

INTRODUCTION

Beech bark disease (BBD) has spread across roughly half of the range of American beech (*Fagus grandifolia*) in North America since it was introduced into Nova Scotia around 1890 (Erllich 1932, 1934; Gwiazdowski and others 2006; Houston 1994). The nonindigenous beech scale insect, *Cryptococcus fagisuga* Lind., mediates BBD by piercing the outer bark of beech trees, facilitating entry of the nonindigenous fungi *Neonectria faginata*, which colonizes only *Fagus* spp., or *Neonectria ditissima* (synonymous with *N. galligena*), which occurs on a variety of hardwood species in North America and Europe (Castlebury and others 2006, Houston and O'Brien 1983). The fungi kill small patches of phloem and cambium, and as dead tissues coalesce, large branches and the trunk are girdled (Burns and Houston 1987, Ehrlich 1934). Terms used to depict the three stages of BBD include the “advancing front” where trees are infested by beech scale, the “killing front” where trees are dying from fungal infection, followed by the “aftermath forest” characterized by beech mortality, infected “cull” trees, and, often, dense thickets of beech sprouts (Houston 1994, Houston and O'Brien 1983, Shigo 1972).

Presence of BBD in Michigan was first noted in 2000 in Mason County in the northwestern Lower Peninsula and Luce County in the eastern Upper Peninsula (UP) (McCullough and others 2001, O'Brien and others 2001). As of 2003, beech scale was present in four counties in northwest Lower Michigan and five counties

in the eastern UP, but there was little evidence of beech decline or mortality related to fungal pathogens (Kearney 2006). Inventory data indicate that more than 15 million merchantable beech [>22 cm diameter at breast height (d.b.h.)] are present on forest land in Michigan (Heyd 2005, McCullough and others 2001). Resource managers, including foresters and wildlife biologists, remain concerned about potential BBD impacts, but their ability to plan and prioritize stand-level operations (e.g., harvest, presalvage, regeneration) is limited by a lack of information about BBD distribution, spread, and effects (Ostrowsky and McCormack 1986). Previous efforts to estimate BBD spread and quantify its impacts have been conducted in Eastern States, typically years after BBD establishment. Differences in topography, climate, soils, and forest attributes between the Lake States region and the Northeast could potentially affect BBD progression and impacts.

This project built on previous efforts undertaken following initial identification of BBD in Michigan. Progression of the advancing fronts in Lower and Upper Michigan were monitored from 2005 through 2009 using an adaptive sampling method to delineate distinct beech scale infestations (Schwalm 2009, Wieferich and others 2011) and iterative modeling processes to estimate spread rates of individual infestations. Results through 2009 indicated that spread rates varied considerably among years and among beech scale populations (Wieferich and others 2011) but were consistently lower than

CHAPTER 11. Beech Bark Disease in Michigan: Spread of the Advancing Front and Stand-Level Impacts (Project NC-EM-09-02)

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published estimates derived from observations in Northeastern States (Griffin and others 2003, Morin and others 2007). In 2002–03, 62 impact sites were established to collect baseline data on composition and condition of the overstory, regeneration, and coarse woody material. Sites represented three levels of beech basal area (low, moderate, and high) and three levels of beech scale infestation (absent, light, and heavy) (Kearney 2006). In 2003, beech scale was absent in 39 sites, 12 sites had light infestations, while 21 sites had moderate or heavy infestations. There was little evidence of beech decline or mortality attributable to BBD in any site in 2003.

Our primary goals in this project were to continue to monitor and delineate the advancing fronts of beech bark disease (BBD) in Lower and Upper Michigan and to assess spread rates. In addition, we resurveyed the original 62 sites to document current condition of beech and other overstory trees, species composition of regeneration, and the amount and composition of coarse woody material.

