BEECH BARK DISEASE IN MICHIGAN: DISTRIBUTION, IMPACTS and DYNAMICS

By

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ABSTRACT

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Beech bark disease (BBD), a *Neonectria* fungal disease mediated by an invasive sap-feeding beech scale insect (*Cryptococcus fagisuga* Lind.), continues to affect American beech (*Fagus grandifolia*) in North America. Beech scale was first identified in Upper and Lower Michigan in 2000. Annual monitoring indicates the rate of spread of the advancing front (beech scale infestation) from 2005 to 2012, varies among Lower Michigan populations, ranging from <1 km to 14.3 km per year. Spread rates are more consistent in Upper Michigan, ranging from 3 to 11 km per year.

In 2002, 62 long term impact sites were established in areas with low, moderate or high beech basal area and beech scale infestations ranging from absent to heavy to collect baseline data on beech condition, overstory and understory species composition and coarse woody material (CWM). Twelve beech trees per site (744 total) were also tagged for future evaluation.

In 2012, I re-visited the original 62 sites to assess impacts of BBD and determine if beech basal area, initial beech scale infestation (in 2002) or differences between Upper and Lower Michigan affected beech mortality, CWM or related variables. In Upper Michigan, up to 55.6% of beech stems and 92.4% of beech basal area have died. In Lower Michigan, however, the highest mortality recorded in a site was 38.9% and dead beech basal area did not exceed 25.6% in any site. Overall, 18.7% of the beech tagged in 2002 have died. Abundance of fresh CWM has doubled since 2002 and 68.2% of the fresh material is beech.

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INTRODUCTION

Beech bark disease (BBD), an etiological complex consisting of the nonindigenous, sap-feeding beech scale insect (*Cryptococcus fagisuga* Lind.) and cambium-killing *Neonectria* spp. fungi (Houston and O'Brien 1994, Castlebury et al. 2006), has caused widespread mortality of American beech (*Fagus grandifolia*) across its northern range in North America (Garnas 2011). *Neonectria* spp. are known to cause perennial cankers on many hardwood trees, but beech are rarely killed by the pathogen unless beech scale is present (Koch 2007).

BBD was discovered in Michigan in 2000 in areas of Luce and Mason counties in Upper and Lower Michigan, respectively. Michigan forests encompass the western range limit of beech in North America and contain 7.16 million acres of maple-beech-birch cover type (Heyd 2005). Beech is a particularly important species for wildlife, especially in late successional northern hardwood stands, where it often provides the only hard mast. Mature beech trees provide cavities and perching branches used by a wide array of birds and mammals. Forest health specialists have estimated that 50% of the 15 million large beech trees (DBH $\geq$ 9 inches) representing 1.67 billion board feet of sawtimber will likely die as the killing front moves through MI (Powell et al. 1993). This mortality represents an enormous, regionally synchronous pulse of coarse woody material (CWM) and the loss of overstory beech may affect aesthetics, productivity, regeneration, biodiversity and overall forest health. The lack of information about the distribution, spread rate of beech scale, impacts and beech scale population dynamics in Michigan limits the ability of resource managers to assess stand susceptibility and vulnerability, and to prioritize risk management operations including pre-salvage, salvage and stand regeneration activities.

My research built on previous studies established to assess change over time. Each chapter will be developed into a separate publication. Chapter One focuses on delineating the spread of beech scale, i.e., the advancing front, and represents a continuation of annual survey efforts dating back to 2005. Chapter Two presents current conditions of beech and overstory and understory species composition in 62 sites with low, moderate, and high levels of beech basal area established in 2002. In 2002, these sites had no, light or heavy beech scale infestations. In 2012, I re-visited the original 62 sites to assess impacts of BBD and determine if beech basal area, initial beech scale infestation (in 2002) or differences between Upper and Lower Michigan affected beech mortality or related variables. I also compared 2012 conditions to data recorded in 2002-03. In Chapter Three, variables related to wildlife habitat were evaluated in these same sites, including coarse woody material (CWM) and conditions of 744 individual beech trees tagged in 2002. As in Chapter Two, current conditions in 2012 were compared to baseline data recorded in 2002-03. Finally, Appendix A present methods and preliminary data acquired by annually monitoring beech scale populations on individual trees in 14 sites since 2007. Data collection and evaluation is ongoing, so the Appendix includes only a brief introduction and overview of the methods and results to date.

CHAPTER 1: PROGRESSION OF THE ADVANCING FRONT OF BEECH BARK DISEASE IN MICHIGAN

ABSTRACT

Beech scale (*Cryptococcus fagisuga* Lind.), an invasive sap-feeding insect associated with beech bark disease (BBD), has spread across roughly half of the range of American beech (*Fagus grandifolia*) in North America since it was introduced in 1890 into Nova Scotia, Canada. In 2000, beech scale was identified in Luce and Mason Counties in Upper and Lower Michigan, respectively. Since 2005, we have monitored the distribution of beech scale annually in Michigan. Beech scale spread results from dispersal of eggs or first instars by wind, birds or other animals and probably long range transport of infested logs or firewood. On average, beech scale spread rates in Upper and Lower Michigan were approximately 4 km per year and 3 km per year since 2005 to 2012, respectively. Some individual populations of beech scale have coalesced in Lower Michigan, but distribution of beech scale in Upper Michigan is nearly continuous. Diameter at breast height of uninfested and infested beech trees in recently infested sites did not differ, indicating that large trees are not necessarily colonized before smaller trees. However, heavily infested trees were significantly larger than uninfested beech or trees with lower densities of beech scale, suggesting beech scale populations build faster on larger trees.

INTRODUCTION

Beech bark disease (BBD), comprised of a nonindigenous, sap-feeding beech scale insect (*Cryptococcus fagisuga* Lind.) and a cambium-killing *Neonectria* fungus (Houston and O'Brien 1994, Castlebury et al. 2006), is an important invasive species affecting American beech (*Fagus grandifolia*) in eastern North America. American beech, a component of eastern North American northern hardwoods, is the only species representing the genus *Fagus* in North America (Fowells 1965, Kitamura and Kawano 2001). American beech and sugar maple (*Acer saccharum* Marsh.) usually dominate beech-maple forests, with a mixture of other species such as red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga canadensis*) and northern red oak (*Quercus rubrum* L.) (Tubbs and Houston 1990). American beech is used for timber and is valued for aesthetics in natural and landscape settings (Burns and Honkala 1990). Beech also is important for wildlife and provides essential food and habitat for a variety of birds and mammals (Burns and Honkala 1990).

Beech scale arrived in Nova Scotia, Canada around 1890 on nursery stock imported from Europe, but is actually native to western Asia (Gwiazdowski et al. 2006, Ehrlich 1932). BBD has spread south to North Carolina and west to Ohio and Tennessee by 1994 (Gwiazdowski et al. 2006, Houston and O'Brien 1994) and is established across much of the northern range of beech in North America (Morin 2007).

Parthenogenic beech scales can produce up to 50 eggs each, enabling populations to build rapidly (Wainhouse and Gate 1988, Ehrlich 1934). Upon hatching, first instars, called "crawlers" (Wainhouse 1980), may disperse a short distance on the tree or they may be carried by wind, birds or other wildlife to other host trees (Felt 1933, Wainhouse 1980). Scale eggs or crawlers may also be transported by humans on infested beech logs or firewood (Ehrlich 1934, Houston

1994, Morin et al. 2007). Crawlers establish in crevices, under branch stubs, patches of lichen or moss, wounds or in other irregularities on the bark, where they are sheltered from the weather (Burns and Houston 1987). Crawlers begin to feed by inserting their stylets, only 2 mm long, through the relatively thin beech bark, into the phloem. Once crawlers molt, they become immobile (Shigo 1972). Development is completed in June and females lay eggs from late summer through October (Ehlrich 1932, Shigo 1972).

Two fungi can be associated with BBD; *Neonectria faginata* and *Neonectria ditissima* (Castlebury et al. 2006). The nonindigenous *N. faginata* is a variation of the European species *Neonectria coccinea* and only colonizes the genus *Fagus*. In contrast, *N. ditissima,* synonymous with *N. galligena*, occurs on a variety of hardwood species in Europe and North America. These two fungi can be distinguished from one another based on colony pigmentation, ascospore size, and conidal size and shape (Castlebury et al. 2006). Small holes in the bark created by feeding beech scales facilitate entry of *Neonectria* spores (Ehrlich 1934, Castlebury et al. 2006). The fungus kills small patches of phloem, cambium, and sapwood (Burns and Houston 1987). As the fungus advances, small patches of dead tissue coalesce, eventually girdling large branches and the trunk (Ehrlich 1934).

Three distinct phases of BBD are used to characterize affected stands (Shigo 1972, Houston and O'Brien 1983, Houston 1994). The first phase, "the advancing front," refers to areas where trees are infested with beech scale, but are not infected with the *Neonectria* pathogen (Houston and O'Brien 1983). The next phase, referred to as the "killing front," is where *Neonectria* has colonized trees, typically killing an estimated 50% of beech trees > 25 cm DBH (Houston 1994). The third phase of BBD, known as the "aftermath forest," is characterized as stands with persisting BBD following the first wave of beech mortality. Beech scale densities typically decline because most live overstory beech are infected by *Neonectria* or have been killed (Shigo 1972, Houston 1994).

Beech scale was first discovered in Michigan in campgrounds in Luce County in Upper Michigan and Mason County in northwest Lower Michigan in 2000 (Figure 1.1). Observations by local residents, including written correspondence with state forestry personnel, indicated that both infestations were present for approximately 10 years before they were identified (O'Brien et al. 2001). Forest inventory and analyses (FIA) data showed that in 2000, 15 million merchantable beech trees (> 22 cm in diameter at breast height (DBH)) were present in Michigan (Heyd 2005). Despite the establishment of BBD, beech trees still increased in abundance by 60% on Michigan timberlands from 2005 to 2009 (Pugh et al. 2009).

Efforts to identify beech scale distribution and assess BBD impacts in Michigan began soon after the discovery of BBD in 2000. By 2003, beech scale had been detected in five counties in eastern Upper Michigan and four counties in central west Lower Michigan (Kearney 2005). In 2004, 244 sites including 191 (78.3%) sites with beech were established in Michigan (Schwalm 2009), in four counties in Upper Michigan (Alger, Schoolcraft, Luce, and Mackinac Counties) and three counties in Lower Michigan (Oceana, Mason, and Manistee Counties). Beech scale was present in a total of 43 sites (17.6%), including 9 and 34 sites in Upper and Lower Michigan, respectively.

Site establishment continued from 2005 through 2009 to monitor the spread of the advancing front. A total of 803 sites were established by 2009 with beech trees present in 696 (86.5%) sites by Wieferich et al. (2011) and Schwalm (2009) (Figure 1.2b). Beech was present in sites in eight of the 11 counties sampled in Upper Michigan and 49 of the 62 counties sampled in Lower Michigan. Sites were predominately in forested areas, but urban and agricultural landscapes were also sampled if beech trees were accessible. Spread rates between 2005 and 2009 varied substantially in different parts of Michigan, but on average, were generally slower than previous reports by Morin 2007 and Griffin et al. 2003 (Figure 1.2). Schwalm (2009) reported average spread rates from 2004 to 2006 as 4.0 and 1.5 km per year in Upper and Lower Michigan, respectively. Wieferich et al. (2011) reported maximum spread rates in Upper and Lower Michigan from 2005 to 2009 reached 11.0 and 14.3 km, respectively, although some populations did not expand between 2006 and 2009. Individual populations in Michigan rarely spread up to 8 km per year. Since the introduction of beech scale in Maine in 1929, scale has spread at a rate of 10 to 15 km per year (Griffin et al. 2003). Morin et al. (2007) compiled historical distribution data from known infestations from 1911 to 2003 as beech scale moved through northeastern North America and reported an average spread rate 14.7 ± 0.9 km per year.

My objectives were to continue to monitor the advancing front of BBD in Michigan, map the distribution of BBD and assess annual spread rates between 2005 and 2012. In addition, I determined whether large beech trees are infested before small trees in newly infested stands. This study took studies by Schwalm (2009) and Wieferich et al. (2011) one step further. The intensive stand level survey provides a high resolution evaluation of spread rates and patterns in Michigan through diffusion or establishing satellite locations, indicating aid in dispersal. Results will enable forest managers and private landowners to integrate potential impacts of BBD into surveys, regeneration and harvest plans, and consider salvage activities where appropriate.

METHODS

Beginning in 2005, locations to monitor the advancing front were selected using adaptive sampling methods (Thompson and Seber 1996). This process involved establishing sample points in concentric circles, 5 to 8 km beyond locations known to be infested. If no beech trees were found within a 5 km radius, a "no beech" point was recorded. Previously uninfested sites within eight km from infested areas were revisited the following year. If the sites had become infested, then the next closest uninfested site was reassessed. This sampling technique continued until a buffer of uninfested sites was established around the perimeter of each infestation. Beech scale populations separated from the main advancing front (Mason and Luce County fronts) by at least 20 km of uninfested habitat were considered to be satellite populations (Wieferich et al. 2011) and these were also delineated. Gaps between fronts were monitored until less than 18 km of uninfested habitat remained between them, determined by maximum dispersal by optimal wind speeds (Wainhouse and Gate 1980).

Schwalm (2009) and Wieferich et al. (2011) using maps and GPS coordinates had mapped the advancing front annually through 2009. In 2011, I continued the adaptive sampling process. I surveyed sites in Upper and Lower Michigan from May to August in 2011 and 2012.

In sites where beech trees were present, one of two types of sites was established. In a forested setting, a variable-radius plot (Panama 10 BAF) was established and a handheld GPS unit (Garmin Etrex Legend HCx) was used to record coordinates of the center plot. Plot centers were established where beech stems, particularly large beech, were most abundant and where the plot encompassed the most beech stems. On rare occasions, two additional plots were established; one was 100 m to the north or south of the center plot and a second plot was 100 m to the west or east, with plot direction determined randomly. Species and diameter at breast height (DBH) were recorded on all trees within each plot. Total basal area and basal area by species were calculated in all sites for each plot from DBH measurements. Every beech tree within each site was visually examined for beech scale. If beech scale was present, infestation levels were estimated based on abundance of wax secreted by beech scale using reference cards to ensure consistency. Beech trees were ranked as:

1) Absent, no beech scale present

2) Trace; a few spots of beech scale were present

3) Patchy; clusters of beech scale on the tree

4) Whitewashed; one or more tree trunk aspects were completely covered with beech scale

A second type of plot was established in locations with limited access and in non-forested areas, such as parks, campgrounds, and roadsides. In these areas, we measured DBH and scale abundance on six beech trees, but up to the first ten beech trees we encountered. Site coordinates were recorded using a handheld GPS unit (Garmin Etrex Legend HCx).

Coordinates were imported into ESRI® ArcGIS 10 to define and map the advancing front and satellite locations. Wieferich et al. (2011) delineated 12 distinct fronts from 2005 to 2009, including six islands, one in Upper Michigan and five in Lower Michigan. By 2009, however, five fronts in Lower Michigan had coalesced, leaving seven advancing fronts to monitor.

For each year, average spread rates and total infested area were calculated for each distinct population and statewide. Average spread rates were calculated by overlaying fifteen points, equally spaced out around the perimeter of each infestation and determining the distance between the current outer infested point and the outer infested point from the previous year. Distances were then averaged for each infestation and statewide. When two independent populations coalesced, the number of points used to calculate spread was summed to ensure accurate spread rates. For example, before infestations in Mason and Wexford Counties coalesced, each infestation was determined by 15 points. After they coalesced, the new infestation (Mason-Wexford) spread rate would be determined using 30 points. Total infested area for each infestation was calculated using the minimum convex polygon (MCP) method in the GeoSpatial Modelling Environment. A MCP represents a complete enclosure of all data points by connecting the exterior sites (Mohr 1947, Kie et al. 1996, Burgman and Fox 2003).

Statistical Analysis

Statistical analyses were performed using SAS 9.2 statistical software (SAS Institute 2003). Normality was tested for DBH classes using the Shapiro-Wilk test and residual plots (Shapiro and Wilk 1965). To determine if tree size affected beech scale establishment in newly infested sites, an ANOVA was used to compare beech scale infestation levels among DBH classes for trees in newly infested sites. Tukey's Honestly Significant Difference was used to separate results that were significant ($\alpha = 0.05$) (Tukey 1977).

RESULTS

Stand Composition

Of the 377 sites, I examined in 2011 and 2012, 89% contained beech including sites in nine counties in Upper Michigan and 28 counties in Lower Michigan (Figure 1.3). Total basal area of all species ranged from 2.3 to 43.6 m^2/ha and averaged 18.8 ± 0.4 m^2/ha. On average, beech made up 50.1 ± 1.3% of the total basal area in sites with beech (Table 1.1). Sites with beech commonly included sugar maple which was present in 57% of the sites. Red maple and red oak were also present in 28.6% and 20.2% of the beech sites, respectively. In total, 26 different species co-occurred with beech trees statewide.

A total of 1395 live beech trees were examined in 2011 and 2012. Beech DBH averaged 30.6 ± 0.5 cm, but ranged from 4.2 to 118.9 cm DBH (Table 1.1). Of the 377 sites established, 119 sites had trees infested with beech scale. In newly infested sites, on average, 82.7 ± 2.3 % of beech trees were infested. Heavily infested, whitewashed trees were significantly larger than other infested or uninfested beech trees ($F = 5.37$; df = 3, 449; $p = 0.0012$) (Table 1.1, Figure 1.4). Beech DBH averaged 30.0 ± 1.9 cm, 30.4 ± 1.2 cm, 35.7 ± 2.2 cm and 44.5 ± 2.9 cm for trees with scale infestation levels ranked as absent, trace, patchy and whitewashed, respectively.

Advancing Front in Upper Michigan

Average size of beech trees did not differ between uninfested and infested sites. However, beech basal area in Upper Michigan was slightly higher in uninfested sites than infested sites. No difference was recorded in species richness, but beech and sugar maple were found to be most abundant. Total and sugar maple basal area did not differ between uninfested and infested sites.

Spread rates of the advancing front in Upper Michigan were variable, averaging 4.2 ± 0.7 km per year from 2005 to 2012. Average annual spread has ranged from 6.2 ± 2.2 km per year in 2005 to 2006 to 2.8 ± 1.8 km per year from 2008 to 09 (Table 1.2). Since 2005,

In 2005, the single advancing front encompassed approximately 6,214 km^2 in Upper Michigan (Table 1.3, Figure 1.2a, Figure 1.5). Every year, the infested area grew, encompassing 132%, 148%, 167%, and finally 183% (11,547 km^2) more area than 2005 in 2006, 2007, 2008, and 2009, respectively (Table 1.3, Figure 1.5)(Wieferich et al. 2011). In 2009, a satellite population of beech scale was found in Vulcan in Menominee County, over 45 km southwest of the leading edge of the main population. By 2009, beech scale had spread through most of the beech dominated stands in Upper Michigan, with the exception of beech in western counties (Figure 1.2b, Figure 1.6). In 2011, the advancing front continued to expand to the west at an average rate of 3.3 ± 1.3 km per year, increasing the affected area to 12,427 km^2 (Table 1.2, Table 1.3, Figure 1.3). In 2012, the infestation expanded further to the southwest at a rate of 2.0 ± 08 km per year (Table 1.2). By the end of 2012, beech scale was present in all Upper Michigan counties with substantial levels of beech (Table 1.3, Figure 1.3, Figure 1.6). Scarce pockets of beech in western Upper Michigan remain uninfested (Figure 1.3, Figure 1.6).

