latty, E.F., Canham, C.D., Marks, P.L. 2003. **Beech bark disease in northern hardwood forests: the importance of nitrogen dynamics and forest history for disease incidence.** Can. J. For. Res. 33, 257-268.

Liebhold, A.M., MacDonald, W.L., Bergdahl, D., Mastro, V.C. 1994. **Invasion by forest pests: a threat to forest ecosystems.** For. Sci. Monogr. 30, 1-49.

Lonsdale, D. 1983. **Wood and bark anatomy of young beech in relation to Cryptococcus attack.** In: Houston, D., Wainhouse, D. (Eds.), Proceedings of IUFRO Beech Bark Disease Working Party Conference. USDA For. Serv. Gen. Tech. Rep. WO-37, pp. 43-49.

Lonsdale, D., Sherriff, C. 1983. **Some aspects of the ecology of *Nectria* on beech.** In: Houston, D., Wainhouse, D. (Eds.), Proceedings of IUFRO Beech Bark Disease Working Party Conference. USDA For. Serv. Gen. Tech. Rep. WO-37, pp. 59-68.

Mayer, M., Allen, D.C. 1983. ***Chilocorus stigma* (Coleoptera: Coccinellidae) and other predators of the beech scale in central New York.** In: Houston, D., Wainhouse, D. (Eds.), Proceedings of IUFRO Beech Bark Disease Working Party Conference. USDA For. Serv. Gen. Tech. Rep. WO-37, pp. 89-98.

McCullough, D.G., Heyd, R.L., O'Brien, J.G. 2001. **Biology and management of beech bark disease.** MSU Ext. Bull. E-2746, East Lansing, MI.

Miller-Weeks, M. 1983. **Current status of beech bark disease in New England and New York.** In: Houston, D., Wainhouse, D. (Eds.), Proceedings of IUFRO Beech Bark Disease Working Party Conference. USDA For. Serv. Gen. Tech. Rep. WO-37, pp. 21-23.

Mize, C.W., 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.

Sheppard, P.R., Caslas, P., Gutierrez, E. 2002. **Relationships between ring-width variation and soil nutrient availability at the tree scale.** Tree-ring Res. 57, 105-113.

Shigo, A.L. 1964. **Organism interactions in the beech bark disease.** Phytopathology. 54, 263-269.

Shigo, A.L. 1972. **The beech bark disease today in the Northeastern United States.** J. For. 70, 286-289.

Tardif, J., Brisson, J., Bergeron, Y. 2001. **Dendroclimatic analysis of *Acer saccharum, Fagus grandifolia*, and *Tsuga canadensis* from an old-growth forest, southwestern Quebec.** Can. J. For. Res. 31, 1491-1501.

Thompson, E.M. 2003. **American Beech (*Fagus grandifolia* Ehrh.) and Northern Hardwood Forests in Michigan: Conditions With and Without Beech Bark Disease.** Master's thesis, University of Michigan, Ann Arbor, Michigan.

Towers, B. 1983. **Status of beech bark disease in Pennsylvania.** In: Houston, D., Wainhouse, D. (Eds.), Proceedings of IUFRO Beech Bark Disease Working Party Conference. USDA For. Serv. Gen. Tech. Rep. WO-37, pp. 24-26.

Wainhouse, D. 1980. **Dispersal of first instar larvae of the felted beech scale, *Cryptococcus fagisuga*.** J. Appl. Ecol. 17, 523-532.

Wainhouse, D., Gate, I.M. 1988. **The beech scale.** In: Berryman, A.A. (Ed.), Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Plenum, New York, pp. 68-82.

Wargo, P.M. 1988. **Amino nitrogen and phenolic constituents of bark of American beech, *Fagus grandifolia*, and infestation by beech scale, *Cryptococcus fagisuga*.** Eur. J. For. Pathol. 18, 279-290.

Yocum, J.L. 2002. **The Effects of Beech Bark Disease on Radial Growth of American Beech (*Fagus grandifolia*, Ehrh.) in Michigan.** Master's thesis, University of Michigan, Ann Arbor, Michigan.

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.

Contains invited papers, short contributions, abstracts, and working group summaries from the Beech Bark Disease Symposium in Saranac Lake, NY, June 16-18, 2004.

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