METHODS

Progression of the Advancing Front

We monitored the advancing fronts of BBD and delineated individual beech scale infestations using adaptive sampling (Thompson and Seber 1996). Sampling points were established in concentric circles 5 to 8 km from the farthest infested sites. If one or more beech were found to be infested with beech scale at a previously

uninfested point, another point was established farther out until an uninfested point was recorded. If no beech were present within 8 km of an infested site, “no beech” points were recorded to ensure the area would not be revisited, and the surveyor moved on. Each year, the uninfested points closest to infested points were revisited and the process was repeated until the infestation was surrounded by a buffer of uninfested sites (with beech). Infestations were considered to be distinct if there was ≥ 20 km of uninfested habitat between the edge of the infestation and the primary beech scale infestation or other satellites. Over time, as beech scale spread, some infestations coalesced and were subsequently considered as a single infestation.

In forested sites, a variable radius plot (determined using a prism with a basal area factor of 10) was established where beech and infested trees (if present) were concentrated, and d.b.h. was recorded by species for overstory trees (>10 cm d.b.h.). In sites with limited access and in nonforested sites (e.g., roadside trees), the first 10 beech trees encountered were measured. In all plots, beech trees were visually examined and ranked as: (1) beech scale absent; (2) trace (scattered, low-density beech scale); (3) patchy (several clumps of beech scale); or (4) whitewashed (one or more aspects of the trunk were heavily infested). Coordinates of plots were imported into ArcGIS® 10.1 (ESRI 2012), and infestations were mapped annually. Spread rates were estimated and areas of beech scale

infestations were calculated using minimum convex polygons for each distinct infestation and statewide.

Impacts of BBD to Date

The 62 sites with BBD impact plots, including 34 sites in 7 counties in Upper Michigan and 28 sites in 14 counties in Lower Michigan, were revisited in 2011–13 to assess impacts of BBD. Similar methods were used in 2002–03 and 2011–13 to assess beech scale and beech condition. The center plot and four subplots, 18.3 m from the center in each cardinal direction (all plots 7.3-m radius), were relocated, and GPS coordinates were recorded at the center plot. Species, d.b.h., and a visual estimate of beech scale abundance were recorded on trees in all five subplots. Twelve additional beech trees growing at equally spaced azimuths and within 60 m of the perimeter of the four subplots were tagged in 2002 and were also reexamined. These trees were originally selected using prioritized criteria: (1) largest tree with dead tissue or at least one canker, (2) any tree (pole-sized or larger) with a canker, (3) largest tree with *C. fagisuga* present, (4) any tree (pole-sized or larger) with *C. fagisuga*, or (5) the largest tree near the azimuth. We measured d.b.h., number of cavities and estimated crown dieback, transparency, and beech scale densities on each tree. Overstory species composition and tree and beech scale abundance were also recorded along three transects (each 25.5 m by 10 m) in the sites.

Frequency, species, size, and decay class of coarse woody material were recorded along

three transects (25.5 m by 1 m wide) in each site. Decay classes for coarse woody material (CWM) were defined as: (0) fresh material with intact bark and no obvious decay; (1) bark sloughing off or absent, but with solid inner sapwood; (2) some decay; small wood chunks break off under impact, but firm center; (3) decaying; loses form under impact; and (4) decayed and form lost (Kearney and others 2005). Regeneration plots were established equidistantly between the center plot and each of the four subplots in the cardinal directions in the sites. Seedlings (<30.5 cm tall), saplings (>30.5 cm tall; <2.5 cm d.b.h.) and recruits (>2.5 cm d.b.h.) were tallied by species within a 2.4-, 3.5-, and 7.3-m radius of the plot center, respectively.

RESULTS

Progression of the Advancing Front

From 2011 through 2013, we established a total of 544 sites (with beech) in 28 counties in Lower Michigan and 9 counties in Upper Michigan to monitor the advancing front. We examined 1,854 live beech trees in these sites; d.b.h. of these beech ranged from 4.2 to 119.5 cm and averaged 30.0 ± 0.4 cm. There were 187 sites with infested beech. On average, 86.0 ± 1.6 percent of the beech trees within infested plots had at least some beech scale. Across all sites, beech made up 53 ± 1.1 percent of the total basal area (all species), which averaged 16.8 ± 0.4 m²/ha. Along with beech, sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and northern red oak (*Quercus rubra*) dominated the overstory.