Advancing Front in Lower Michigan

In 2005, beech scale infestations in Lower Michigan were limited to mostly the northwestern region, with one satellite in north central Lower Michigan, just south of the Mackinac Bridge (Figure 1.2a). Three distinct populations delineated in Mason, Wexford and in Emmet counties encompassed a total of approximately 2,667 km^2 (Table 1.2, Figure 1.2a). In 2006, another small (< 2 km^2) satellite population was discovered in Charlevoix County. Through 2012, this infestation had not expanded (Table 1.3). Another distinct satellite was discovered in Crawford County in 2009, encompassing an area of 196 km^2 (Table 1.3). The most recent infestation of beech scale was detected in Isabella County in 2010 (Figure 1.3).

Spread of infestations between 2005 and 2009 varied considerably (Table 1.2). The Emmet infestation increased 14-fold from 77 km^2 in 2005 to 1,155 km^2 in 2009, expanding at an average rate of 3.0 ± 0.8 km per year from 2005 to 2009 and a maximum spread of 14.4 km. Wexford County, expanded in area rapidly, spread at an average of 1.4 ± 0.8 km per year from 2005 to 2009 and a maximum rate of 8 km per year, increasing its initial area (51 km^2) by 390% before coalescing with the Mason front (Table 1.2 and Table 1.3). In contrast, the infestation in Mason County spread at 2.1 ± 0.3 km per year, at a maximum rate of only 3.3 km per year from

2005 to 2009, increasing its area by only 40% before coalescing with the Wexford population since 2005 (Table 1.2 and Table 1.3).

By the end of 2012, the Wexford and Mason county infestations, and the Crawford and Emmet County infestations had merged, reducing the number of distinct advancing fronts in Lower Michigan from five to three (Figure 1.5). The infested area in Mason and Wexford counties in 2012 now encompasses 8,438 km^2 (Table 1.3). The Crawford and Emmet infestations also expanded, across a total of 6,345 km^2 by 2012 (Table 1.3). The new infestation in Isabella County was delineated in 2012 and encompasses an area of 151 km^2. Throughout Lower Michigan between 2011 and 2012, the advancing front spread at an average rate of 3.3 ± 0.6, a minimum of < 2 km and a maximum rate of 12 km. From 2005 to 2012, average spread of beech scale across Lower Michigan was 2.7 ± 0.6 km per year (Table 1.2).

Beech Scale Distribution on Islands

In 2005, approximately 16 km^2 on Beaver Island were infested with beech scale and in 2006, the infestation had increased to 36 km^2, although some stands with beech remained uninfested (Table 1.3). In 2012, all beech stands across the island were infested, encompassing a total of 144.4 km^2. Both Mackinac Island and Bois Blanc Island were infested in 2006, but the combined total area was only 3 km^2. Unfortunately, these islands have not been revisited since then. Beech scale was not found on Drummond Island in 2006, but scale was present in two sites in 2008 and spread into two previously uninfested sites in 2009 (Wieferich et al. 2011). In 2012, all stands on Drummond Island with beech were infested (Table 1.3). Beech scale was not detected in 2005 or 2006, on either North or South Manitou Islands. In 2012, however, Keri

Deneau, Forest Health Specialist at Sleeping Bear Dunes National Lakeshore, reported beech scale was present throughout both islands (Table 1.3).

DISCUSSION

Three types of spread patterns have been used to describe the expansion of invasive species (Shigesada and Kawasaki 1997). Type 1 spread refers to invasive species that expand linearly with time, exemplified by muskrats (*Ondatra zibethicus*) and gypsy moth (*Lymantria dispar*). Type 2 spread depicts an initially slow start, followed by an increase to a higher linear expansion rate, generally attributed to satellite populations coalescing with the main front. Japanese beetles (*Popillia japonica*) and European starling (*Sturnus vulgaris*) are examples of Type 2 spread rates. Type 3 expansion occurs when a species increases exponentially, mimicking a convex curve (Shigesada and Kawasaki 1997). This type of expansion is depicted by cheatgrass (*downy brome*) and rice water weevil (*Lissorhoptrus oryzophilus*) (Shigesada and Kawasaki 1997). To date, the type of spread represented by beech scale, *Cryptococcus fagisuga*, has not been characterized.

Using historical data from 1911 to 2003, Morin et al. (2007) projected the spread of beech scale in North America from 2003 to 2010, using an average spread of 14.7 ± 0.9 km per year. In comparison with the actual beech scale distribution recorded in 2009 by Wieferich et al. (2011), Morin's model was relatively accurate at a large scale. The spread rate used by Morin et al. (2007) was similar to the findings of Griffin et al. (2003), who showed spread rates in the northeast United States ranged from 10 to 15 km per year. However, spread rates by Morin and Griffin were estimated using coarse data reported by a variety of studies and actual populations were not monitored annually. Their average spread rates were double than those of infestations in Michigan. My colleagues and I have closely monitored the advancing front of BBD in Michigan annually from 2005 to 2012.

To characterize the spread of beech scale, establishment of beech scale should be considered. In Lower Michigan, beech scales have dispersed long distances establishing satellite populations. Beech scale, a parthenogenic insect, is not affected by mate-finding success and is likely to establish if hosts are present. Predators of beech scale, primarily twice-stabbed lady beetles (*Chilocorus stigma*), are not known to have major effects on scale populations (Houston and O'Brien 1983, McCullough et al. 2001). At low densities, environmental stochasticity could affect persistence of low density of newly established populations (Shigesada and Kawasaki 1997). Extremely cold winter temperatures dipping under -35 °F and severe autumn rainfall are known to reduce the abundance of scale (Houston and O'Brien 1983, Houston 1994). Unlike Upper Michigan, where the advancing front exhibits a type 1 spread, with long distance dispersal, like Lower Michigan, spread of beech scale is better represented by type 2 expansion, where satellites coalesce, increasing spread.

Schwalm (2009) concluded from surveys in 2005 and 2006 that beech scale spread at 4 and 1.5 km per year in Upper and Lower Michigan, respectively. However, data collected from 2005 to 2012 showed spread of distinct scale populations in Upper Michigan have been consistent at 4 to 6 km per year, but has only slowed down in recent years, while spread in Lower Michigan were highly variable, ranging from < 1 to 14.3 km (Wieferich et al. 2011). This may reflect limited beech availability to the west of current infestation in Upper Michigan and south and east in Lower Michigan (Tubbs and Houston 1990). In some regions of Lower Michigan, spread rates were as low as < 1 km per year, particularly around Muskegon and

Charlevoix Counties. In Emmet County, however, spread reached 14.3 km (Wieferich et al. 2011).

Area occupied by beech scale infestations was estimated by MCPs. MCPs have been widely used to compare results of multiple studies and assessing change overtime (Kie et al. 1996). A limitation of MCPs, however, is that size of populations with irregular perimeters can be overestimated and uninfested areas are sometimes encompassed within a polygon (Burgman and Fox 2003). To avoid this problem, I used multiple MCPs to delineate irregular areas, eliminating sites known to be uninfested within the polygons.

Host availability appears to affect rate of spread of beech scale. In Upper Michigan, overall spread rates were generally higher than in Lower Michigan, perhaps due to the high beech volume in the eastern and central Upper Michigan (Figure 1.6). High beech volume may reflect decades of selective harvesting of maple in Upper Michigan, leaving less valuable beech. Spread rates in Upper Michigan have decreased between 2009 and 2012 compared to 2005 to 2009, probably because the population of beech scale has reached the edge of the western range of beech (Figure 1.6). In Lower Michigan, the Mason County infestation, first identified in 2000, has expanded through adjacent areas that include low to moderate levels of beech, but further spread may now be limited by areas with poorly drained soils that lack beech or only have low beech volume (Stanley et al. 2007)(Figure 1.6). In contrast, the infestations in Wexford and Emmet Counties spread relatively quickly through regions characterized by abundant beech typically on well-drained sandy soils (Figure 1.6). In Lower Michigan, the advancing front is still expanding south and east. Unlike Upper Michigan, average spread rates have recently increased in Lower Michigan, but beech volume is lower in neighboring Counties, which also may slow expansion (Figure 1.6).

Large diameter beech trees have been thought to be colonized first in newly infested sites (Fernandez and Boyer 1988). The probability of large beech trees becoming infested first may simply reflect the larger surface area to intercept dispersing crawlers compared to small trees (Fernandez and Boyer 1988). Large diameter beech trees with rough bark, abundant branch scars, cracks and fissures also make it easier for crawlers to establish and survive (Shigo 1972, McCullough et al. 2001). My data, showed no significant difference between the DBH of uninfested or infested beech in recently infested sites, but heavily infested, "whitewashed" trees were significantly larger than other uninfested trees and trees with lower scale densities. This may indicate that beech scale populations build up faster on large beech trees than on smaller beech trees, either because small trees have smooth bark or they are more resistant to scale survival (Fernandez and Boyer 1988). Although, because we surveyed using variable radius plots and a 10 baf prism, we may have underestimated the abundance of small beech trees and cannot accurately estimate what proportion of these small trees were infested early in newly infested sites. Another explanation could be that large diameter trees with tall dominant or co-dominant canopies are more likely to be infested by crawlers carried by birds or wind-borne scale crawlers than smaller trees (Ehrlich 1934, Wainhouse and Gates 1988, Houston 1994).

Information about the advancing front of BBD and its expansion from 2005 to 2012 provides forest managers and landowners the opportunity to incorporate BBD into their management strategies. Harvesting dominant and co-dominant beech trees, as proposed by Mielke et al. (1987), could perhaps reduce the spread of beech scale through the stand and into adjacent areas. Not all stands encompassed by the perimeter of the minimum convex polygons should be assumed to be infested and pockets of uninfested beech may still occur. Stands with a high beech component that are within or adjacent (< 16 km away) to the areas delineated by the polygons, however, should be considered at high risk for BBD. Distribution maps of the advancing front can be helpful when establishing guidelines for log transport during timber harvests, or salvage or for firewood cutting. Preparation for BBD arrival and annual monitoring are recommended for any states or regions with uninfested beech resource to reduce unwanted impacts from BBD.

Table 1.1: Basal area of beech and sugar maple, species richness and beech DBH in sites grouped by *Cryptococcus fagisuga* (beech scale) infestation levels surveyed in 2011 and 2012 of beech trees in Lower and Upper Michigan. Within columns, different letters (A, B, C) indicate a difference in standard error in basal area, species richness and DBH means.

	Sites					Individual beech trees			
Beech scale level	No. of sites	Mean basal area					DBH (cm)		
Lower Michigan	2011-12	Beech	Sugar maple	Total	Species richness	No. of beech	Mean	Min.	Max.
Absent[1]	191	9.3 ± 0.4 B	4.0 ± 0.4 A	19.3 ± 0.5 B	2.9 ± 0.1 B	84	32.7 ± 2.1 AB	7.2	111.1
Trace	62	9.1 ± 0.7 AB	3.6 ± 0.8 A	19.2 ± 1.0 AB	2.9 ± 0.1 B	240	30.3 ± 1.2 A	4.2	88.6
Patchy	32	9.1 ± 1.0 AB	3.4 ± 0.8 A	17.8 ± 1.3 AB	1.3 ± 0.2 A	98	35.6 ± 2.2 B	7.7	118.9
Whitewashed	19	7.6 ± 1.0 A	3.9 ± 1.0 A	16.3 ± 2.2 A	2.7 ± 0.3 B	31	43.4 ± 2.8 C	21.7	79.2
Upper Michigan									
Absent	24	7.7 ± 0.7 B	4.8 ± 0.8 A	18.5 ± 1.0 A	3.2 ± 0.2 A	6	41.2 ± 5.4 A	24.9	60.5
Trace	6	6.5 ± 0.4 A	6.9 ± 1.7 A	16.8 ± 1.7 A	3.2 ± 0.4 A	12	38.0 ± 5.4 A	11.3	69.8
Patchy	0	NA	NA	NA	NA	0	NA	NA	NA
Whitewashed	0	NA	NA	NA	NA	0	NA	NA	NA

[1] Scale infestation level recorded as absent (no beech scale), trace (a few spots of beech scale), patchy (beech scale clusters on the tree) or whitewashed (one or more tree trunk aspects completely covered with beech scale).

Table 1.2: Average (±SE) spread rates (km per year) of beech scale (*Cryptococcus fagisuga*) in infestations in Upper and Lower Michigan from 2005 to 2012.

Infestation	Year (km per year)						
Upper Michigan	2005-06	2006-07	2007-08	2008-09	2010-11	2011-12	2005-12
Menominee	---	---	---	---	---	1.1 ± 1.1	1.1 ± 1.1
Luce	6.2 ± 2.2	6.1 ± 2.6	4.9 ± 2.2	2.8 ± 1.8	3.3 ± 1.3	2.9 ± 1.2	4.4 ± 0.6
Total Upper Michigan	6.2 ± 2.2	6.1 ± 2.6	4.9 ± 2.2	2.8 ± 1.8	3.3 ± 1.3	2.0 ± 0.8	4.2 ± 0.7
Lower Michigan							
Wexford	1.2 ± 0.7	0.6 ± 0.3	0.3 ± 0.3	3.6 ± 1.6	6.0 ± 2.0[1]	4.1 ± 1.9	2.9 ± 0.8
Mason	2.5 ± 1.3	2.3 ± 1.1	1.3 ± 0.8	2.2 ± 1.2			
Charlevoix	---	---	0	0	0	0	0
Cheboygan	---	---	---	---	---	5.0 ± 2.3[2]	3.1 ± 0.8
Emmet	0.9 ± 0.7	5.1 ± 2.5	0.6 ± 0.5	2.9 ± 1.3	3.8 ± 2.0		
Crawford	---	---	---	---	2.2 ± 0.7	2.7 ± 1.1	2.5 ± 0.3
Isabella	---	---	---	---	---	2.9 ± 1.4	2.9 ± 1.4
Total Lower Michigan	1.5 ± 0.5	2.7 ± 0.9	0.7 ± 0.3	2.9 ± 0.8	4.5 ± 0.9	3.8 ± 0.8	2.7 ± 0.6
Statewide Total	2.7 ± 0.7	3.5 ± 1.0	1.8 ± 0.6	2.9 ± 0.7	4.2 ± 0.8	3.3 ± 0.6	3.1 ± 0.3

[1] Wexford and Mason beech scale infestations coalesced in 2010.

[2] Cheboygan and Emmet beech scale infestations coalesced in 2011.

Table 1.3: Area (km^2) of distinct beech scale infestations by year estimated by minimum convex polygon method. "< 2" = Insufficient points to create minimum convex polygon (MCP). "---" = indicates this was not sampled that year.

Infestation				**Year**			
Upper Michigan	2005	2006	2007	2008	2009	2011	2012
Menominee	---	---	---	---	255	12,427[2]	13,100
Luce	6,214	8,203	9,187	10,373	11,547		
Total Upper Michigan	6,214	8,203	9,187	10,373	11,802	12,427	13,100
Lower Michigan							
Wexford	51	136	144	199	6,245[1]	7,727	8,438
Mason	2,539	2,813	3,287	3,560			
Charlevoix	0	≤ 2	≤ 2	≤ 2	≤ 2	≤ 2	≤ 2
Cheboygan	0	---	---	---	≤ 2	3,007[3]	6,345[4]
Emmet	77	149	739	841	1,155		
Crawford	0	---	---	---	196	308	
Isabella	---	---	---	---	---	≤ 2	151
Total Lower Michigan	2,667	3,100	4,172	4,602	7,600	11,046	14,936
Islands							
Beaver	16	36	---	---	---	---	145
Bois Blanc	---	4	---	---	---	---	---
Drummond	---	---	---	≤ 2	12	12	48
Mackinac	---	3	---	---	---	---	---
North Manitou	0	---	---	---	---	---	22
South Manitou	0	0	---	---	---	---	21
Statewide Total	8,897	11,344	13,357	14,973	19,414	23,485	28,272

[1] Wexford and Mason beech scale infestations coalesced in 2010.

[2] Menominee and Luce beech scale infestations coalesced in 2011.

[3] Cheboygan and Emmet beech scale infestations coalesced in 2011.

[4] Cheboygan, Emmet and Crawford beech scale infestations coalesced in 2012.

Table 1.4: Number of plots sampled each year and total number of plots infested with *Cryptococcus fagisuga* from 2005-2012. Michigan island information on the lake it occurs in, if residents live on the island and the distance from mainland.

Island	No. of plots sampled	Total plots with beech scale	Lake	Residents	Distance from mainland (km)
Beaver			Michigan	Yes	24
2005	12	3			
2006	15	5			
2012	2	7			
Bois Blanc			Huron	Yes	6
2006	9	4			
Drummond			Huron	Yes	<2
2006	10	0			
2008	9	2			
2009	8	3			
2012	2	5			
Mackinac			Huron	Yes	4
2006	13	7			
N. Manitou			Michigan	No	11
2005	14	0			
2012	49	49			
S. Manitou			Michigan	No	11
2005	3	0			
2006	6	0			
2012	32	32			

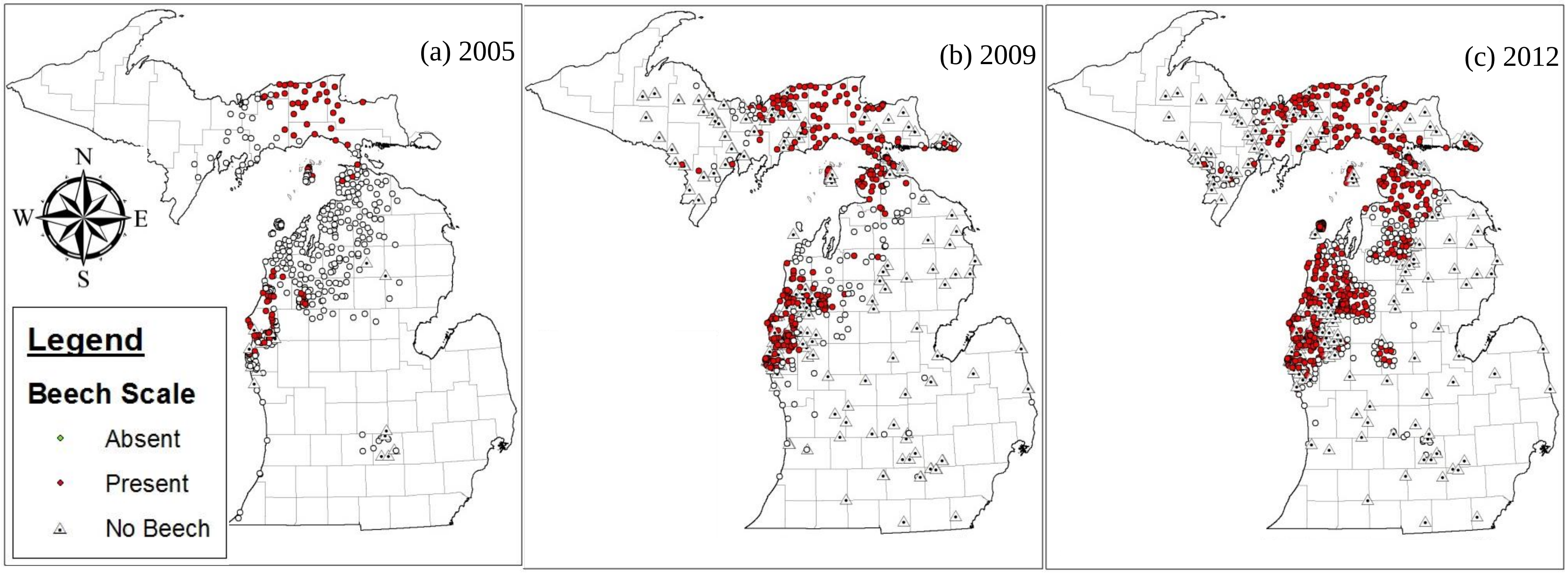

Figure 1.1: Distribution of sites with and without overstory beech trees and beech scale (*Cryptococcus fagisuga*) in (a) 2005, (b) 2009, and (c) 2012. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