In Lower Michigan, we continued to survey four distinct beech scale infestations that were monitored from 2005 through 2009 (Wieferich and others 2011). The Mason-Wexford infestation, which encompassed 7727 km² in 2009, had expanded to 9200 km² in 2013. The Charlevoix-Crawford-Emmet infestation encompassed <3010 km² in 2011 but had expanded to 7088 km² in 2013. In addition, a relatively new infestation in Midland County occupied <2 km² when detected in 2011 but had increased to 287 km² by 2013. The most recent detection occurred early in 2014, when a small area in a nature center near Grand Rapids (Kent Co.) was found to be infested. More than 16 575 km² in Lower Michigan are now infested. Advancing fronts in Lower Michigan spread at an average rate of 3.3 ± 0.4 km/year from 2011 through 2013 and 3.1 ± 0.3 km/year from 2005 through 2013, but the rate of spread of individual infestations ranged from <2 to 14.8 km/year.

In the UP of Michigan, a single and nearly continuous beech scale infestation has been monitored since 2005. A distinct satellite population encompassing 255 km² was identified in Menominee County in 2009, more than 45 km west of the leading edge of the main front. This infestation coalesced with the primary infestation in 2011. The beech scale-infested area in the UP, estimated at 6214 km² in 2005, encompassed at least 13 530 km² in 2013. The leading edge of the infestation in the central Upper Peninsula is now ringed by no-beech points, although a few scattered areas with beech occur in the northwestern portion of the UP. Annual spread rates of the advancing front in

Upper Michigan have ranged from 6.2 ± 2.2 km/year between 2005 and 2007 to 2.0 ± 0.8 km/year between 2011 and 2013. On average, the infestation spread at 3.9 ± 0.7 km/year from 2005 through 2013.

Impacts of BBD to Date

In 2002–03, beech scale was present in 23 of the 62 sites, but by 2013, 55 sites were infested, including 44 sites that were heavily infested. Overall, 18 percent of the 1,440 beech trees examined in the 62 sites had died by 2013. There was little difference in the size of dead beech (average 34 ± 0.8 cm d.b.h.) and live beech (average 30 ± 0.4 cm d.b.h.). The killing front is progressing in Upper Michigan; 23 percent of the beech trees and 26 percent of the beech basal area in our plots are dead. In the Upper Peninsula sites that were infested with beech scale in 2002, 49 percent of the trees were dead in 2013. In contrast, in Lower Michigan, only 9 percent of the beech trees and <7 percent of the beech basal area was dead by 2013. Even in sites that had beech scale in 2002, only 8 percent of the trees had died. Canopy dieback and transparency levels were generally higher in Upper Peninsula sites (average of 12 percent and 16 percent, respectively) than in Lower Michigan sites (average of 7 and 13 percent, respectively).

We were able to find 724 of the 744 beech trees around the perimeter of the subplots that were tagged in 2002. Most trees (79 percent) were alive, 5 had died and fallen, 80 were dead but standing, and 46 had broken along the trunk (e.g., beech snap). Only 11 of the 314 beech in

Lower Michigan had died, while roughly 30 percent of the 368 beech in the Upper Peninsula were dead. In 2002, 500 of the tagged trees were not yet infested by beech scale, but by 2013, only 189 trees had not been colonized. Average d.b.h. of live and dead beech trees was 33.5 ± 1.0 cm and 23.5 ± 4.7 cm in Lower Michigan and 34.3 ± 0.8 cm and 39.5 ± 1.1 cm in the UP, respectively. Radial growth was higher for trees that were uninfested in 2003 than for trees that were already colonized by beech scale in 2003 (2.5 ± 0.2 and 1.6 ± 0.2 cm, respectively).

Coarse woody material (CWM) was encountered in every site in 2011–13, and 732 pieces were recorded. Beech made up 68 percent of the 310 fresh, identifiable pieces, and beech CWM was most abundant in heavily infested sites. Total CWM volume ranged from 7 to 312 m³/ha and averaged 74 ± 10.5 and 50 ± 8.4 m³/ha in sites in the Upper Peninsula and Lower Michigan, respectively. Beech CWM volume averaged 14.7 ± 3.2 m³/ha across all sites.

A total of 4,978 overstory trees, representing 19 species, were measured in subplots and transects in the 62 sites in 2011–13. Beech and sugar maple dominated the overstory. Other common species (from most to least dominant) included red maple, eastern hemlock (*Tsuga canadensis*), paper birch (*Betula papyrifera*), and red oak. As in 2002, regeneration was dominated by beech and maple. Beech accounted for only 11 percent of seedlings but made up 63 percent of all saplings, followed by sugar maple, which accounted for 18 percent of the saplings.

DISCUSSION

Spread rates of the advancing front of BBD in Michigan, monitored since 2005, have varied among years and among distinct beech scale infestations. Between 2005 and 2007, Schwalm (2009) reported populations spread at rates of 4.0 and 1.5 km/year in Upper and Lower Michigan, respectively. Wieferich and others (2011) monitored 12 distinct infestations and reported spread rates of individual infestations varying from 1.0 to 8.0 km/year in Lower Michigan. The highest spread rate was recorded when two originally distinct infestations coalesced and subsequently expanded at a rate of 14.3 km/year. In Upper Michigan, Wieferich and others (2011) reported the maximum spread rate of the single advancing front was 11.0 km/year. Our estimates indicate spread in the Upper Peninsula has slowed, probably because nearly the entire range of beech has been colonized. Spread rates in Lower Michigan remain highly variable, however, which may reflect the fragmented distribution of beech and forested land in general in this part of the State. We expect spread rates will slow as the advancing front reaches areas in the central and eastern Lower Peninsula where beech volume is relatively low. Recent identification of localized infestations in Midland and Kent Counties indicates long-range dispersal of beech scale continues, probably as a result of birds transporting eggs or crawlers. Uninfested beech within 15 km of beech scale infestations should be treated as high-risk sites, and BBD impacts should be considered as management plans are developed.

Effects of BBD are most pronounced in the Upper Peninsula, where the killing front continues to advance. Little beech mortality attributable to BBD was present in 2002–03 (Heyd 2005, Kearny and others 2005, McCullough and others 2001), but almost 25 percent of the beech trees we examined had been killed. In Northeastern States, 50 percent or more of the overstory beech reportedly died during the first wave of BBD (Kasson and Livingston 2012, Krasny and Whitmore 1992). This mortality rate is comparable to what we observed in our sites that were infested in 2003.

Beech thickets, which are common in many Northeastern forests, may proliferate following the relatively rapid death of previously healthy beech trees caused by BBD, increasing the abundance of susceptible beech stems (Griffin and others 2003, Hane 2003, Houston 1994). Thickets reduce light availability and survival rates of nonbeech seedlings and saplings, including sugar maple and red maple (Hane 2003, Kobe and others 1995, Twery and Patterson 1984). Although beech saplings were common, we observed a single beech thicket in only three sites in the Upper Peninsula, and none were present in Lower Michigan. In Upper Michigan, overstory composition will likely change as overstory beech die. Sugar maple was consistently abundant in our sites, and previous studies indicate canopy gaps resulting from BBD can increase radial growth and recruitment of young sugar maples into the overstory (DiGregorio and others 1999).

Beech mortality in the Upper Peninsula has resulted in an increase in snags and a pulse of coarse woody material. These changes may provide habitat for numerous birds, mammals, and salamanders (Davis 1983, Gilbert and others 1997, Kahler and Anderson 2006, Morrison and others 1986, Strojny and others 2010), although such benefits may be offset by reduced production of mast as overstory trees succumb (Hamelin 2011, Tubbs and Houston 1990). Studies in Northeastern States, for example, indicate bear reproduction is associated with abundance of beech nuts (Hamelin 2011). Our data also indicate beech scale infestation has reduced radial growth. Radial growth rates of trees that were not infested in 2003 were almost 65 percent higher than those of trees that were infested in 2003. Reduced growth of trees infested by beech scale has been similarly noted in other studies (Erlach 1934, Mencuccini and others 2005, Mize and Lea 1979).

It is not clear why beech mortality is so much greater in the Upper Peninsula sites than in Lower Michigan. Beech scale has been present in Lower Michigan for at least as long as it has been present in the Upper Peninsula, and in many of our sites, all or nearly all of the beech have been colonized by beech scale. The difference likely involves *Neonectria* sp. infection rates or virulence. Fruiting bodies have been observed more frequently in the Upper Peninsula than in Lower Michigan, while evidence of *Neonectria* remains difficult to find in Lower Michigan (O'Brien and others 2001). Further study will be needed to understand why beech mortality rates

remain relatively low in Lower Michigan despite the presence of beech scale for more than 15 years.