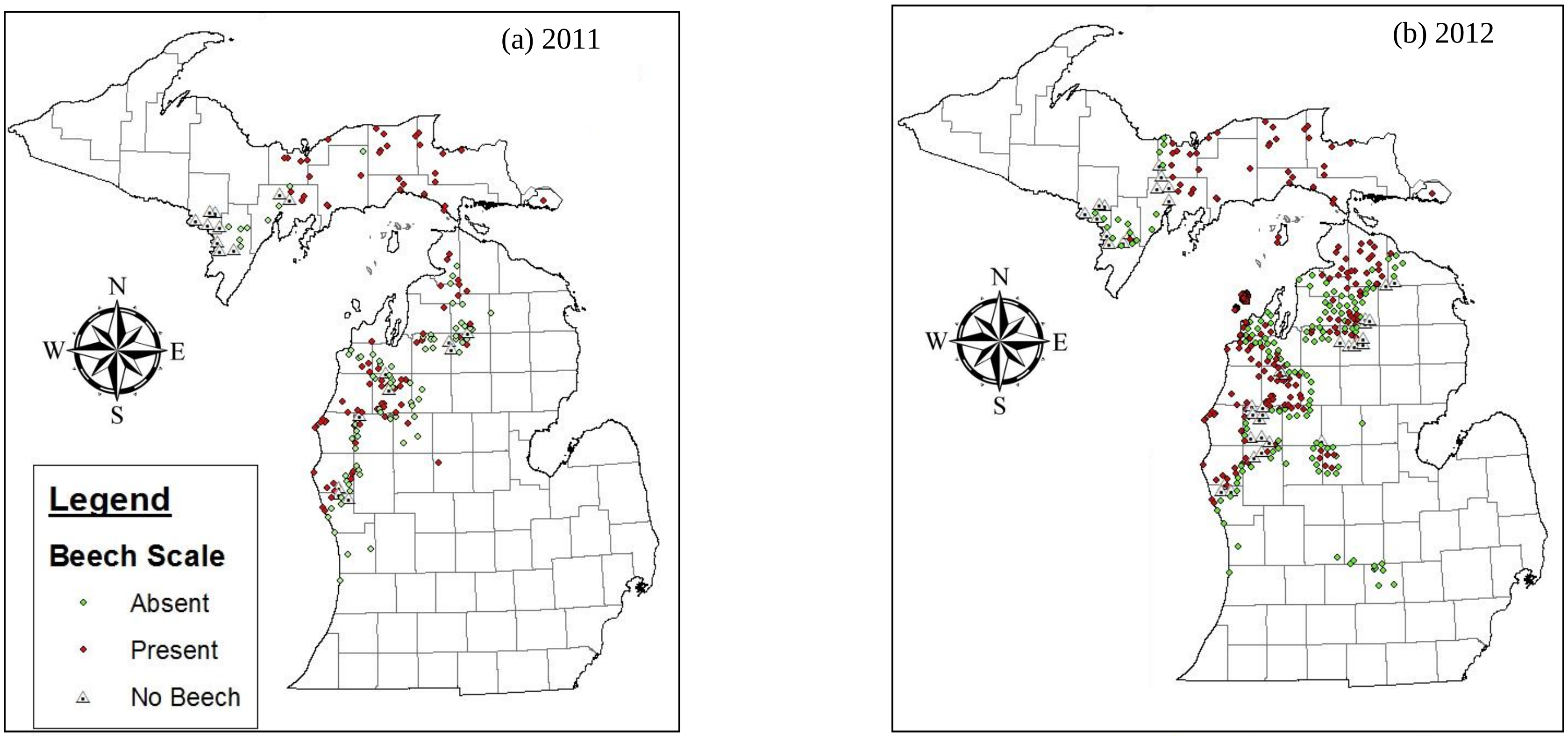

Figure 1.2: Distribution of beech scale (*Cryptococcus fagisuga*) represented as point data in sites surveyed in (a) 2011 and (b) 2012.

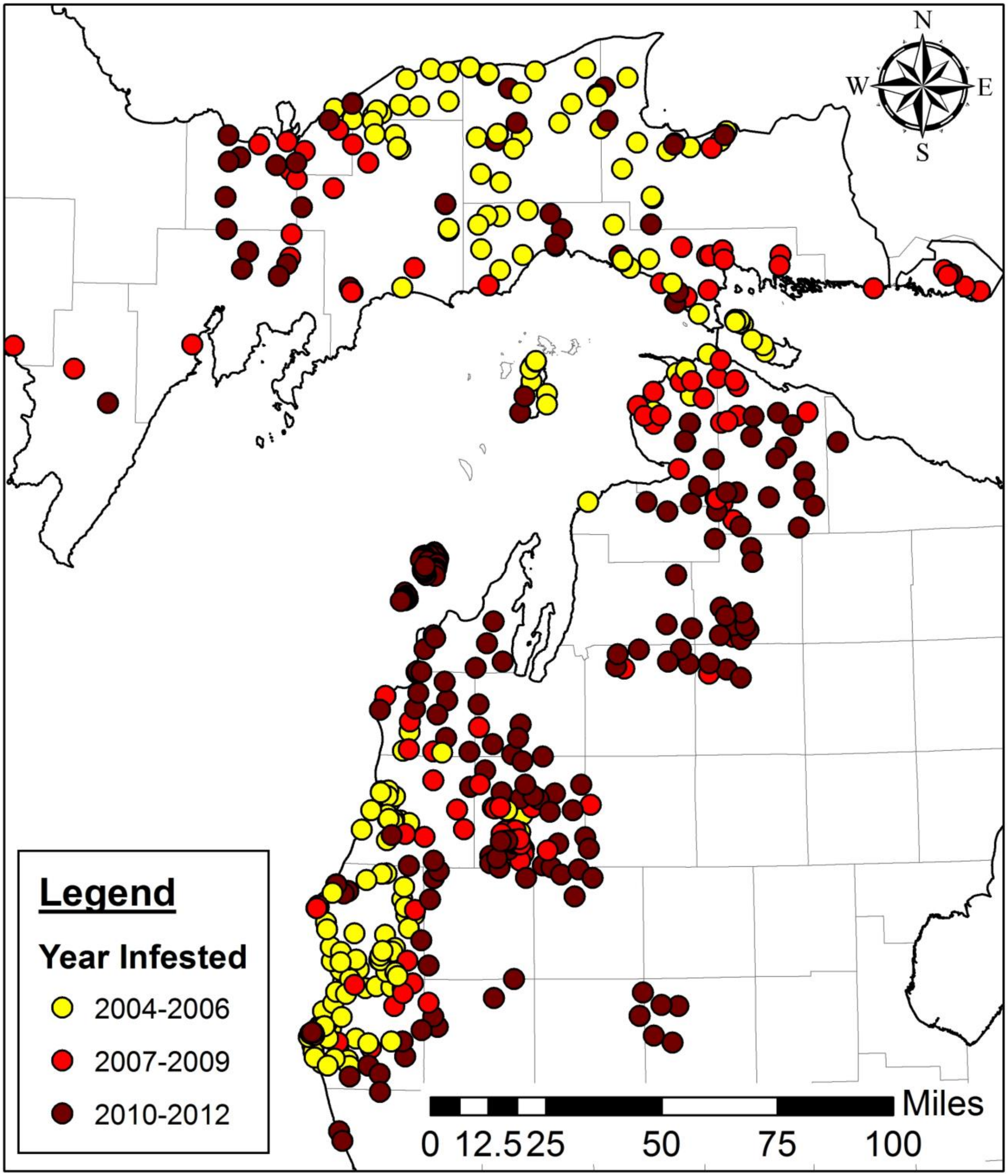

Figure 1.3: Point data showing detection of beech scale (*Cryptococcus fagisuga*) over time from 2004 to 2012.

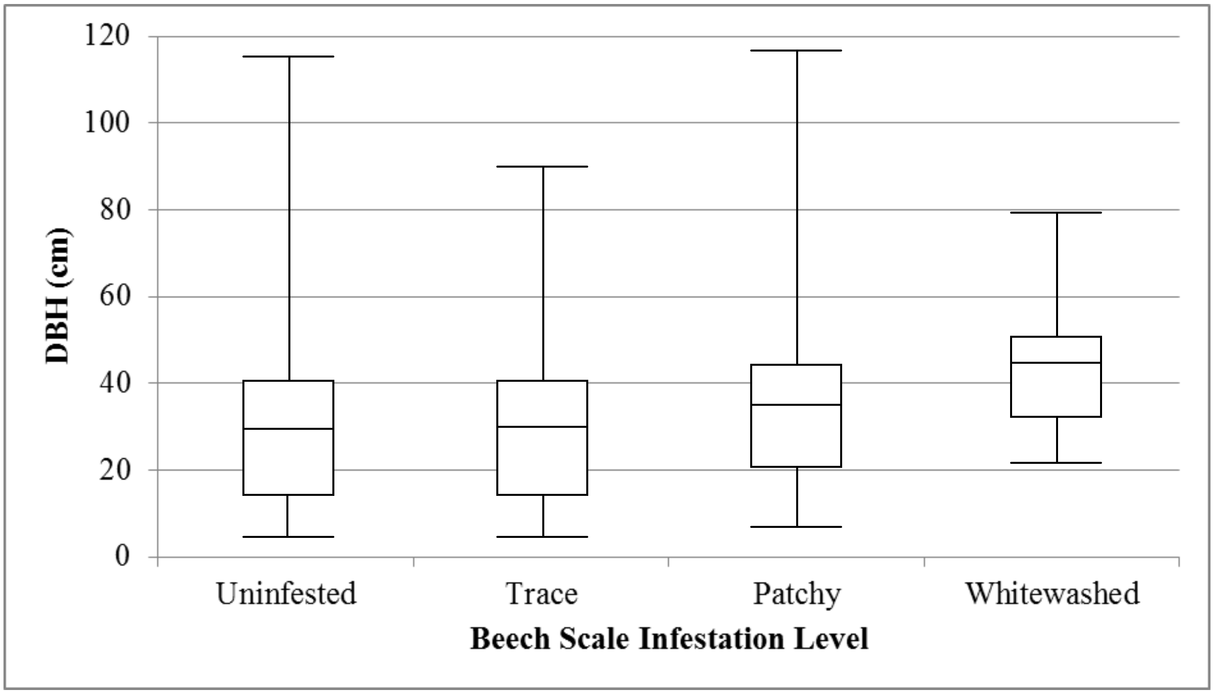

Figure 1.4: Boxplot distribution of beech DBH grouped by uninfested (no beech scale), trace (a few spots of beech scale), patchy (beech scale clusters on the tree) or whitewashed (one or more tree trunk aspects completely covered with beech scale).

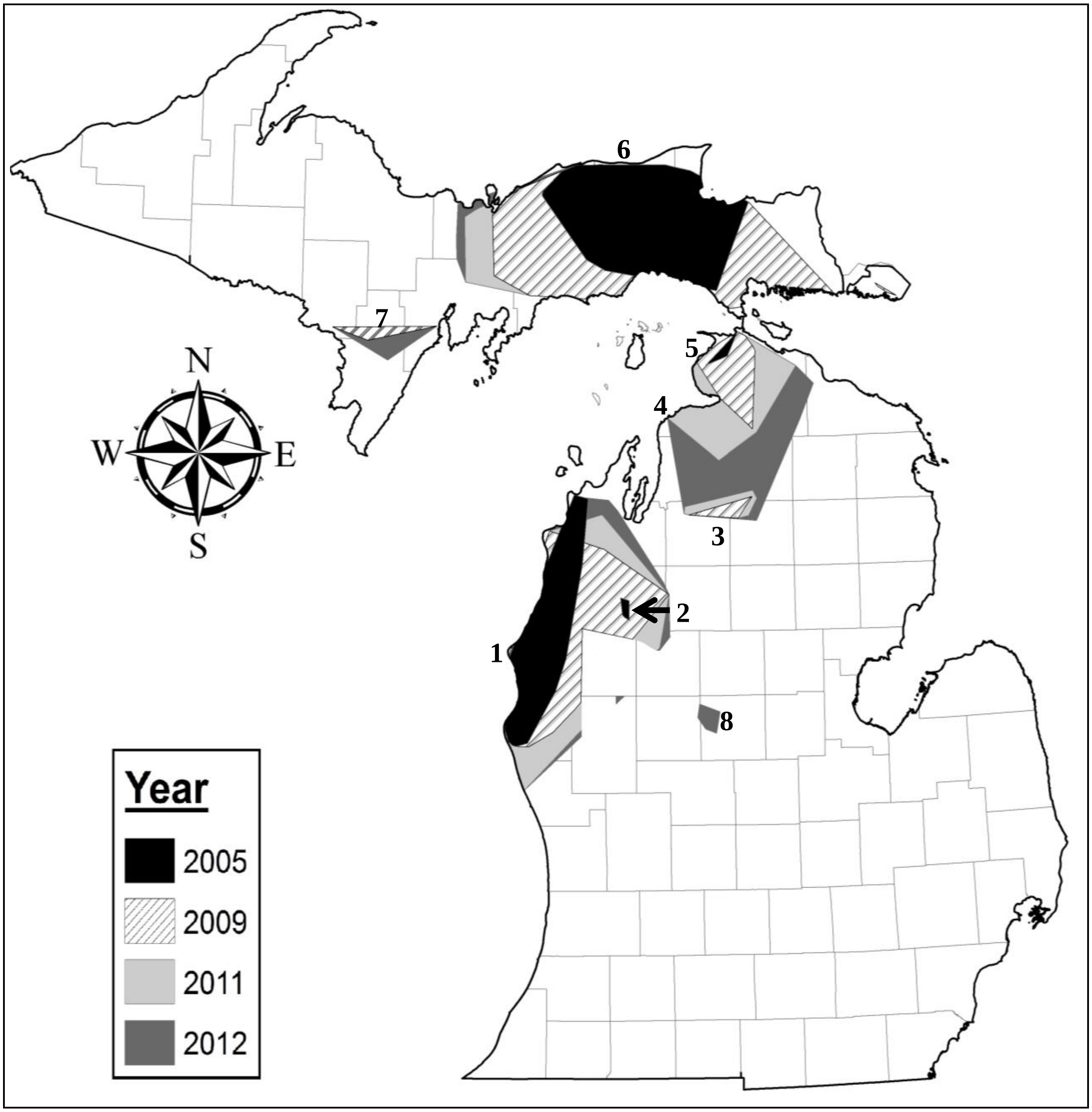

Figure 1.5: Areas with beech scale (*Cryptococcus fagisuga* Lind.) populations as delineated by minimum convex polygons in years 2005, 2009, 2011 and 2012. Numbers represent initial identifications of beech scale over 20 km from an existing advancing front (beech scale population). 1 = Mason, 2 = Wexford, 3 = Crawford, 4 = Charlevoix, 5 = Emmet, 6 = Luce, 7 = Menominee and 8 = Isabella.

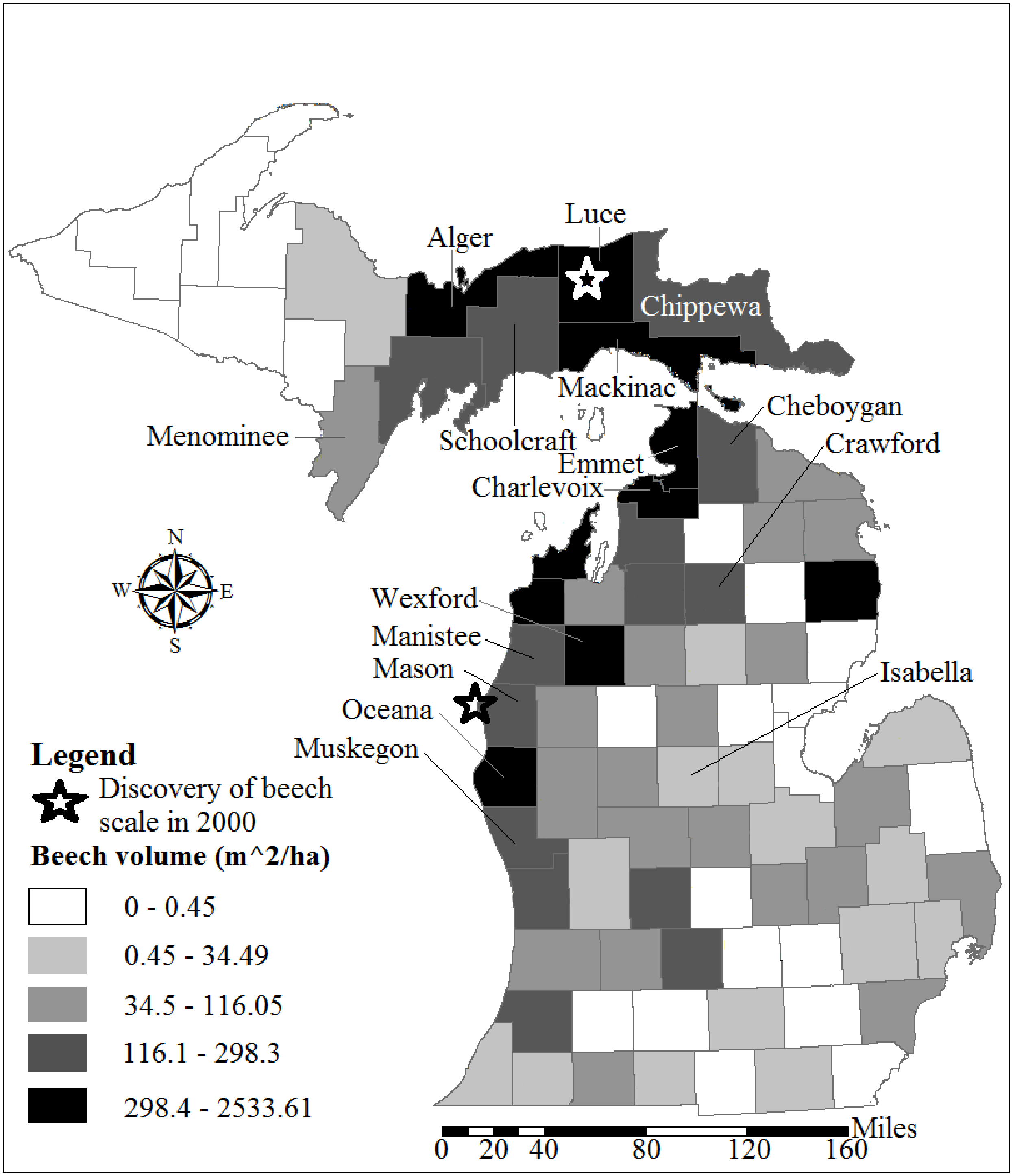

Figure 1.6: Original sites of beech scale (*Cryptococcus fagisuga*) were first identified in 2000 in Upper Michigan in Luce County and in Mason County in Lower Michigan (Indicated by star). American beech (*Fagus grandifolia*) volumes per county, separated by shades were acquired from www.fs.fed.us/ne/morgantown/4557/AFPE/

CHAPTER 2: IMPACTS OF BEECH BARK DISEASE ON OVERSTORY SPECIES COMPOSITION AND REGENERATION IN HARDWOOD FORESTS

ABSTRACT

Beech bark disease (BBD) was first identified in Michigan in 2000. In 2002, 62 sites were established to collect baseline data in and around areas with beech scale (*Cryptococcus fagisuga* Lind.) to assess overstory and understory composition. In 2012, the original 62 sites were re-visited to assess impacts of BBD among stands with different initial beech scale infestations, beech basal area and between Upper and Lower Michigan. The number of sites infested with beech scale have increased from 23 sites in 2002 to 55 sites in 2012. Differences in the proportion of beech basal area killed by BBD as of 2012 differed between Upper and Lower Michigan. In Upper and Lower Michigan, 26.0 ± 5.3% and 6.6 ± 1.7% of beech basal area was dead, respectively. In Upper Michigan sites, beech mortality in individual sites reached a maximum of 55.6% of beech stems and 92.4% of the beech basal area. Overall, in Upper Michigan, dead beech basal area has increased an average of 4-fold since 2002 and mortality rates are similar to those recorded in northeastern states with a long history of BBD. Mortality has progressed more slowly in Lower Michigan and did not differ significantly from 2002. I recorded a maximum of 33.8% dead beech stems and 25.6% of the beech basal area dead in 2012. Species composition of regeneration was similar to that recorded in 2002, except that red maple (*Acer rubrum*) regeneration increased in 12 sites that had heavy beech scale infestations in 2002.

INTRODUCTION

In the northeastern United States, northern hardwoods are an important forest cover type (Leak 1969). American beech (*Fagus grandifolia*), the only native *Fagus* species in North America, is often a major component of northern hardwood stands and can occur in 20 forest cover types (Tubbs and Houston 1990). Beech is a slow growing, deciduous tree that can live upwards of 400 years (Tubbs and Houston 1990, Heyd 2005). The native range of beech extends from southern Canada to areas of Mexico (Tubbs and Houston 1990).

American beech is monoecious and can also reproduce asexually through root suckers. Beech nuts are dispersed initially by barochory, and then secondary dispersers such as black bear, deer, rodents and birds may carry the nuts further from the seed tree (Kitamura & Kawano 2001). Mature beech trees produce mast every two to three years. Two ripe seeds will normally form in each cupule (Tubbs and Houston 1990, Kitamura & Kawano 2001). Following a successful mast, beech may produce flowers the following year that become seeds, but these seeds rarely germinate because of insufficient nutrients. As a juvenile, American beech is highly shade tolerant and able to persist for decades in the understory in shaded areas (Kitamura & Kawano 2001).

A non-indigenous, sap-feeding insect (*Cryptococcus fagisuga* Lind.) and a cambium-killing *Neonectria* spp. fungus comprise the invasive pest known as beech bark disease (BBD), which affects American beech in eastern North America (Houston and O'Brien 1994, Castle bury et al. 2006). Since arriving in Nova Scotia, Canada around 1890 on imported nursery stock, BBD has spread across much of the northern range of beech in North America (Ehrlich 1932, Houston and O'Brien 1994, Gwiazdowski et al. 2006, Morin 2007).

First instar beech scales, called crawlers, are the only mobile stage and can disperse by wind or crawling around the tree (Felt 1933, Wainhouse 1980). Birds, wildlife and human transportation of infested beech logs may also transport crawlers (Ehrlich 1934, Houston 1994, Morin et al. 2007). Once beech scales become established in a suitable location, they insert their mouthparts through the fairly thin bark on the tree trunk or branches to begin feeding. The insects molt and become immobile for the remainder of their life span (Shigo 1972, Burns and Houston 1987). As they feed, the microscopic insects secrete a waxy layer, the first visual indication of their presence (Shigo 1972). Beginning in mid-summer, each parthenogenic beech scale may lay up to 50 eggs (Ehrlich 1932, Ehrlich 1934, Shigo 1972, Wainhouse and Gate 1988).

Beech scales facilitate entry of one or both fungi associated with BBD, *Neonectria faginata* and *N. ditissima*, by creating microscopic holes in the outer bark when feeding (Ehrlich 1934, Castlebury et al. 2006). *N. faginata,* a variation of the European species *Neonectria coccinea*, only attacks the genus *Fagus*. In contrast, the native *N. ditissima,* aka *N. galligena*, infects a variety of hardwood species in Europe and North America (Castlebury et al. 2006). Both *N. faginata* and *ditissima* fungi kill small patches of cambium tissue and as they coalesce, large branches and the trunk are girdled (Ehrlich 1934).

BBD is categorized into three distinct phases known as the advancing front, the killing front and the aftermath forest (Shigo 1972, Houston and O'Brien 1983, Houston 1994). Stands with trees infested by beech scale, but not yet infected by the *Neonectria* fungi, make up the first phase of BBD, the "advancing front" (Houston and O'Brien 1983). As *Neonectria* moves into the stand, BBD progresses into the second phase the "killing front." In this phase, roughly 50% of beech trees are expected to succumb to BBD and most infected beech that survive are defective (Ostrofsky & McCormack 1986, Houston 1994). The final phase of BBD the "aftermath forest," represents the stand after the initial wave of beech mortality. *Neonectria* and beech scale usually persist, but most large beech trees are dead (Shigo 1972, Houston 1994).

Since the arrival of BBD, efforts have been made to evaluate its impacts on forests. In northern Pennsylvania, about half of the beech trees over 23 cm diameter at breast height (DBH) were lost during the first wave of BBD (Houston and O'Brien 1983, McCullough et al. 2001, Heyd 2005). Stands with BBD generally have substantial beech mortality and decline (Griffin 2003). When weakened by BBD, beech trees become susceptible to high winds and large limbs or trunks may break, a condition referred to as "beech snap" (Shigo 1972, Houston et al. 1979). A study in New York suggested that without disturbance, beech abundance in the canopy would be favored over sugar maple (*Acer saccharrum*), but when sites were disturbed, sugar maple would outcompete beech (Canham 1988, Griffin 2003). Mortality of large beech trees and beech snap act as a canopy-level disturbance, leading to competition between sub-canopy species to fill the gaps and increased radial growth on the edge of the gaps (DiGregorio et al. 1999, Griffin 2003).

In Maine, where BBD has been monitored for 50 years, three major changes in affected stands have been reported (Ostrofsky and McCormack 1986). Initial impact comes from the mortality of large diameter beech trees. Second, trees that were not heavily infested or those that were somewhat tolerant of BBD survived, but became defective trees. A few beech, < 5%, that are genetically resistant to beech scale also remain (Koch 2007). Lastly, BBD caused major changes in species composition, both in the overstory and understory. Dying and declining beech may produce root or stump sprouts, often resulting in dense, impenetrable beech thickets.

Sprouts are genetically the same as the parent, therefore, if the parent is susceptible to beech scale, so are all sprouts (Ostrofsky and McCormack 1986).

The native range of American beech in North America extends west into Michigan and northeast Wisconsin. In Michigan, there are 7.16 million acres of maple-beech-birch forest type, encompassing approximately 1.67 billion board feet of beech timber (Powell et al. 1993, Heyd 2005). Roughly 138 million beech trees, including over 15 million beech trees greater than 23 cm DBH and 0.9 million larger than 53 cm DBH, occur in Michigan forests.

Beech scale was first identified in Luce and Mason County in Michigan in 2000 (McCullough et al. 2001) (Figure 2.1). In Upper Michigan, beech scale has spread west across most of the range of beech and in 2009 was found in northeastern Wisconsin (Schwalm 2009, Wieferich et al. 2011). In Lower Michigan, the range of beech scale has expanded and now encompasses the majority of beech in the northwest (Wieferich et al. 2011). To date, however, relatively little is known about BBD and its impacts in forests in the Great Lakes Region.

In 2002-03, 62 sites were established and sampled by Amy Kearney, then a graduate student at Michigan State University (MSU), to collect baseline data on overstory and understory composition in Michigan (Figure 2.1). Kearney focused her assessments around the newly identified beech scale populations in Mason and Luce Counties. Sites were selected to represent three levels of beech basal area (low, moderate, and high) and three levels of beech scale infestation (absent, light, and heavy). In 2003, there was no evidence of any beech scale infestation in 63% of Kearney's sites (39 sites), while trees in 11 of the remaining 23 sites had heavy infestations of beech scale. There was little evidence of beech mortality attributable to BBD in any of the plots in 2003 (Kearney 2005). Kearney reported live beech basal area ranged from 1.4 to 39.0 m^2 per ha in the 62 sites.

Given the well-documented conditions in 2002-03, we now have a unique opportunity to assess BBD impacts over a ten year period. My objectives were to reassess the overstory and understory composition in the same 62 sites and determined whether BBD impacts varied among sites with low, moderate, and high beech basal area and among sites where beech scale was absent, light and heavy in 2002. I quantified frequency, abundance, basal area and canopy condition of species in the overstory and tally abundance of stems in the understory by species. Overstory and understory composition in 2012 were then compared to records from 2002.

METHODS

Site Establishment

We located and re-visited the original 62 sites established in 2002-03 in Upper and Lower Michigan in 2011-12 (Figure 2.1). Thirty-four sites were established in Upper Michigan in seven counties and 28 sites were established in Lower Michigan in 14 counties. Of the 21 counties sampled in 2002, 23 sites in five counties were infested with beech scale (Chippewa, Manistee, Mason, Luce, and Oceana). Within these 62 stands in 2002, sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*) and red oak (*Quercus rubra*) were common. Basswood (*Tilia americana*), ash (*Fraxinus* sp.), black cherry (*Prunus serotina*), ironwood (*Ostrya virginiana*), birch (*Betula* sp.) and aspen (*Populus* sp.) were also present, but not as abundant.

In 2002, Kearney selected 62 stands based on two factors; beech basal area and beech scale infestation levels. Sites were grouped into three basal area classes including low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha), based on data provided by Michigan

Department of Natural Resources (MI-DNR). Beech scale density per tree was visually estimated based on the maximum percentage of one aspect of the trunk covered by white wax secreted by the scales. Trees were assigned to one of the following categories: absent (no wax present), light (<10% wax coverage), or heavy (>10% wax coverage). Sites were then grouped based on percentage of infested trees within the stands and placed into one of the three following groups: absent (no infested trees), light (less than 50% of beech trees with scale), or heavy (greater than 50% of beech trees infested). In addition to these criteria, Kearney selected stands that had not been harvested since 1998.

Overstory Composition

Within each stand, five circular plots were established, including a center plot (7.3 m radius) and four plots of equal size, located 18.3 m away from the center plot in each cardinal direction (Figure 2.2). The center of each plot was marked with a buried metal turf stake and geographic positioning coordinates were recorded at each plot center. I recorded DBH, species and scale densities on tagged trees in each plot.

I also assessed overstory species composition in three transects, each 25.5 m long and ten m wide (Figure 2.2). The northern two transects established by Kearney in 2002 ran perpendicular to each other. To more thoroughly sample trees within each site, I added a third transect which ran south from the center of the southern plot (Figure 2.2). All live trees (> 12.5 cm DBH) and snags (> 12.5 cm DBH and > 2 m high) in each transect were tallied by species, and DBH and canopy dieback were recorded. Basal area per ha was calculated for each species using the sum of DBH measurements from plots and transects. Crown dieback was measured for all trees using five percent classes following guidelines developed by the USDA Forest Service, Forest Health Monitoring System (USDA For. Serv. 2007). I used a foliage transparency card when estimating canopy dieback to ensure readings were consistent. Dieback recorded for individual trees was then averaged by species for each site and standardized per ha. Beech scale presence and density, and evidence of fungal infection (e.g. fruiting bodies) were recorded for beech trees in each transect. Following the methods described by Wieferich et al. (2011), I recorded scale density as;

1) Absent, no beech scale present

2) Trace; a few spots of beech scale were present

3) Patchy; clusters of beech scale on the tree

4) Whitewashed; one or more tree trunk aspects were completely covered with beech scale

We also recorded the height of snags (dead trees) using a clinometer.

Frequency, abundance and basal area data from transects were pooled per site then used to calculate relative importance values. Relative importance values represent the contribution of a given species to the overstory and are calculated as the sum of relative frequency (number of transects containing the species as a percentage of the total number of occurrences for all species within all transects), relative density (number of stems of the species as a percentage of the total number of stems of all species) and relative dominance (total basal area of the species as a percentage of the total basal area for all species) (Kent and Coker 1992).

Regeneration

Four regeneration plots were established equidistantly between the center plot and the four plots in each cardinal direction to minimize effects of trampling (Figure 2.2). Within each regeneration plot, we tallied seedlings by species (< 30.5 cm tall) within a 2.4 m radius, saplings (> 30.5 cm tall; <2.5 cm DBH) within a 3.5 m radius and recruits (2.5 to 12.5 cm DBH) within a 7.3 m radius.

Statistical Analysis

Statistical analyses were performed using SAS 9.2 statistical software (SAS Institute 2003). Basal area and number of stems were summed by site, then standardized per ha. Normality was tested for all variables using the Shapiro-Wilk test and residual plots (Shapiro and Wilk 1965). A three way ANOVA was used to determine if beech basal area, initial beech scale infestation level or differences between sites in Upper and Lower Michigan influenced current number of stems of beech and maple in the overstory, the current basal area of overstory beech and maple, and canopy condition of beech. To determine if beech basal area, initial beech scale infestation level or differences between Upper and Lower Michigan affected current conditions of overstory stems and basal area of beech and maple and understory stems of beech and maple, I compared them to conditions in 2002 using an ANCOVA. To ensure that significant differences were not based on the variability of the southern transect that was not sampled in 2002, data from the southern transect was not used in the ANCOVA analysis. Tukey's Honestly Significant Difference was used to separate differences when ANOVA or ANCOVA results were significant ($\alpha = 0.05$) (Tukey 1977).

RESULTS

Since 2003, beech scale representing the advancing front of BBD, has spread to encompass most of the original 62 sites. In 2003, beech scale was present in only 23 of the 62 sites, including 14 sites in Upper Michigan and nine in Lower Michigan. Twelve sites had light infestations and 11 were heavily infested (Figure 2.3). In 2012, beech scale was present in 55 of the 62 sites, including 33 of the 34 sites in Upper Michigan and 22 of the 28 sites in Lower Michigan (Table 2.1, Figure 2.3). Overall, 26 sites in Upper Michigan and 18 sites in Lower Michigan are now heavily infested.

Overstory Beech Condition

Overall, the 1,440 beech trees encountered in the 62 sites in 2012, 256 beech (17.8%) were dead. Beech trees ranged from 3 to 71 per site with an average of 23 ± 2 beech per site. Relative importance values indicate beech was second only to the more dominate sugar maple in the overstory (Table 2.2). On average, 15.5 ± 2.7% of beech stems per site were dead (Figure 2.4). Overall, 207 of the 896 beech trees (23.1%) examined in Upper Michigan were dead, compared to 50 of the 544 beech trees (9.2%) examined in Lower Michigan. Mortality of beech stems was affected by beech basal area ($F = 10.58$; $df = 2, 45$; $p = 0.0002$), initial scale infestation level ($F = 17.74$; $df = 2, 45$; $p < 0.0001$) and differences between Upper and Lower Michigan ($F = 18.84$; $df = 1, 45$; $p < 0.0001$) (Table 2.3). Mortality of beech stems was higher in areas with high beech basal area than in low beech basal area. In sites with low or heavy beech scale infestations in 2002 mortality of beech stems were greater than uninfested sites. Upper Michigan sites also had higher beech stem mortality than Lower Michigan sites. Interactions between Upper and Lower Michigan and initial scale infestation levels were significant ($F = 8.37$; $df = 2, 45$; $p = 0.0008$). Mortality of beech stems was highest in Upper Michigan sites that were infested in 2002 and lowest in Lower Michigan sites that were uninfested in 2002. Interactions between initial scale infestation level and beech basal area were also significant ($F = 4.13$; $df = 4, 45$; $p = 0.0062$). Mortality of beech stems in infested sites with beech scale in 2002, beech basal area was greatest. Uninfested sites in 2002 that had low beech basal area had the lowest beech stem mortality.

Average DBH of dead beech across all sites was 33.7 ± 0.8 cm, ranging from 12.2 to 79.3 cm. Living beech averaged 29.6 ± 0.4 cm DBH and ranged from 11.1 to 82.9 cm. Beech basal area ranged from 1.0 to 35.4 m^2/ha in the 62 sites and averaged, 21.3 ± 1.1% of the beech basal area was dead. In Upper Michigan, 26.0 ± 5.3% of the total beech basal area was dead (Figure 2.5); in one site, 92.4% of the beech basal area was dead. Total dead beech basal area in Upper Michigan exceeded 50% in nine of the 34 sites in four counties (Chippewa, Luce, Mackinaw and Schoolcraft Counties). In contrast, only 6.6 ± 1.7% of beech basal area was dead in Lower Michigan; mortality was highest in Ludington State Park, Mason County, where 25.6% of the trees died.

Basal area of dead beech differed among sites classed as low, moderate, and high beech basal areas ($F = 7.28$; $df = 2, 45$; $p = 0.0018$), initial scale infestation levels ($F = 11.84$; $df = 2, 45$; $p < 0.0001$) and between Lower and Upper Michigan ($F = 11.55$; $df = 1, 45$; $p = 0.0014$) (Table 2.3, Figure 2.5). Dead beech basal area was significantly higher in sites with high beech basal area, in sites that were heavily infested in 2002 and sites in Upper Michigan than in sites with low beech basal area, sites where beech scale was light or absent in 2002 or sites in Lower Michigan. On average, the proportion of beech basal area that was dead was 12.2%, 23.1%, and 26.5% in low, moderate, and high beech basal area, respectively. Interactions between initial scale infestation levels and Upper and Lower Michigan were significant ($F = 4.23$; $df = 2, 45$; $p < 0.0207$). Upper Michigan sites that were heavily infested with beech scale in 2002 had more dead beech basal area than uninfested sites in Lower Michigan. Interactions between initial scale infestation level and beech basal area were also significant ($F = 3.32$; $df = 2, 45$; $p < 0.0183$). Sites with high beech basal area and heavy beech scale infestations in 2002 had more dead beech basal area sites with low beech basal area that were uninfested in 2002.

Crown condition of live beech trees was assessed in each site. Canopy dieback was generally low, averaging 9.1 ± 1.1% across all sites, but varied from 0 to 95% per tree. More canopy dieback was recorded in sites with high beech basal area than in sites with low beech basal area ($F = 5.00$; df = 2, 1042; $p = 0.0069$). Sites with heavy initial scale infestations in 2002 had higher canopy dieback than sites that were uninfested in 2002 ($F = 6.25$; df = 2, 1042; $p < 0.002$). Average dieback in Upper Michigan sites had more dieback than Lower Michigan ($F = 9.55$; df = 1, 1042; $p = 0.0021$).

Overstory Composition

A total of 4,978 trees > 12.5 cm DBH were recorded in plots and transects, representing 19 species. Overstory species richness averaged 4.6 ± 0.2 species across all sites. DBH of all species averaged 30.0 ± 0.6 cm ranging from 10.6 to 94.2 cm. Sugar maple, the most important species in these stands based on relative importance values, was present in 49 of the 62 stands (Table 2.2). Sugar maple basal area ranged from 0.7 to 33.3 m^2/ha except for one site with 51.2 m^2/ha, an almost pure sugar maple stand. Sugar maple basal area was greater in sites in Upper Michigan than Lower Michigan ($F = 7.16$; df = 1, 56; $p<0.0098$), but less abundant in stands that had heavy beech scale infestations in 2002 than stands with light or no beech scale infestations ($F = 12.26$; df = 2, 56; $p < 0.0001$). The next most common species, red maple, was present in 38 sites, with basal area ranging from 0.3 to 24.0 m^2/ha, except for one virtually pure red maple stand with a basal area of 51.0 m^2/ha. Red maple basal area was not affected by beech basal area, 2002 scale infestation or differences between Upper and Lower Michigan. Other species present in 10 to 20 sites (from most to least dominant) were eastern hemlock, paper birch, red oak, black cherry, yellow birch, ironwood, aspen and white ash.