CONTACT INFORMATION

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LITERATURE CITED

- Burns, B.S.; Houston, D.R. 1987. Managing beech bark disease: evaluating defects and reducing loss. *Northern Journal of Applied Forestry*. 4: 28-33.
- Castlebury, L.A.; Rossman, A.Y.; Hyten, A.S. 2006. Phylogenetic relationships of *Neonectria/Cylindrocarpon* on *Fagus* in North America. *Canadian Journal of Botany*. 84: 1417-1433.
- Davis, J.W. 1983. Snags are for wildlife. *Sialia: The Quarterly Journal of the North American Bluebird Society*. 7(3): 83-90. <http://nabluebirdsociety.org/PDF/Sialia%20Bluebird%20Journals/7.3.pdf>. [Date accessed: July 2013].
- DiGregorio, L.M.; Krasny, M.E.; Fahey, T.J. 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. 1932. The occurrence in the United States of *Cryptococcus Fagi* (Baer.) Dougl., the insect factor in a menacing disease of beech. *Journal of the Arnold Arboretum*. 13: 75-80.
- Ehrlich, J. 1934. The beech bark disease: a *Nectria* disease of *Fagus*, following *Cryptococcus Fagi* (Baer.). *Canadian Journal of Forest Research*. 10: 593-690.
- ESRI. 2012. ArcGIS® 10.1. Redlands, CA: Environmental Systems Research Institute.
- Gilbert, J.H.; Wright, J.L.; Lauten, D.J.; Probst, J.R. 1997. Den and rest-site characteristics of American marten and fisher in northern Wisconsin. In: Proux, G.; Bryant, H.N.; Woodward, P.M., eds. *Martes: taxonomy, ecology, techniques, and management*. Edmonton, Alberta, Canada: Provincial Museum of Alberta: 135-145.
- Griffin, J.M.; Lovett, G.M.; Arthur, M.A.; Weathers, K.C. 2003. The distribution and severity of beech bark disease in the Catskill Mountains, N.Y. *Canadian Journal of Forest Research*. 33: 1754-1760.
- Gwiazdowski, R.A.; Van Driesche, R.G.; Desnovers, A. [and others]. 2006. Possible geographic origin of beech scale, *Cryptococcus fagisuga* (Hemiptera: Eriococcidae), an invasive pest in North America. *Biological Control*. 39: 9-18.
- Hamelin, P.L. 2011. VT ANR management guidelines for optimizing mast yields in beech mast production areas. 23 p. http://www.vtfishandwildlife.com/Library/Reports_and_Documents/Fish_and_Wildlife/VT%20ANR%20Beech%20MPA%20Guideline%203-22-2011.pdf. [Date accessed: May 6, 2013].
- Hane, E.N. 2003. Indirect effects of beech bark disease on sugar maple seedling survival. *Canadian Journal of Forest Research*. 33: 806-813.
- Heyd, R.L. 2005. Managing beech bark disease in Michigan. In: Evans, C.A.; Lucas, J.A.; Twery, M.J., eds. *Beech bark disease: proceedings of the beech bark disease symposium*. Gen. Tech. Rep. NE-331. Newtown Square, PA: U.S. Department of Agriculture Forest Service, Northeastern Research Station: 128-132.
- Houston, D.R. 1994. Major new tree disease epidemics: beech bark disease. *Annual Review of Phytopathology*. 32: 75-87.
- Houston, D.R.; O'Brien, J.T. 1983. Beech bark disease. *Forest Insect & Disease Leaflet 75*. U.S. Department of Agriculture Forest Service. <http://www.na.fs.fed.us/spfo/pubs/fidls/beechnectria/fidl-beech.htm>. [Date accessed: March 15, 2015].
- Kahler, H.A.; Anderson, J.T. 2006. Tree cavity resources for dependent cavity-using wildlife in West Virginia forests. *Northern Journal of Applied Forestry*. 23: 114-121.
- Kasson, M.T.; Livingston, W.H. 2012. Relationships among beech bark disease, climate, radial growth response and mortality of American beech in northern Maine, USA. *Forest Pathology*. 42: 199-212.
- Kearney, A. 2006. Impacts of beech bark disease on stand composition and wildlife resources in Michigan. East Lansing, MI: Michigan State University Department of Forestry. 118 p. M.S. thesis.