Canopy dieback of all species averaged 9.9 ± 0.6% across all sites, with a range of 0 to 95%. Sugar maple dieback ranged from 0 to 60% and averaged 3.7 ± 0.2%. Dieback in red maple averaged 6.6 ± 0.5%, ranging from 0 to 80%. Sugar or red maple dieback was not affected by beech basal area, 2002 scale infestation or differences between Upper and Lower Michigan.

Of the 4,978 trees surveyed, nine percent (248 trees) were dead. In addition to beech, birch, sugar maple and red maple trees and occasionally red oak, black cherry, white pine, hemlock, aspen and basswood snags were also recorded. Size of dead trees ranged from 13.2 to 112.1 cm DBH, averaging 31.4 ± 0.9 cm DBH. Average density of snags in the 62 sites was 51.8 ± 6.0 per ha representing an average basal area of 4.8 ± 0.9 m^2/ha. Dead trees averaged 8.1 ± 0.2 m in height, with some reaching 20 m high.

Change in Overstory Since 2002

Average basal area of live beech declined from 30.6 ± 3.1% in 2002 to 23.9 ± 2.4% in 2012 across all sites. In 2002, 7.4% of beech stems in the 62 sites were dead, including 5.4% of beech stems in Upper Michigan and 10.8% beech stems in Lower Michigan (Figure 2.5). On average, beech mortality has doubled since 2002 and is especially high in eastern Upper Michigan (Figure 2.5), where the killing front is advancing. Beech mortality in Lower Michigan did not differ between 2002 and 2012, while in Upper Michigan, beech mortality has increased three fold. In the 14 Upper Michigan stands that were infested with beech scale in 2002, 49.4% of beech trees are now dead. In contrast, only 8.5% of beech trees are dead in the nine previously infested stands in Lower Michigan. Upper Michigan had significantly more beech mortality in terms of stems ($F = 14.48$; df = 1, 35; $p = 0.0005$) and basal area ($F = 13.01$; df = 1, 35; $p = 0.001$) than Lower Michigan. Sites infested with beech scale in 2002 had significantly higher beech mortality in stems ($F = 14.78$; df = 2, 35; $p < 0.0001$) and basal area($F = 13.51$; df = 2, 35; $p < 0.0001$) in 2012 than originally uninfested sites ($F = 5.42$; df = 22, 38; $p < 0.0001$). Interactions for both beech stems ($F = 5.39$; df = 2, 35; $p = 0.0091$) and beech basal area ($F = 4.50$; df = 2, 35; $p = 0.018$) mortality were significant; beech mortality was highest in Upper Michigan sites with heavy initial beech scale infestation and lowest in Lower Michigan sites that were uninfested in 2002.

Abundance of sugar maple stems has significantly increased since 2002 ($F = 14.39$; df = 2, 34; $p < 0.0001$) in sites that had no or light initial beech scale infestation levels. Red maple has also increased from an average basal area of 8.4 ± 1.8% in 2002 to 15.3 ± 2.7% in 2012 across all sites. Number of red maple stems has significantly increased in sites infested in 2002 ($F = 9.79$; df = 2, 35; $p = 0.0004$) and have increased more in stands with high beech basal area than stands with low beech basal area ($F = 6.17$; df = 2, 35; $p = 0.0051$).

Regeneration

Species richness in the seedling strata averaged 3.7 ± 0.2 species per site and did not differ from 2002. Beech seedlings were present in 59 of the 62 sites and accounted for 11.4% of the total number of seedlings recorded (Table 2.4). Sugar maple and red maple seedlings, however, dominated regeneration, accounting for 86.4% and 67.9% of all seedlings in Upper Michigan and Lower Michigan sites, respectively (Table 2.4). Sugar maple seedlings were more common in Upper Michigan than Lower Michigan ($F = 24.64$; df = 1, 34; $p < 0.0001$) and were more abundant in sites with no or light levels of beech scale in 2002 than in sites with heavy levels of beech scale in 2002 ($F = 12.34$; df = 2, 34; $p < 0.0001$). Sites with heavy beech scale infestations in 2002 had significantly more red maple seedlings in 2012 than sites that were uninfested or lightly infested in 2002 ($F = 16.0$; df = 2, 33; $p < 0.0001$) (Table 2.4).

Beech dominated the sapling stratum, accounting for 62.7% of all saplings, followed by sugar maple (18.3%) and ironwood (4.9%) (Table 2.5). Species richness averaged 2.7 ± 0.2 species per site and did not differ from 2002. Beech ($F = 15.38$; $df = 1, 32$; $p = 0.0004$) and sugar maple ($F = 8.16$; $df = 1, 35$; $p = 0.0072$) saplings were more abundant in Upper Michigan than in Lower Michigan (Table 2.5). Sites with heavy beech scale infestations in 2002 had more red maple saplings in 2012 than uninfested or lightly infested sites in 2002 ($F = 108.1$; $df = 2, 38$; $p < 0.0001$).

Species richness of recruits averaged 2.9 ± 0.1 species per site and was not significantly different than in 2002. Sugar maple and beech were the most abundant recruits in all stands, comprising 27.1 and 50.1% of the total stems, respectively (Table 2.6). Beech recruits in high beech basal areas were more abundant than in low beech basal areas ($F = 19.49$; $df = 2, 32$; $p < 0.0001$). Beech ($F = 52.6$; $df = 1, 32$; $p < 0.0001$) and sugar maple ($F = 7.72$; $df = 1, 34$; $p = 0.0088$) recruits were also more abundant in Upper Michigan than Lower Michigan. Sugar maple recruits were more common in sites with absent or light scale infestations in 2002 than in sites with heavy scale levels ($F = 7.32$; $df = 2, 34$; $p = 0.0022$). The interaction of site location and 2002 beech scale infestation was significant. More sugar maple recruits were in Upper Michigan sites that had absent or light scale levels in 2002 than in Lower Michigan sites with similarly absent or light scale levels ($F = 5.53$; $df = 2, 34$; $p = 0.0083$). Red maple recruits were more abundant in sites heavily infested with beech scale in 2002 than uninfested or lightly infested sites in 2002 ($F = 169.69$; $df = 2, 38$; $p < 0.0001$) (Table 2.6).

DISCUSSION

Beech bark disease continues to expand through the native range of American beech (Garnas 2011, Griffin 2003, Morin et al. 2007, Garnas 2001) and was first identified in both

Upper and Lower Michigan in 2000. In Michigan, the progression of beech scale has been monitored annually at a finer resolution than in other studies (Schwalm 2009, Wieferich et al. 2011). Results show spread of the advancing front differs between Upper and Lower Michigan and stands have been impacted differently (Schwalm 2009, Wieferich et al. 2011). Kearney (2005) reported little beech mortality and there were no differences in beech mortality in 2002-03 among sites varying in beech scale infestation levels, beech basal area or between Upper and Lower Michigan. In contrast, by 2012, more overstory beech trees in Upper Michigan were dead or dying in areas where beech scale was present in 2002 than in more recently invaded sites. In some Upper Michigan sites, mortality of beech stems and beech basal area are high affecting up to 55.6% of beech stems and 92.4% of beech basal area. In Lower Michigan, beech mortality rates were generally lower and did not differ from 2002. The sites with the highest beech mortality occurred in Mason and Manistee Counties, not far from locations where BBD was first identified.

In northeastern states, up to 85% of beech stems are killed by BBD (Krasny and Whitemore 1992). As of 2012, beech mortality rates in Upper Michigan are similar to estimates from Pennsylvania and northern Maine, where 50% of overstory beech stems were dead and half of the surviving beech were either heavily infested with beech scale or infected with *Neonectria* (McCullough et al. 2001, Heyd 2005, Kasson & Livingston 2012). Surviving beech in Pennsylvania stands were weakened by patches of dead tissue and had substantially declined (Ostrofsky and McCormack 1986). Furthermore, like Upper Michigan, most beech mortality attributed to BBD occurs among large beech trees (Mize and Lea 1979, Fernandez and Boyer 1988, Gruerrier et al. 2003).

The difference in beech mortality rates between Upper and Lower Michigan may be explained by the *Neonectria* fungi, which may be less abundant or less virulent in Lower Michigan. *Neonectria* has been cultured by a number of pathologists from trees in Upper Michigan, but was reported as being scarce and difficult to find in Lower Michigan (O'Brien et al. 2001). Another possible explanation could simply be that *Neonectria* is spreading more slowly in Lower Michigan than in Upper Michigan due to forest fragmentation and parcelization in Lower Michigan (Leefers et al. 2007). If fragmentation and parcelization affects the spread of BBD from stand to stand, however, we would still expect to see high mortality in areas such as Ludington State Park that were invaded early. However, 2012 data from sites in Ludington State Park indicate only 25.6% of beech have died, so this is probably not the case. A third explanation could simply be that Upper Michigan beech trees are more susceptible to the *Neonectria* fungi, whereas beech populations in Lower Michigan are tolerant to the *Neonectria* strand (Burns and Houston 1987, Hamelin 2011). The reason behind the difference in mortality in Upper and Lower Michigan is unclear, but more research on *Neonectria* fungi is clearly needed.

As dominant beech die in Upper Michigan, other overstory species may compete to replace beech in the overstory. Sugar maple and red maple were abundant in nearly all sites and will most likely fill gaps as beech die. Canopy disturbance by beech bark disease has shown to significantly increase radial growth of sugar maple growing in gaps (DiGregorio et al. 1999). However, radial growth of existing overstory trees canopies may occupy gaps created by dying beech (Poage and Peart 1993). Historically, disturbances such as disease and harvesting have increased red maple stocking in northern hardwood stands (Trimble 1970, Leak and Filip 1977, Reynolds et al. 1979, Walter and Yawney 1990), but sub-canopy species and understory do not typically respond to gaps less than 500 m^2 (Poage and Peart 1993, DiGregorio et al. 1999). As a mid-successional species, red maple is likely to fill gaps more quickly than more shade tolerant, late successional species such as sugar maple, especially when red maple stands are more abundant than sugar maple (Walters and Yawney 1990). Eventually, sugar maple and other long-lived shade tolerant species will probably replace red maple trees, which rarely live over 150 years (Godman et al. 1990, Walters and Yawney 1990). In summary, stands impacted by beech bark disease will most likely become more dominated by sugar or red maple.

In northeastern North America, beech thickets often arise following high beech mortality due to the relatively rapid death of previously healthy beech trees, increasing the number of beech in the understory roughly five-fold (Ostrofsky and McCormack 1986, Houston 1994, McCullough et al. 2001, Hane 2003, Guerrier et al. 2003). Thickets arise from root sprouts produced by the parent rootstock, resulting in proliferation of susceptible beech stems within the stand (Ostrofsky and McCormack 1986, Griffin et al. 2003). As beech thickets develop, they create a dense layer of foliage, reducing light that reaches the forest floor (Hane 2003). Species survival in the understory is dependent on light availability and advanced regeneration (Kobe 1995, Hane 2003). Survival rates of non-beech seedling and sapling species, including sugar and red maple, are reduced in beech thickets (Twery and Patterson 1984, Hane 2003). However, I observed only a single beech thicket in three sites in Upper Michigan and saw none in Lower Michigan. Beech reproduction in the western portion of the beech range in the United States may be more likely to occur by seed than by root sprouts, but further study will be needed to assess this.

In time, significant changes may occur in the understory, as BBD progresses and more sites move into the aftermath forest (Shigo 1972). Like the overstory, saplings and recruits are dominated by sugar maple and beech. Some understory beech will probably replace dead overstory beech for at least one generation (Twery and Patterson 1984, Gruerrier et al. 2003). To date, there are few changes in regeneration since 2002 except that red maple regeneration is increasing in all strata in the sites that were heavily infested in 2002. If gaps remain open allowing for light penetration into lower strata, red maple with its rapid release, has a better chance to outcompete beech and sugar maple recruits for overstory space (Walters & Yawney 1990).

Table 2.1: Basal area of live and dead beech (m^2/ha) recorded in 2012 and abundance of beech scale recorded in 2002 and in 2011-2012 transects in 62 sites in Michigan. Beech scale infestation level was ranked as 0 if no scale was present, 1 if the sites were lightly infested, 2 if the infestation was patchy and 3 if trees were heavily infested.

Peninsula	**County**	**Beech basal area (m^2/ha)**			**Beech Scale Infestation Level**	
		Total	**Live**	**Dead**	**2002**	**2012**
Lower	Emmet	4.27	4.27	0.00	0	3
Lower	Emmet	6.98	6.98	0.00	0	3
Lower	Kalkaska	3.55	3.55	0.00	0	0
Lower	Wexford	25.49	24.63	0.86	0	3
Lower	Benzie	3.12	3.12	0.00	0	0
Lower	Mason	23.48	19.65	3.83	2	3
Lower	Mason	17.30	13.19	4.11	2	3
Lower	Mason	6.83	1.61	5.22	2	3
Lower	Mason	11.15	11.15	0.00	1	3
Lower	Mason	3.64	3.64	0.00	2	3
Lower	Mason	2.64	2.64	0.00	1	3
Lower	Manistee	4.92	4.92	0.00	0	1
Lower	Manistee	29.07	29.07	0.00	1	3
Lower	Allegan	5.30	4.63	0.67	0	0
Lower	Ottawa	32.99	32.57	0.42	0	0
Lower	Muskegon	2.05	2.05	0.00	0	0
Lower	Oceana	21.09	20.27	0.82	2	3
Lower	Oceana	3.54	3.54	0.00	0	3
Lower	Mason	10.35	9.95	0.40	2	2
Lower	Wexford	0.00	0.00	0.00	0	3
Lower	Leelanau	7.07	7.07	0.00	0	3
Lower	Antrim	3.01	3.01	0.00	0	2
Lower	Emmet	1.04	1.04	0.00	0	1
Lower	Charlevoix	0.00	0.00	0.00	0	1
Lower	Charlevoix	28.47	24.88	3.59	0	3
Lower	Wexford	8.77	8.77	0.00	0	2
Lower	Cheboygan	3.45	3.45	0.00	0	3
Lower	Montmorency	1.97	1.97	0.00	0	0
Upper	Luce	9.88	6.75	3.13	1	3
Upper	Luce	9.42	5.27	4.15	2	3
Upper	Luce	2.57	2.57	0.00	2	3
Upper	Alger	10.71	10.71	0.00	0	1
Upper	Delta	19.26	19.26	0.00	0	1
Upper	Schoolcraft	5.00	5.00	0.00	0	1

Table 2.1 (continued)

Peninsula	County	Beech basal area (m^2/ha)			Beech Scale Infestation Level	
		Total	Live	Dead	2002	2012
		24.19	24.19	0.00	0	1
Upper	Schoolcraft	16.69	16.69	0.00	0	1
Upper	Luce	19.38	9.99	9.39	2	2
Upper	Luce	23.29	9.99	13.30	2	2
Upper	Chippewa	21.53	2.88	18.65	2	3
Upper	Luce	24.02	9.03	14.99	1	3
Upper	Chippewa	4.09	4.09	0.00	0	3
Upper	Chippewa	6.61	4.25	2.36	1	3
Upper	Chippewa	12.31	3.81	8.50	1	3
Upper	Mackinac	12.43	12.00	0.43	0	3
Upper	Mackinac	13.42	13.09	0.33	0	3
Upper	Mackinac	10.44	7.02	3.42	1	3
Upper	Chippewa	8.30	8.30	0.00	0	2
Upper	Mackinaw	8.98	8.98	0.00	1	3
Upper	Mackinaw	9.16	3.62	5.54	1	3
Upper	Mackinaw	10.12	3.89	6.24	1	3
Upper	Mackinaw	29.99	7.71	22.28	1	3
Upper	Alger	24.79	24.79	0.00	0	3
Upper	Alger	23.46	23.46	0.00	0	2
Upper	Delta	17.78	17.78	0.00	0	1
Upper	Delta	11.19	11.19	0.00	0	1
Upper	Delta	13.13	13.13	0.00	0	0
Upper	Alger	35.35	31.93	3.42	0	3
Upper	Alger	2.40	2.40	0.00	0	3
Upper	Schoolcraft	19.61	4.51	15.10	0	3
Upper	Marquette	7.06	7.06	0.00	0	1
Upper	Chippewa	6.27	6.27	0.00	0	3
Upper	Mackinaw	16.44	12.69	3.75	0	3

Table 2.2: Relative importance values of dominant overstory species in the original 62 sites based on 2002 and 2011-2012 sampling.

Species	Year	Relative density[1]	Relative frequency[2]	Relative dominance[3]	Relative importance value[4]
Sugar Maple	2012	**36.1 ± 3.3**	**74.2 ± 5.2**	**33.4 ± 3.3**	**143.6**
	2002*	33.4 ± 3.5	-	32.4 ± 3.5	-
	2012*	35.2 ± 3.5	73.4 ± 5.2	32.7 ± 3.5	141.3
American Beech	2012	**24.7 ± 2.2**	**76.3 ± 3.7**	**23.8 ± 2.2**	**124.9**
	2002*	30.7 ± 3.0	-	30.6 ± 3.1	-
	2012*	24.7 ± 2.4	76.1 ± 4.5	23.9 ± 2.4	124.7
Red Maple	2012	**15.6 ± 2.5**	**47.3 ± 5.6**	**15.6 ± 2.5**	**78.5**
	2002*	8.7 ± 1.7	-	8.4 ± 1.8	-
	2012*	16.0 ± 2.8	46.8 ± 5.7	15.3 ± 2.7	78.2
Eastern Hemlock	2012	**5.8 ± 1.6**	**20.4 ± 4.4**	**5.7 ± 1.5**	**31.9**
	2002*	5.2 ± 1.5	-	5.9 ± 1.6	-
	2012*	5.9 ± 1.7	21.8 ± 4.8	5.3 ± 1.5	32.9
Red Oak	2012	**4.4 ± 1.3**	**17.2 ± 4.2**	**6.3 ± 1.8**	**28.0**
	2002*	5.4 ± 1.8	-	6.0 ± 2.0	-
	2012*	4.3 ± 1.3	17.7 ± 4.5	6.5 ± 1.9	28.5
Basswood	2012	**2.9 ± 1.0**	**11.3 ± 3.6**	**3.2 ± 1.1**	**17.4**
	2002*	1.8 ± 0.8	-	1.7 ± 0.8	-
	2012*	3.0 ± 1.1	12.1 ± 3.9	3.3 ± 1.2	18.4

* rows = Only data from the northern two transects were used.

[1] Relative density is the number of stems of the species as a percentage of the total number of stems of all species.

[2] Relative frequency is the number of transects containing the species as a percentage of the total number of occurrences for all species within all transects.

[3] Relative dominance is the total basal area of the species as a percentage of the total basal area for all species.

[4] Relative importance value is the sum of relative density, relative frequency and relative dominance.

Table 2.3: Average (±SE) number of live and dead beech stems (per ha) and live and dead beech basal area (m^2/ha) in 62 sites in 2011-12 grouped by beech basal area, initial scale infestation levels in 2002 and site location in Upper or Lower Michigan. Within groups (column), different letters (A,B,C) indicate a significant ($\alpha \leq 0.05$) difference among sites.

		No. of beech stems		**Beech basal area**	
	No. of sites	Live	Dead	Live	Dead
Beech Basal Area*					
Low	25	74.0 ± 9.3 A	8.7 ± 3.7 A	31.7 ± 4.4 A	4.4 ± 1.9 A
Moderate	24	131.1 ± 13.1 B	28.0 ± 7.5 B	68.4 ± 7.5 B	18.6 ± 5.6 B
High	13	181.5 ± 33.6 C	52.2 ± 12.4 C	96.3 ± 14.9 C	34.8 ± 12.4 B
Initial Beech Scale Infestation**					
Absent	39	131.8 ± 14.9 B	8.7 ± 2.5 A	65.3 ± 7.5 A	5.0 ± 1.9 A
Light	12	102.5 ± 14.9 AB	55.9 ± 13.7 B	47.9 ± 7.5 A	34.8 ± 9.9 B
Heavy	11	90.1 ± 20.5 A	51.0 ± 13.1 B	52.8 ± 13.1 A	36.0 ± 12.4 B
Peninsula					
Lower	28	109.4 ± 16.8 A	11.2 ± 3.1 A	60.3 ± 8.7 A	5.6 ± 1.9 A
Upper	34	126.2 ± 13.7 A	36.7 ± 7.5 B	59.0 ± 7.5 A	24.9 ± 6.2 B

* Beech basal area recorded as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha).