- Kearney, A.; McCullough, D.G.; Walters, M. 2005. Impacts of beech bark disease on wildlife resource abundance in Michigan. In: Evans, C.A.; Lucas, J.A.; Twery, M.J., eds. Beech bark disease: proceedings of the beech bark disease symposium. Gen. Tech. Rep. NE-331. Newtown Square, PA: U.S. Department of Agriculture Forest Service, Northeastern Research Station: 92-93.
- Kobe, R.K.; Pacala, S.W.; Silander, J.A., Jr.; Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*. 5: 517-532.
- Krasny, M.E.; Whitmore, M.C. 1992. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. *Canadian Journal of Forest Research*. 22: 139-143.
- McCullough, D.G.; Heyd, R.L.; O'Brien, J.G. 2001. Biology and management of beech bark disease: Michigan's newest exotic forest pest. Michigan State University Extension Bulletin E-2746. East Lansing, MI: Michigan State University. 11 p.
- Mencuccini, M.; Martínez-Vilalta, J.; Vanderklein, D. [and others]. 2005. Size-mediated ageing reduces vigour in trees. *Ecology Letters*. 8: 1183-1190.
- Mize, C.W.; Lea, R.V. 1979. The effect of the beech bark disease on the growth and survival of beech in northern hardwoods. *European Journal of Forest Pathology*. 9: 242-248.
- Morin, R.; Liebhold, A.; Tobin, P. [and others]. 2007. Spread of beech bark disease in the Eastern United States and its relationship to regional forest composition. *Canadian Journal of Forestry Research*. 37: 726-736.
- Morrison, M.L.; Dedon, M.F.; Raphael, M.G.; Yoder-Williams, M.P. 1986. Snag requirements of cavity-nesting birds: are USDA Forest Service guidelines being met? *Western Journal of Applied Forestry*. 1(2): 38-40.
- O'Brien, J.G.; Ostry, M.E.; Mielke, M.E. 2001. First report of beech bark disease in Michigan. *Plant Disease*. 69: 905.
- Ostrowsky, W.D.; McCormack, M.L. 1986. Silvicultural management of beech and the beech bark disease. *Northern Journal of Applied Forestry*. 3: 89-91.
- Schwalm, N. 2009. The beech scale (*Cryptococcus fagisuga*) in Michigan: distribution, models of spread and relation to forest and wildlife resources. East Lansing, MI: Michigan State University Department of Fisheries and Wildlife. 147 p. M.S. thesis.
- Shigo, A.L. 1972. The beech bark disease today in the Northeastern United States. *Journal of Forestry*. 70: 286-289.
- Strojny, C.A.; Hunter, M.L. 2010. Log diameter influences detection of eastern red-backed salamanders (*Plethodon cinereus*) in harvest gaps, but not in closed-canopy forest conditions. *Herpetological Conservation and Biology*. 5(1): 80-85.
- Thompson, S.K.; Seber, G.A.F. 1996. Adaptive sampling. New York: Wiley. 288 p.
- Twery, M.J.; Patterson, W.A., III. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. *Canadian Journal of Forest Research*. 14: 565-574.
- Tubbs, C.H.; Houston, D.R. 1990. American beech. In: Burns, R.M.; Honkala, B.H., tech. coords. *Silvics of North America: Vol. 2, hardwoods*. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture Forest Service: 325-332. http://www.na.fs.fed.us/pubs/silvics_manual/volume_2/fagus/grandifolia.htm. [Date accessed: March 15, 2015].
- Wieferich, D.J.; McCullough, D.G.; Hayes, D.B.; Schwalm, N.J. 2011. Distribution of American beech (*Fagus grandifolia*) and beech scale (*Cryptococcus fagisuga* Lind.) in Michigan from 2005 to 2009. *Northern Journal of Applied Forestry*. 28: 173-179.