** Initial beech scale infestation level recorded in 2002 as absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

Table 2.4: Average (±SE) density of beech, sugar maple, red maple and total seedlings (< 30.5 cm tall) in 62 sites in 2011-12 grouped by beech basal area, initial scale infestation levels in 2002 and site location in Upper or Lower Michigan. Within groups (column), different letters (A,B,C) indicate a significant (α≤0.05) difference.

	No. of sites	Beech	Sugar maple	Red maple	Total
Beech Basal Area[1]			**Thousands per ha**		
Low	25	11.9 ± 4.1 A	31.2 ± 9.3 A	41.6 ± 14.3 A	101.0 ± 15.7 A
Moderate	24	10.5 ± 2.2 A	52.8 ± 14.9 A	53.3 ± 20.5 A	121.8 ± 22.2 A
High	13	16.3 ± 7.0 A	39.0 ± 18.5 A	34.1 ± 11.5 A	97.3 ± 17.2 A
Initial Beech Scale Infestation[2]					
Absent	39	12.5 ± 2.8 A	38.8 ± 7.1 B	13.3 ± 4.0 A	77.0 ± 7.9 A
Light	12	15.2 ± 7.6 A	84.8 ± 29.8 C	81.1 ± 28.5 B	189.6 ± 27.6 B
Heavy	11	8.5 ± 3.8 A	2.0 ± 1.2 A	115.2 ± 35.6 B	130.2 ± 37.8 B
Peninsula					
Lower	28	12.7 ± 3.4 A	17.3 ± 5.3 A	46.9 ± 15.6 A	94.4 ± 16.0 A
Upper	34	11.9 ± 3.3 A	60.8 ± 12.7 B	42.6 ± 13.2 A	119.6 ± 15.5 A

[1] Beech basal area recorded as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha).

[2] Initial beech scale infestation level recorded in 2002 as absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

Table 2.5: Average (±SE) density of beech, sugar maple, red maple and total saplings (> 30.5 cm tall and < 2.5 cm DBH) in 62 sites in 2011-12 grouped by beech basal area, initial scale infestation levels in 2002 and site locations in Upper or Lower Michigan. Within groups (column), different letters (A,B,C) indicate a significant (α≤0.05) difference.

	No. of sites	Beech	Sugar maple	Red maple	Total
Beech Basal Area[1]			**Hundreds per ha**		
Low	25	25.3 ± 5.0 A	11.6 ± 9.4 A	2.1 ± 1.6 AB	45.2 ± 11.7 A
Moderate	24	28.0 ± 7.0 A	5.7 ± 2.3 A	0.5 ± 0.4 A	40.8 ± 7.1 A
High	13	35.5 ± 11.2 A	6.7 ± 3.5 A	2.7 ± 1.3 B	54.3 ± 12.7 A
Initial Beech Scale Infestation[2]					
Absent	39	32.2 ± 5.7 A	11.7 ± 6.2 B	0.3 ± 0.2 A	50.4 ± 8.6 A
Light	12	22.1 ± 5.2 A	4.3 ± 2.8 B	0.6 ± 0.5 A	37.0 ± 8.6 A
Heavy	11	22.1 ± 9.5 A	0.5 ± 0.4 A	7.4 ± 3.7 B	37.0 ± 12.1 A
Peninsula					
Lower	28	18.7 ± 4.0 A	1.7 ± 1.3 A	0.3 ± 0.2 A	27.4 ± 4.9 A
Upper	34	36.5 ± 6.4 B	13.7 ± 7.0 B	2.8 ± 1.3 B	60.2 ± 9.6 B

[1] Beech basal area recorded as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha).

[2] Initial beech scale infestation level recorded in 2002 as absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

Table 2.6: Average (±SE) density of beech, sugar maple, red maple and total recruits (between 2.5 and 12.5 cm DBH) in 62 sites in 2011-12 grouped by beech basal area, initial scale infestation levels in 2002 and site location in Upper or Lower Michigan. Within groups (column), different letters (A,B,C) indicate a significant (α≤0.05) difference.

	No. of sites	Beech	Sugar maple	Red maple	Total
Beech Basal Area[1]				**Per ha**	
Low	25	141.6 ± 24.8 A	170.3 ± 26.3 A	25.7 ± 14.9 A	432.7 ± 37.5 A
Moderate	24	392.8 ± 89.3 B	122.0 ± 28.0 A	33.0 ± 18.2 A	630.0 ± 91.2 B
High	13	268.9 ± 98.4 B	132.2 ± 56.1 A	56.3 ± 33.4 A	534.4 ± 108.8 AB
Initial Beech Scale Infestation[2]					
Absent	39	250.2 ± 53.5 AB	163.6 ± 21.1 B	4.2 ± 2.6 A	504.1 ± 56.7 A
Light	12	413.4 ± 126.9 B	168.1 ± 60.5 B	39.8 ± 16.7 B	709.7 ± 116.9 B
Heavy	11	158.9 ± 51.6 A	46.2 ± 30.3 A	138.5 ± 51.9 C	427.8 ± 77.4 A
Peninsula					
Lower	28	146.2 ± 30.4 A	109.4 ± 26.1 A	39.5 ± 16.4 A	371.4 ± 44.4 A
Upper	34	363.8 ± 70.8 B	171.8 ± 26.6 B	31.2 ± 16.2 A	661.3 ± 66.6 B

[1] Beech basal area recorded as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha).

[2] Initial beech scale infestation level recorded as absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

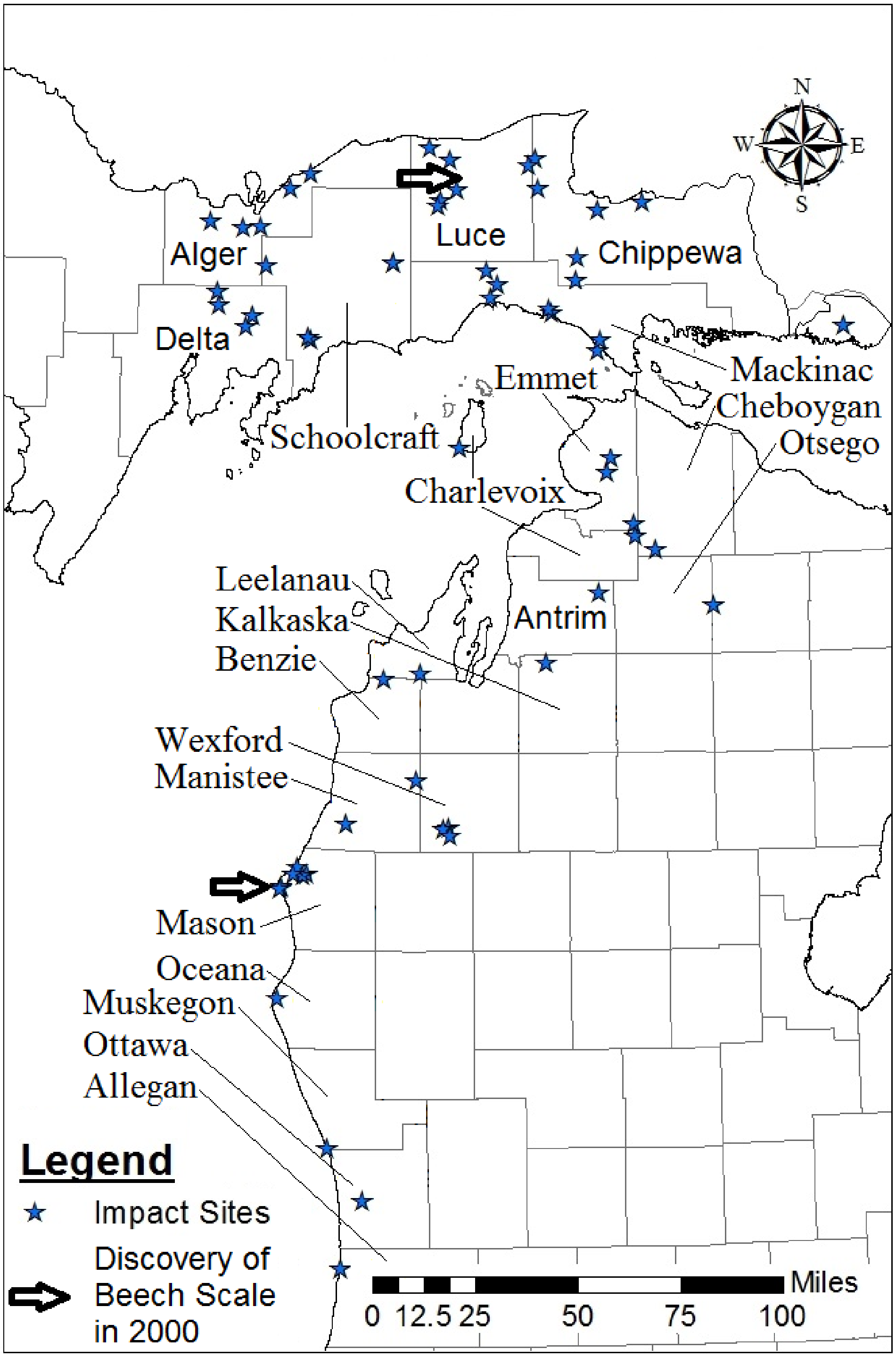

Figure 2.1: Original sites in 2000, where beech scale (*Cryptococcus fagisuga*) was first identified in Upper Michigan in Luce County and in Mason County in Lower Michigan are indicated by arrows. Distribution and county names of the 62 long term impact sites established in 2002-2003 by Amy Kearney and re-surveyed in 2011-2012 are indicated by stars.

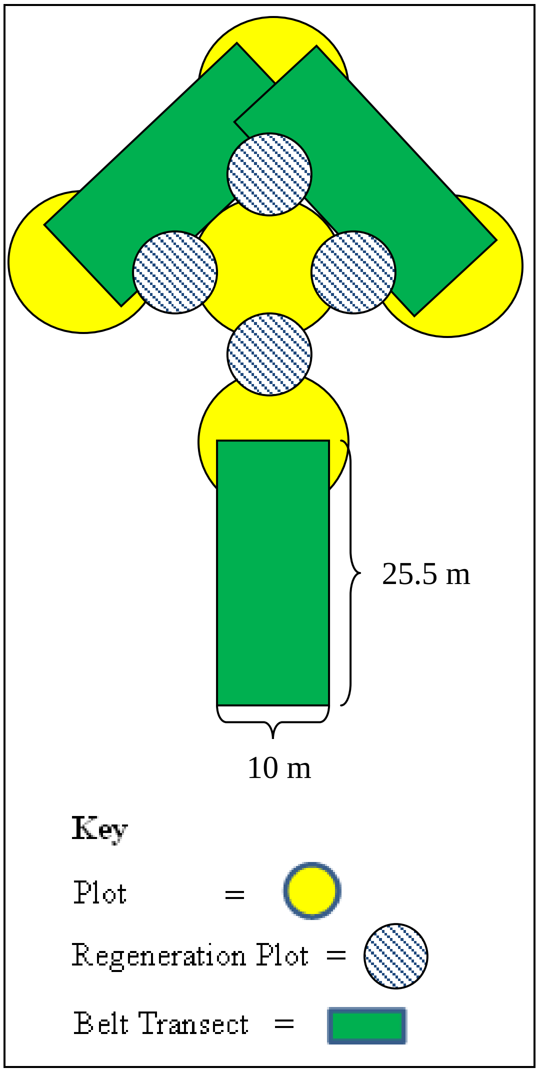

Figure 2.2: Configuration of transects to subplots at each long term impact plot.

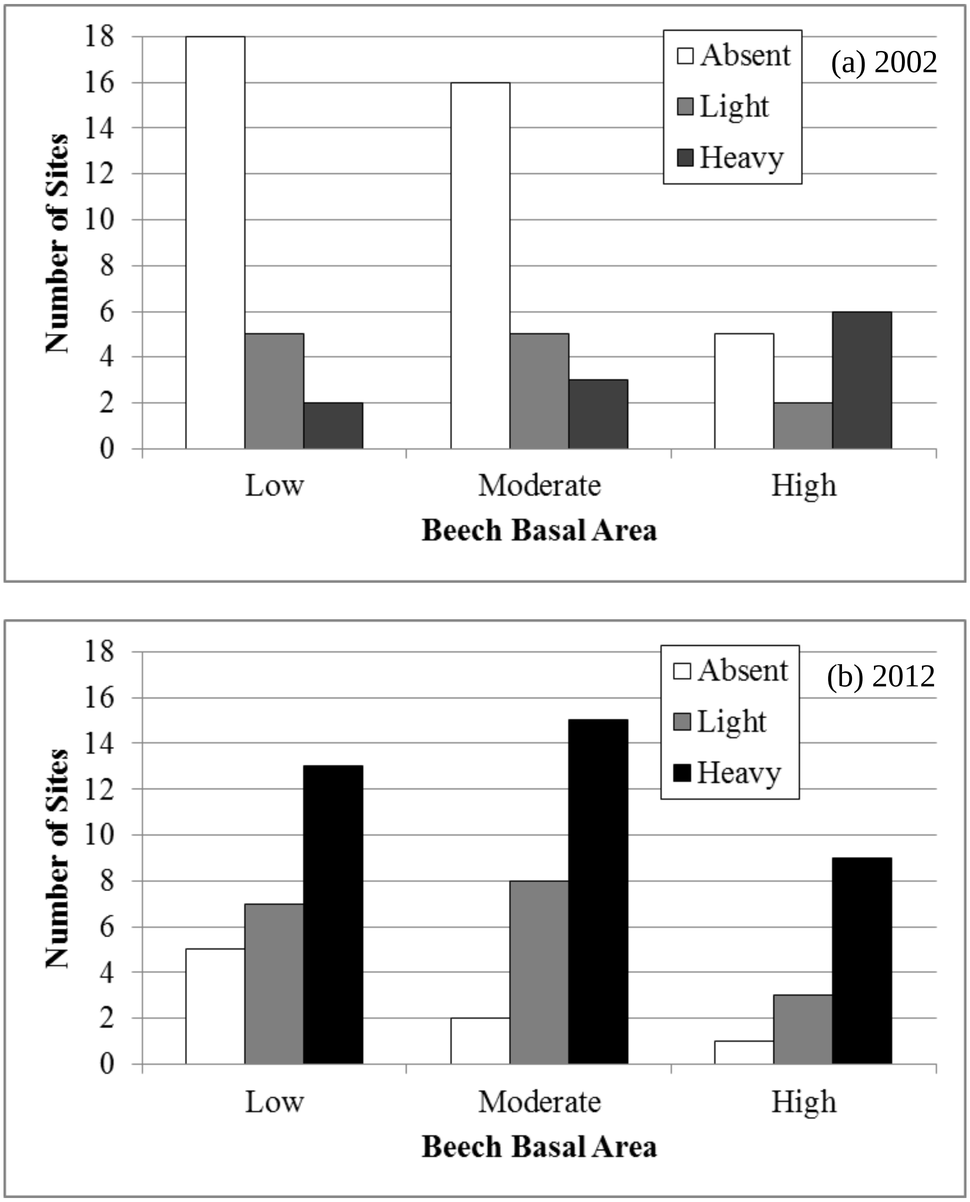

Figure 2.3: Beech scale infestation levels in (a) 2002 and (b) 2012 stands in 62 sites with low, moderate or high beech basal area. Beech basal area was classed as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha).

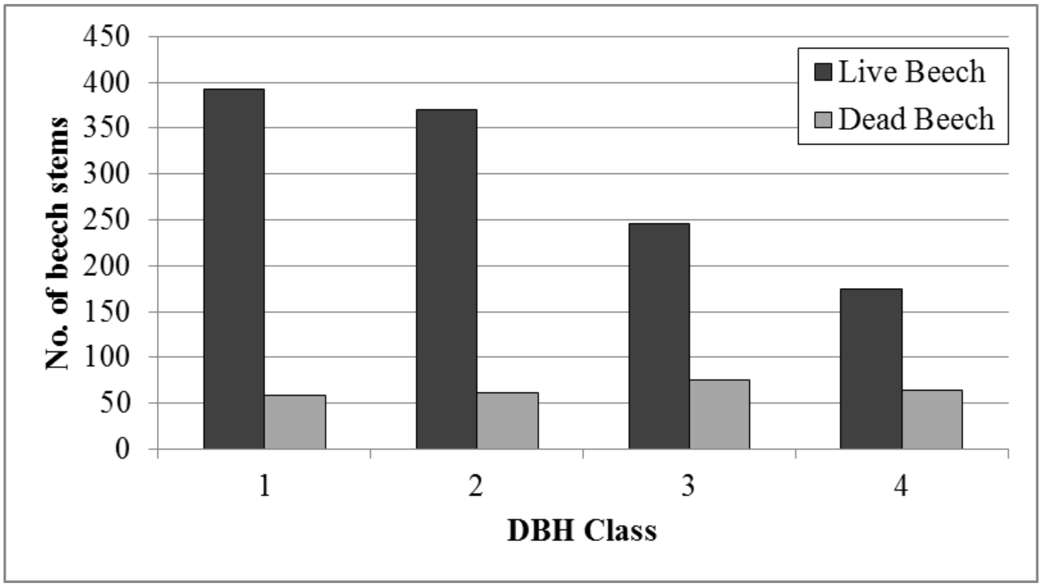

Figure 2.4: Distribution of live and dead beech stems by DBH class in 62 sites in Michigan in 2012. DBH class was recorded as 1 (>12.5 and < 22.5 cm DBH), 2 (≥ 22.5 and < 32.5 cm DBH), 3 (≥ 32.5 and < 42.5 cm DBH) or 4 (≥ 42.5 cm DBH).

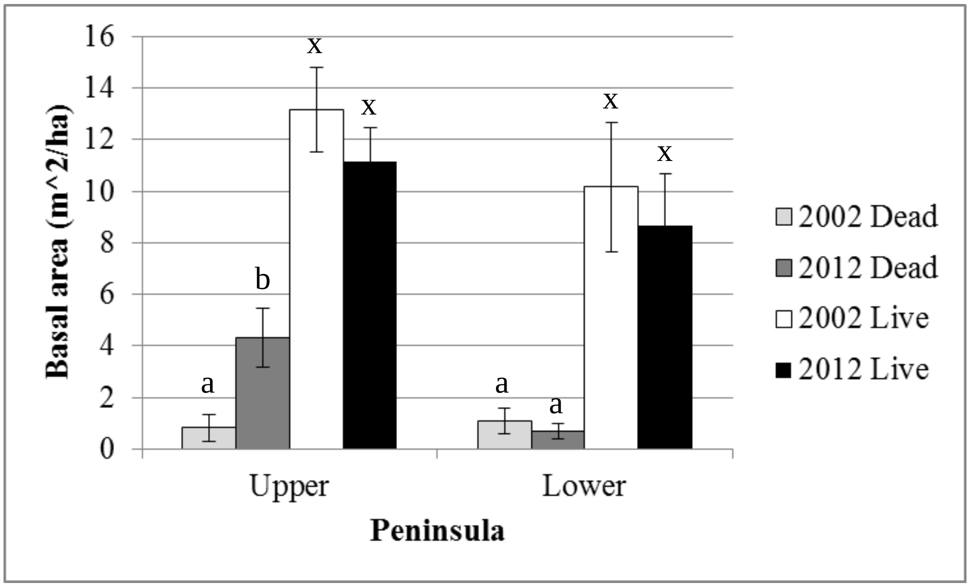

Figure 2.5: Live and dead beech basal area (m^2/ha) in Upper and Lower Michigan in 2002 and 2012. Different letters indicate a significant ($\alpha \leq 0.05$) difference between beech basal area of dead (a,b) and live beech (x,y) between years.

CHAPTER 3: INFLUENCE OF BEECH BARK DISEASE ON VARIABLES RELATED TO WILDLIFE HABITAT

ABSTRACT

Beech bark disease continues to spread through Michigan forests, potentially altering overstory composition and habitat condition for wildlife. In 2002-03, following the 2000 identification of BBD in Michigan, condition of 744 beech trees and abundance of coarse woody material (CWM) were recorded in 62 sites. I re-visited the original 62 sites in 2012 to evaluate condition of the same trees and the amount, composition and condition of CWM. Radial growth of trees that were heavily infested by beech scale in 2003 averaged 1.6 ± 0.2 cm compared to trees that were uninfested in 2003, which averaged 2.5 ± 0.2 cm. Overall, 18.1% of the trees tagged in 2003 were dead in 2012. Beech mortality rates were affected by beech scale infestation levels in 2002, beech basal area and differed between sites in Upper and Lower Michigan. Abundance of CWM pieces was significantly higher in areas with high beech basal area and heavy initial beech scale infestation levels. However, volume of CWM did not differ among beech basal area, initial beech scale infestation level or between Upper and Lower Michigan. In 2002, only 20.2% of the CWM pieces were fresh. In 2012, 62.6% of the CWM pieces were fresh and 68.3% of the fresh pieces were beech. In the short-term, many wildlife species may benefit from snags created by mortality of large diameter beech and a pulse in fresh CWM as BBD progresses. However, in the long-term, mortality of overstory beech trees will reduce the availability of hard mast, nesting locations and perching branches for a variety of birds and mammals.

INTRODUCTION

American beech (*Fagus grandifolia*) is an important species for wildlife in North America across its range which runs from southern Canada to Florida (Tubbs and Houston 1990). As the only *Fagus* species in North America, beech occurs in mesic deciduous forests, more commonly referred to as northern hardwoods (Fowells 1965, Kitamura and Kawano 2001). Northern hardwood forests typically are dominated by beech (*Fagus* sp.), maple (*Acer* sp.), birch (*Betula* sp.) hemlock (*Tsuga* sp.), and in some areas, northern red oak (*Quercus rubrum* L.) (Dickmann and Leefers 2003, Woods and Davis 1989, Tubbs and Houston 1990).

Over 40 species of wildlife including birds, mammals and amphibians use American beech for shelter, cavities, perching branches and hard mast (Tubbs and Houston 1990, McCullough et al. 2001, Heyd 2005). Mature beech and beech snags often have large cavities, where birds and mammals may seek shelter, nest or hibernate (Allen 1990, Kahler and Anderson 2006). Numerous species also feed on hard mast produced by beech including black bears (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), white-footed mice (*Peromyscus leucopus*), deer mice (*Peromyscus* Sp.), red-backed voles (*Myodes* Sp.) and a wide diversity of birds (Horsley et al. 2000, Schnurr et al. 2002, Faison and Houston 2004). Heavy mast production occurs every two to three years (Fowells 1965, Tubbs and Houston 1990). Beech nuts ripen during one growing season, dropping in the fall after the first heavy frost. Ripe beech nuts have a high fat content needed by many species like black bear to attain the weight required to hibernate and produce offspring (Rogers 1987, Faison and Houston 2004).

Unfortunately, beech in North America have been severely affected by beech bark disease (BBD), comprised of a nonindigenous, sap-feeding beech scale insect (*Cryptococcus fagisuga* Lind.) and a cambium-killing *Neonectria* fungus (Houston and O'Brien 1994). BBD begins when beech scales infest beech trees. Native to western Asia, beech scale arrived in Nova Scotia, Canada in 1890 on nursery stock from Europe (Gwiazdowski et al. 2006). Beech scale insects are only 0.5 mm long, and feed on sap in the phloem tissue, facilitating entry of the *Neonectria* fungi. Parthenogenic beech scales produce an average of 50 eggs per adult in late summer and fall (Ehrlich 1934, Wainhouse and Gate 1988). Upon hatching, first instars, called crawlers, may disperse by wind to nearby beech trees or may find suitable feeding locations on the tree where they hatched (Wainhouse 1980, Felt 1933). Crawlers drive their 2 mm long stylets into the beech bark to feed on sap, then molt and are thereafter immobile (Shigo 1972). Openings in the outer bark left by the scales enable *Neonectria faginata* and *Neonectria ditissima* spores to colonize the tree (Castlebury et al. 2006). *N. faginata*, variation *N. coccinea*, is a nonindigenous fungus that only attacks the genus *Fagus*, while the native *N. ditissima* (formerly *N. galligena*) infects a variety of hardwoods in North America (Castlebury et al. 2006). *Neonectria* fungi kill small patches of cambium tissue that eventually coalesce, disrupting transportation of water and nutrients, weakening the trees, leading to canopy dieback and ultimately mortality (Ehrlich 1934). Beech trees weakened by BBD, are also more susceptible to high winds that cause large limbs or trunks to break, a condition referred to as "beech snap" (Shigo 1972, Houston et al. 1979).

Stands affected by BBD are classed into three phases; the advancing front, the killing front, and the aftermath forest (Shigo 1972, Houston and O'Brien 1983, Houston 1994). The advancing front refers to areas where beech trees are becoming infested or are infested with beech scale, but have not been affected by the *Neonectria* pathogen (Houston and O'Brien 1983). Areas are classified as "the killing front" where trees are dead, dying or heavily infected by *Neonectria*. After BBD has spread through the stand, it is referred to as "the aftermath forest."

Species composition can be altered in stands where BBD causes substantial mortality (Ostrofsky and McCormack 1986). Northern Pennsylvania, Maine and New York have reported substantial declines in beech tree abundance due to BBD (Heyd 2005, McCullough et al. 2001, Ostrofsky and McCormack 1986, Griffin 2003, Canham 1988). Large diameter beech trees are typically infested early (Fernandez and Boyer 1988) and mortality is reported higher in large beech trees than in small trees or recruits (Heyd 2005, McCullough et al. 2001, Ostrofsky and McCormack 1986).

Snags and dying beech trees in the killing front represent a potential short-term pulse of coarse woody material (CWM), a term that refers to down woody material > 7.6 cm in diameter (Gilbert 1997). CWM has implications for wildlife habitat, food sources and moisture retention. Many wildlife species occupy down logs for thermal shelter, hunting locations, and maternal dens (Gilbert et al. 1997), while others may use large diameter logs for cover in large gaps (Strojny et al. 2010). Furthermore, down woody material is decomposed by arthropods that break down the plant material, mineralizing nutrients for other plants to uptake. A pulse in the amount of CWM could benefit some arthropod populations subsequently influencing other wildlife species that feed on arthropods (Niwa 2001). However, a pulse in CWM driven by BBD would be short lived and the long term repercussions would outweigh the short term benefits.

Michigan presented an unique opportunity to assess effects of BBD on overstory beech condition and CWM over time. BBD was first identified in Michigan in two localized areas in 2000 (O'Brien et al. 2001). In 2002-03, 62 long term impact sites were established across much of the beech range to collect baseline data on overstory beech condition, CWM, the frequency of beech snags and presence of cavities in beech trees (Kearney 2005). In 2012, individual beech trees in the 62 sites originally tagged in 2002 were re-assessed to quantify canopy condition, radial growth, abundance of cavities and current beech scale infestation levels. Abundance, frequency, size class, volume and decay class of CWM were also determined in the 62 sites. Condition of individual beech trees and CWM estimated in 2012 were then compared to records from 2002 to illustrate the progression and effects of BBD over the past ten years.

METHODS

In 2002, 62 sites were established based on beech basal area and beech scale infestation levels across 21 counties in Michigan. No harvesting activity had occurred in the 62 sites after 1998. Sites were grouped into three classes based on beech basal area data provided by the Michigan Department of Natural Resources; Low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha). Beech trees were assigned to one of the following categories based on a visual estimate of percent wax coverage on the side of the tree with the most scale: absent (no wax present), light (<10% coverage), or heavy (>10% coverage). Sites were then grouped based on percentage of individual trees infested within the plot and placed into one of the three following groups: absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

Long Term Impact Trees

In 2002, 12 beech trees were selected in each of the 62 sites around the perimeter of the plot (Figure 3.1). A turf stake was buried 18.3 m from the plot's center, in each cardinal direction. Three beech trees within 60 m of the corresponding turf stake were tagged in each azimuth other than the direction leading back to the plot's center. Tree selection was based on the following prioritized criteria: 1) largest tree with a canker, 2) any tree (pole-sized or larger) with a canker, 3) large tree with *C. fagisuga* present, 4) any tree (pole-sized or larger) with *C. fagisuga*, or 5) any large tree (closest to the azimuth used).

In 2012, I measured DBH, estimated crown dieback and transparency, counted cavities, and estimated beech scale density on each tree. Crown dieback and transparency were measured using five percent classes following guidelines developed by the USDA Forest Service, Forest Health Monitoring System (USDA For. Serv. 2007). I used a foliage transparency card when estimating canopy transparency to keep readings consistent. Cavities were counted and their size was visually estimated from the ground. Cavities were classed as: small (cavity < 7 cm at the widest point), moderate (cavity 7-30 cm at the widest point), or large (cavity > 30 cm at widest point). Scale density was classed into one of four categories: absent (no scale present), trace (a few spots of beech scale present), patchy (patches of beech scale clusters on the tree) or whitewashed (one or more aspects of the tree trunk completely covered with beech scale). For analysis, individual trees were pooled by site to assess current conditions and individual trees were compared to conditions in 2002 on a tree by tree basis.

Coarse Woody Material

Frequency, species, size and decay class of CWM, > 7.6 cm in diameter, were recorded along three transects, each 25.5 m long by one m wide (Figure 3.1). Each piece was recorded as: (0) for fresh material with intact bark and no obvious decay; (1) bark starting to fall off, or the bark may be absent, but the inner sapwood was still solid; (2) some decay; under impact, small wood chunks break off, but the center remained firm; (3) decaying; maintained original shape, but under impact loses form; and (4) decayed and form lost (Kearney 2005). CWM pieces and volume were summed over area surveyed in each site, then standardized by ha for analysis.

Statistical Analysis

Statistical analyses were performed using SAS 9.2 statistical software (SAS Institute 2003). Proportion of living beech, average DBH of live and dead beech were calculated for each site. Abundance, frequency, volume and decay class of CWM were standardized per ha for each site. Normality was tested for all variables using the Shapiro-Wilk test and residual plots (Shapiro and Wilk 1965). Abundance, frequency, volume and decay class of CWM, radial growth, proportion of beech alive and diameters of live and dead beech were normally distributed. A natural log transformation ($\ln(x + 2)$) on number of cavities, canopy dieback and transparency were successful to normalize distributions. A three-way ANOVA was used to determine if initial beech basal area, 2002 beech scale infestation level or differences between Upper and Lower Michigan influenced beech mortality, condition of beech trees, radial growth or CWM variables. Tukey's Honestly Significant Difference was used to separate differences when ANOVA results were significant ($\alpha = 0.05$) (Tukey 1977). A t-test was used to determine if tree or CWM variables differed significantly between 2002 and 2012.

RESULTS

Long Term Impact Trees

A total of 744 beech trees were tagged and evaluated in the 62 sites in 2002-03 and 724 of these trees were re-located in 2012. Of the 724 beech, five trees had fallen, 21 had been felled, 80 were dead snags and 46 had snapped, leaving 572 (79%) live beech trees. Of the live beech, 5.8% were classed as suppressed and 20.0% were intermediate in 2012. Co-dominant trees were most abundant, accounting for 61.5% of the live trees, while 12.7% of the beech were classed as dominant. To assess beech mortality attributable to BBD, the 26 trees that were felled or fallen were excluded from analysis. In Lower Michigan sites, 11 of the 314 beech were dead, while 108 out of 368 beech trees were dead in Upper Michigan sites. Beech mortality was affected by initial scale infestation in 2002 ($F = 8.5$; $df = 2, 45$; $p = 0.0007$), beech basal area ($F = 5.1$; $df = 2, 45$; $p = 0.0101$) and between sites in Upper and Lower Michigan ($F = 23.59$; $df = 1, 45$; $p < 0.0001$) (Table 3.1). Beech mortality was higher in sites with moderate and high beech basal area than in sites with low beech basal area and in sites infested in 2002 than in initially uninfested sites. Beech mortality was also greater in Upper Michigan than in Lower Michigan. The only significant interaction occurred between initial scale infestation level and Upper and Lower Michigan. Beech mortality was highest in initially infested sites in Upper Michigan and generally lower in Lower Michigan regardless of initial scale infestation ($F = 6.89$; $df = 2, 45$; $p = 0.0025$).

Average DBH of live beech trees was 33.9 ± 0.6 cm, and ranged from 4.5 to 96.2 cm. Average tree DBH was similar in Lower Michigan (33.5 ± 1.0 cm) and Upper Michigan (34.3 ± 0.8 cm) (Table 3.1). DBH of beech trees did not significantly differ from DBH in 2002 ($t(678) = 1.09$; $p = 0.25$). However, beech snags and snapped beech trees averaged 38.1 ± 1.2 cm DBH and were significantly smaller in Lower Michigan than Upper Michigan ($F = 17.53$; $df = 1, 117$; $p < 0.0001$). Dead beech trees in Lower Michigan averaged 23.5 ± 4.7 cm DBH, compared to Upper Michigan, where dead beech averaged 39.5 ± 1.1 cm DBH.

Radial growth of uninfested beech trees in 2002 grew an average DBH of 2.5 ± 0.2 cm, while heavily infested beech grew slower at 1.6 ± 0.2 cm (Table 3.1). Uninfested beech trees in 2012, had grown 2.6 ± 0.1 cm DBH since 2002. Radial growth varied significantly among trees in the 62 sites ($F = 2.03$; $df = 61, 620$; $p < 0.0001$) and among trees in sites with absent, light or heavily infestations in 2002 ($F = 4.92$; df = 2, 665; $p = 0.0076$), but did not differ between trees in Upper and Lower Michigan. Eight outlier trees were not used for radial growth analysis due to sampling error. Outlier DBH either reduced in size by over ten cm or increased over 40 cm indicating sampling error in either 2002 or 2012.

Many of the originally uninfested beech trees in 2002-03, have since been colonized by beech scale. In 2002, 500 live beech trees were uninfested, but only 189 trees remained uninfested in 2012, including 117 trees in 16 sites in Lower Michigan and 72 of the 132 trees in 11 sites in Upper Michigan. Of the 500 initially uninfested trees, 228 had a trace or patchy beech scale infestation in 2012. Beech scale infestation was classed heavy on the remaining 83 beech trees.

Canopy condition was variable among trees. Dieback ranged from 5 to 95%, averaging $9.9 \pm 0.6\%$ across sites (Table 3.1). Canopy transparency was similarly variable, ranging from 5 to 95% transparent and averaged $15.6 \pm 0.6\%$. Canopy dieback ($F = 40.78$; df = 1, 524; $p < 0.0001$) and transparency ($F = 6.98$; df = 1, 513; $p = 0.0085$) varied between peninsulas. Significantly more canopy dieback and transparency were recorded in Upper Michigan than in Lower Michigan (Table 3.1). Dieback also varied among initial scale infestation levels ($F = 4.6$; df = 2, 523; $p = 0.01$) and beech basal area ($F = 6.55$; df = 2, 523; $p = 0.0016$), but not among interactions. In moderate and high beech basal area, dieback was greater than in low beech basal area. Sites with light beech scale infestations had significantly higher dieback than other sites (Table 3.1). Transparency did not differ among initial scale infestation or among beech basal area.

Cavities were observed on a total of 68 of the 698 beech trees (Table 3.2). A total of 108 cavities were recorded, 99 of the cavities were on living beech. Overall, 52 small cavities (< 7 cm diameter) were found on 40 beech trees ranging from 14.9 to 84.3 cm DBH, with an average of 40.4 ± 2.5 cm. Moderate-sized cavities (> 7 cm and < 30 cm diameter) were found on 22 beech trees ranging from 19.7 to 84.3 cm DBH, with an average DBH of 49.7 ± 3.3 cm. Large cavities (> 30 cm diameter) were less common, accounting for 24.1% of all cavities recorded (Table 3.2). Large cavities occurred on 24 beech trees; no more than two large cavities were on any individual tree. Beech trees with large cavities ranged from 19.7 to 96.2 cm DBH, with an average DBH of 50.1 ± 3.9 cm.

Coarse Woody Material

We encountered CWM (> 7.6 cm in diameter) in every site and recorded a total of 732 pieces in the 62 sites. Only 310 (42%) of the pieces could be identified to genus or species (Figure 3.2). Unidentifiable CWM occurred in transects 85.0 ± 2.7 % of the time. American beech comprised 25% of the total pieces of CWM and 68.3% of the identifiable pieces, more than any other species. Although the abundance of beech CWM did not differ between Upper and Lower Michigan, more pieces were recorded in high beech basal area than low or moderate beech basal area ($F = 8.53$; $df = 2, 45$; $p = 0.0007$) and in sites with initially heavy beech scale infestation than in other sites ($F = 6.44$; $df = 2, 45$; $p = 0.0035$) (Table 3.3). Paper birch and sugar maple each accounted for four percent of the CWM pieces, while black cherry, eastern hemlock, fir, ironwood, aspen, red maple, white ash, and yellow birch were occasionally encountered.

American beech was the most common identifiable CWM, occurring in 34.9 ±4.3% of sites, including 25 of the 34 sites in Upper Michigan and 14 of the 28 sites in Lower Michigan. Frequency of beech CWM pieces was significantly higher in sites with moderate and high beech basal area than sites with low beech basal area ($F = 3.60$; $df = 2, 45$; $p = 0.0355$) (Table 3.3).

Initial scale infestation level also showed a significant increase in beech CWM pieces from uninfested plots to lightly infested and then to heavily infested ($F = 7.44$; df = 2, 45; $p = 0.0016$). Beech CWM did not differ between Upper and Lower Michigan (Table 3.3).

Diameters of all CWM pieces ranged from 7 to 70 cm; 59% of all pieces were ≤ 15 cm, 34% were between 15 and 30 cm in diameter, while only 7% were over 30 cm. Beech CWM averaged 17.9 ± 1.9 cm in diameter and ranged from 8 to 65 cm. Beech CWM diameter did not differ among initial beech scale infestation levels, beech basal area, or between Upper and Lower Michigan. Only pieces of hemlock CWM were consistently larger than beech. However, paper birch and sugar maple made up the next largest portion of CWM diameters.

Total CWM volume ranged from 7.3 to 312.5 m^3/ha and exceeded 144.0 m^3/ha in three sites in Upper Michigan and one in Lower Michigan. Volume of CWM averaged 63.0 ± 7.0 m^3/ha. In Upper Michigan sites, CWM averaged 73.6 (± 10.5) m^3/ha compared to 50.1 (± 8.4) m^3/ha in Lower Michigan. CWM volume did not vary among initial beech scale infestation levels ($F = 1.69$; df = 2, 45; $p = 0.20$), beech basal area ($F = 1.59$; df = 2, 45; $p = 0.22$), between peninsulas ($F = 0.02$; df = 1, 45; $p = 0.90$) nor were there any significant interactions. Volume of beech CWM ranged from 0 to 112.8 m^3/ha and averaged 14.7 ± 3.2 m^3/ha across all sites. Beech CWM volume did not differ among initial scale infestation levels ($F = 2.63$; df = 2, 45; $p = 0.08$), by beech basal area ($F = 1.25$; df = 2, 45; $p = 0.29$) or between Upper and Lower Michigan sites ($F = 0.43$; df = 1, 45; $p = 0.52$).

Most CWM pieces were fresh (62.6%), followed by moderately decayed at 25% and severely decayed at 12.5% (Figure 3.2). Of the fresh CWM, 94.3% were identifiable and of those 68.3% were beech (Figure 3.3, Figure 3.4). The abundance of CWM in decay classes 0, 1, 2, 3 and 4 did not differ among beech scale infestation levels or among beech basal area. However, in decay class 2, CWM pieces were recorded more often in Upper Michigan than Lower Michigan ($F = 4.73$; $df = 1, 45$; $p = 0.0349$). In decay class 1, beech CWM was significantly higher in sites where beech scale infestation was heavy in 2002 ($F = 8.1$; $df = 2, 45$; $p = 0.001$) (Table 3.5).

Identifiable CWM was similar in 2002, with beech (24%) and paper birch (12%) most abundant, but sugar maple, hemlock, aspen, and black cherry were also common. Large diameter pieces of CWM were more abundant in 2012 than in 2002. Volume did not differ among sites between 2002 and 2012 ($t(61) = 1.42$; $p = 0.17$). Overall, 24.8% of the CWM pieces in 2012 were over 20 cm in diameter, compared to only 15.8% in 2002. The total number of CWM encountered along two transects dropped from 746 logs in 2002 to 501 logs in 2012. In 2002, 42.6% of the logs were moderately decayed and 37.1% were severely decayed, while only 20.2% were fresh (Figure 3.3).

DISCUSSION

Before BBD arrived in Michigan, American beech, with its thin outer bark, was already an easy target for many decay fungi and insects. More than 70 species of decay fungi and several aphids, scales and wood-boring insects take advantage of the relatively thin beech bark (Tubbs and Houston 1990). Most of these pests, however, only attack weakened or dying trees (Tubbs and Houston 1990), unlike BBD, where beech scales colonize relatively healthy beech trees, which then become weakened or dying trees.

Studies in the northeastern U.S. have shown radial growth of beech trees declines in areas with BBD (Mize and Lea 1979, Twery and Patterson 1984, Gavin and Peart 1993, Gove and

Houston 1996). Whether this decrease is attributable to effects of beech scale or the effects of the fungal pathogen is not clear, but a reduction from 2.5 cm per year to 1.6 cm per year in Michigan uninfested and heavily infested stands with beech scale is noteworthy. Ehrlich (1934) speculated that growth reduction could be attributed to beech scale, as well as fungal infection.

Mize and Lea (1979) in the Adirondack Region of New York, concluded that BBD reduced DBH growth substantially over time on 295 beech trees, but were unable to relate growth reduction with any variables examined. The value of my study is that the same 724 individual beech trees were assessed in 2002 and again in 2012. Growth of living beech trees is diminishing in stands that were colonized by beech scale in 2002 and radial growth differed among trees that had heavy, light or absent beech scale infestations in 2002.

The decline in radial growth was consistent regardless of tree size. In other words, smaller trees would normally grow faster than larger, older trees (Mencuccini et al. 2005). My data, however, showed radial growth of smaller trees that were heavily infested was less than growth of larger trees in lightly infested sites and those trees had lower growth rates than trees in uninfested sites.

Canopy dieback and transparency did reflect patterns observed in radial growth and beech mortality. Canopy condition of overstory beech trees was highly variable within and between sites. Typically, symptoms of BBD, particularly fungal infection, include yellowing or thinning foliage, and dieback of large branches, before the entire tree succumbs (Shigo 1972, McCullough et al. 2001). There were relatively few trees with high dieback or thinning estimates that exceeded 50% (18 trees), occurring in stands with higher beech mortality. Most sites (50 of the 62) had relatively low estimates of dieback (< 20%) and 53 of the 62 sites had <

20% thinning. In heavily beech scale infested sites, canopy dieback and transparency may have been low due to higher mortality rates, leaving only more tolerant beech alive.

Dead and dying beech trees no longer produce hard mast, which is an important food resource for a wide variety of birds and mammals (Tubbs and Houston 1990, Hamelin 2011). With a decline in mature beech trees, hard mast production will drop considerably and beech is often the only mast-producing species in many stands within the Beech-Maple cover type. *Quercus* spp. also provide hard mast, but the northern range of many oak species, like white (*Q. alba*) and black oak (*Q. velutina*) ends in Lower Michigan (Rogers 1990, Sanders 1990). The only other hard mast species recorded in our sites was red oak, which was present in only seven of the 62 sites. Beechnuts contain approximately twice as much crude protein as red oak acorns and beech nuts and red oak acorns have twice as much fat as white oak acorns (Hamelin 2011). Black bears, for example, may not be able to acquire enough food to produce offspring without the nutrition beechnuts add to their diet (Faison and Houston 2004, Rogers 1987). Four times as many female black bears reproduce in years with high beechnut production than in years with poor beechnut production (Hamelin 2011).

Birds and small mammals use American beech for shelter as well. Cavities in living trees are generally overlooked, but they can have as much influence on birds and small mammals in a forested stand as snags (Allen 1990, Kahler and Anderson 2006). Birds such as red-breasted nuthatch (*Sitta canadensis*) and the federally endangered northern flying squirrel (*Glaucomys sabrinus*) are among numerous species that rely on cavities for nesting to breed (Kahler and Anderson 2006). Most of my sites had at least one beech tree with cavities and I recorded a total of 108 cavities, 99 cavities on living beech plus another 9 cavities on beech snags. As large beech trees succumb to beech bark disease or break, cavities in these stands will likely become less abundant. Whether other overstory species will provide adequate cavities for birds and other wildlife in these areas remains to be seen.

In the short-term, beech snags will become more abundant as large diameter beech trees die benefiting a wide range of animals. Snags are essential for over 135 species of birds, small mammals, reptiles, amphibians and invertebrates in North America (Davis 1983). Some birds are primary excavators, creating their own cavities for nesting in dead tree snags and providing cavities for secondary excavators later on (Morrison et al. 1986). However, snags will eventually fall. Snags and CWM may also increase fuel loads for wildfires (Brown et al. 2003), although wildfires rarely occur in northern hardwood forests and when they occur, have historically been trivial (Cardille and Ventura 2001).

In sites where beech scale was already present in 2002-03, CWM increased substantially by 2012. In New York, volume of CWM normally ranged from 15 to 45 m^3/ha in stands without beech bark disease, but exceeded 166 ± 42 m^3/ha in areas with BBD (Carbonneau 1986, McGee 2000). In Michigan, beech bark disease is more recent and most sites have been infested for < 10 years. CWM volume has only exceeded 124 m^3/ha in only four sites in Upper Michigan and one site in Lower Michigan under the influence of BBD since 2002. However, as indicated by the long term impact trees and mortality in Chapter 2, beech is declining and dying in Upper Michigan, leading to a pulse of fresh beech CWM as overstory beech fall. In the short-term, arthropods will have more material to decompose, mineralizing more nutrients for plants and increasing soil fertility, potentially increasing productivity and health (Niwa 2001).

Diameter and decay class of CWM can influence survival of many species. Overall, the diameter of CWM pieces and abundance of CWM in the sites sampled in 2012 is similar to that recorded in 2002. The decay class of CWM, however, has shifted to more recently downed material with a notable increase in fresh beech CWM. Large decayed logs act as moisture sinks on the forest floor and serve as a critical nutrient source for surrounding plants (Fraver et al. 2002). Protected by CWM from large herbivores like white-tailed deer (*Odocoileus virginianus*), seedlings have an optimal location to flourish (Horsley et al. 2000). Furthermore, larger diameter logs increase habitat for small amphibians and mammals such as eastern red-backed salamander (*Plethodon cinereus*) and American marten (*Martes americana*), directly influencing their survival (Strojny et al. 2010, Gilber et al. 1997). In the long term, however, as overstory beech die, CWM will decompose, leaving the stands with short lived benefits from BBD.

Table 3.1: Average (±SE) DBH in 2002-03 and 2011-12, radial growth, canopy dieback, transparency and survival of beech trees (*Fagus grandifolia*) in 62 sites in 2012 grouped by beech basal area, initial scale infestation levels and between Upper and Lower Michigan. Within groups (column), different letters indicate a significant (α≤0.05) difference between DBH (A,B,C). Within years (row), different letters indicate a significant (α≤0.05) difference between DBH (x,y).

	DBH (cm) 2002-03	DBH (cm) 2011-12	Radial growth (cm)	Canopy dieback (%)	Transparency (%)	Survival (% alive)
Beech Basal Area*						
Low	29.7 ± 0.9 A x	32.3 ± 0.9 A y	2.6 ± 0.2 B	7.6 ± 0.8 A	14.5 ± 0.8 A	91.1 ± 3.5 B
Moderate	33.7 ± 0.8 B x	35.8 ± 0.8 B y	2.1 ± 0.3 A	12.0 ± 1.2 B	17.2 ± 1.1 A	74.4 ± 6.7 A
High	33.7 ± 1.0 B x	36.7 ± 1.0 B y	2.3 ± 0.2 AB	11.2 ± 1.6 B	15.2 ± 1.5 A	74.9 ± 8.1 A
Initial Beech Scale Infestation**						
Absent	32.5 ± 0.6 B x	35.0 ± 0.7 B y	2.5 ± 0.2 C	8.9 ± 0.6 B	15.4 ± 0.7 A	91.8 ± 2.9 B
Light	34.1 ± 2.9 B x	36.2 ± 3.1 B x	2.1 ± 0.2 B	17.0 ± 2.8 C	17.8 ± 1.9 A	56.9 ± 8.8 A
Heavy	28.2 ± 1.3 A x	30.7 ± 1.3 A x	1.6 ± 0.2 A	4.2 ± 1.5 A	9.2 ± 2.4 A	71.4 ± 10.4 A
Peninsula						
Lower	30.3 ± 0.9 A x	33.2 ± 0.9 A y	2.5 ± 0.2 B	7.4 ± 0.8 A	13.0 ± 0.7 A	95.6 ± 1.3 B
Upper	33.7 ± 0.6 B x	35.8 ± 0.6 B y	2.1 ± 0.2 A	12.4 ± 1.0 B	18.2 ± 1.0 B	69.7 ± 5.6 A

* Beech basal area classed as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha) in 2002.

** Initial beech scale infestation classed as absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

Table 3.2: Long term individual trees containing cavities grouped by DBH and frequency of cavities and separated by cavity size among stands with low, moderate, and high beech basal area, initial *C. fagisuga* infestation levels (absent, light or heavy) and by peninsula in 2011-12. Within groups (column), different letters indicate a significant (α≤0.05) difference between DBH and frequency of cavites (A,B,C). Within cavity sizes (row), different letters indicate a significant (α≤0.05) difference between DBH and frequency of cavities (x,y,z).

	Cavity Size*							
	Small	Moderate	Large	Total	Small	Moderate	Large	Total
Beech Basal Area**	**DBH of trees with Cavities**				**Frequency of trees with Cavities**			
Low	37.9 ± 5.0Ax	45.9 ± 5.5Ay	53.9 ± 8.7Ay	41.6 ± 4.0A	0.7 ± 0.1Ay	0.5 ± 0.2Axy	0.3 ± 0.1Ax	1.5 ± 0.2B
Moderate	40.7 ± 4.4Ax	50.1 ± 5.7Ax	48.2 ± 5.4Ax	47.4 ± 3.5A	0.9 ± 0.2Ay	0.5 ± 0.1Bx	0.5 ± 0.1Ax	1.9 ± 0.2B
High	44.1 ± 4.3Ax	49.4 ± 2.3Ax	49.6 ± 8.0Ax	46.2 ± 3.1A	0.6 ± 0.1Ay	0.2 ± 0.1Ax	0.3 ± 0.1Ax	1.2 ± 0.1A
Initial Scale Infestation Level***								
Absent	41.6 ± 2.7Bx	49.9 ± 3.7Ay	49.3 ± 4.5Ay	45.6 ± 2.2A	0.8 ± 0.1Ay	0.4 ± 0.1Ax	0.4 ± 0.1Ax	1.6 ± 0.1A
Light	28.4 ± 8.9Ax	48.9 ± 6.8Ay	55.5 ± 0.5By	41.0 ± 6.2A	0.7 ± 0.3Ax	0.4 ± 0.2Ax	0.4 ± 0.2Ax	1.6 ± 0.3A
Heavy	NA	NA	NA	NA	NA	NA	NA	NA
Peninsula								
Lower	40.9 ± 3.2Ax	49.8 ± 4.7Ay	57.5 ± 7.1By	46.7 ± 3.0A	0.9 ± 0.1By	0.4 ± 0.1Ax	0.3 ± 0.1Ax	1.6 ± 0.2A
Upper	39.7 ± 4.1Ax	49.7 ± 4.7Ay	43.8 ± 3.5Axy	42.5 ± 2.6A	0.6 ± 0.1Ax	0.5 ± 0.2Ax	0.5 ± 0.1Bx	1.6 ± 0.2A

* Cavity size recorded as small (< 7 cm), moderate (> 7 cm and < 30 cm), or large (> 30 cm).

** Beech basal area recorded as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha).

*** Initial scale infestation level recorded as absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

Table 3.3: Coarse woody material (CWM) frequency (% of pieces per transect), abundance (No. of pieces) and size (cm dia.) among stands with low, moderate, and high beech basal area, initial *C. fagisuga* infestation levels (absent, light or heavy) and by peninsula in 2011-12. Within groups (column), different letters indicate a significant ($\alpha \leq 0.05$) difference between frequency, abundance and size of CWM (A,B,C).

	Frequency	Abundance	Size
Beech Basal Area*			
Low	18.0 ± 5.3A	1.3 ± 0.5A	19.0 ± 3.1B
Moderate	40.3 ± 6.3B	2.3 ± 0.5B	16.8 ± 3.0AB
High	56.4 ± 10.9B	7.5 ± 1.9C	14.7 ± 1.0A
Initial Scale Infestation Level**			
Absent	22.8 ± 4.9A	1.5 ± 0.4A	17.7 ± 3.5AB
Light	44.4 ± 8.5B	4.0 ± 1.6B	22.0 ± 4.3B
Heavy	66.7 ± 9.0C	7.3 ± 1.5C	15.2 ± 1.2 A
Peninsula			
Lower	27.4 ± 6.4A	2.4 ± 0.7A	18.7 ± 3.7A
Upper	41.2 ± 5.6B	3.5 ± 0.8A	17.5 ± 2.2A

* Beech basal area recorded as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha).

** Initial scale infestation level recorded as absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

Table 3.4: Average (± SE) coarse woody material (CWM) volume (m^3/ha) in 2012 grouped by decay class among sites with absent, light, and heavy *C. fagisuga* (beech scale) infestation and low, moderate and high beech basal area in 2002. Different letters indicate a significant ($\alpha \leq 0.05$) difference in CWM volume within columns (A,B,C) and rows (x,y,z).

	Initial *C. fagisuga* infestation			
Beech BA	Absent	Light	Heavy	All sites
		Decay Class 0*		
low	20.0 ± 13.4 B y	14.1 ± 6.4 A y	0.4 ± 0.4 A x	17.3 ± 9.7 A
moderate	3.7 ± 1.1 A x	28.3 ± 23.4 A y	2.2 ± 2.2 A x	8.6 ± 5.0 A
high	4.5 ± 2.8 AB x	39.2 ± 26.2 A y	11.8 ± 2.8 B y	13.2 ± 4.7 A
all stands	11.4 ± 6.3 xy	24.2 ± 10.4 y	7.1 ± 2.3 x	13.1 ± 4.5
		Decay Class 1		
low	15.1 ± 3.7 A x	26.5 ± 8.0 A x	13.5 ± 9.2 A x	17.2 ± 3.2 A
moderate	15.6 ± 3.4 A x	28.4 ± 21.5 A x	28.7 ± 12.5 AB x	19.9 ± 5.0 A
high	14.9 ± 3.1 A x	24.8 ± 11.2 A xy	35.4 ± 10.9 B y	25.8 ± 5.8 A
all stands	15.3 ± 2.2 x	27.0 ± 9.0 y	29.6 ± 7.0 y	20.1 ± 2.6
		Decay Class 2		
low	14.9 ± 3.6 A y	11.5 ± 5.3 A xy	4.9 ± 4.9 A x	13.4 ± 2.8 A
moderate	12.8 ± 3.5 A xy	51.2 ± 17.3 B z	9.4 ± 5.8 A x	20.7 ± 5.3 A
high	9.6 ± 1.8 A x	12.3 ± 4.0 A xy	19.8 ± 6.9 B y	14.7 ± 3.4 A
all stands	13.4 ± 2.2 x	28.2 ± 9.2 y	14.2 ± 4.4 x	16.4 ± 2.4
		Decay Class 3		
low	5.8 ± 2.0 A xy	44.4 ± 39.3C y	2.1 ± 2.1 A x	13.2 ± 8.0 A
moderate	15.2 ± 6.0 B y	1.2 ± 0.9 B x	1.4 ± 0.7 A x	10.6 ± 4.2 A
high	9.9 ± 4.7 AB y	0 ± 0 A x	4.2 ± 2.8 A y	5.7 ± 2.3 A
all stands	10.2 ± 2.7 y	19.0 ± 16.6 xy	3.0 ± 1.5 x	10.6 ± 3.6
		Decay Class 4		
low	4.5 ± 1.1 B x	8.8 ± 5.4 B x	3.5 ± 3.5 A x	4.6 ± 1.3 B
moderate	2.7 ± 1.3 B y	0 ± 0 A x	1.3 ± 1.3 A xy	2.0 ± 0.9 A
high	0.5 ± 0.5 A xy	0 ± 0 A x	4.1 ± 3.3 A y	2.1 ± 1.6 AB
all stands	2.8 ± 0.7 x	3.7 ± 2.5 x	3.2 ± 1.9 x	3.1 ± 0.7
		Decay Classes Pooled		
low	59.4 ± 15.6 A y	105.3 ± 36.1 A y	24.3 ± 15.2 A x	65.8 ± 13.7 A
moderate	49.2 ± 6.9 A x	109.1 ± 38.7 A y	43.0 ± 16.4 AB x	60.9 ± 10.2 A
high	39.5 ± 7.1 A x	76.3 ± 11.0 A y	75.2 ± 17.4 B y	61.6 ± 9.6 A
all stands	52.7 ± 7.7 x	102.0 ± 21.0 y	57.2 ± 12.0 x	63.0 ± 7.0

* Decay was classed as 0 (fresh material with intact bark and no obvious decay), 1 (bark starting to fall off, or the bark may be absent, but the inner sapwood was still solid), 2 (some decay; under impact, small wood chips break off, but the center remained firm), 3 (decaying; maintained original shape, but under impact loses form) or 4 (decayed; no structural integrity).

Table 3.5: Average (± SE) volume (m^3/ha) of beech coarse woody material (CWM) in 2012 grouped by decay class among stands with absent, light, and heavy *C. fagisuga* (beech scale) infestation and low, moderate and high beech density in 2002. Within groups (column), different letters indicate a significant (α≤0.05) difference between CWM volume (A,B,C). Within initial *C. fagisuga* infestation (row), different letters indicate a significant (α≤0.05) difference between CWM volume (x,y,z).

	Decay Class*			
	0	**1**	**2**	**3**
Beech Basal Area**				
Low	3.1 ± 1.8 A y	4.1 ± 1.7 A y	0.03 ± 0.03 A x	0 ± 0 A x
Moderate	7.5 ± 5.0 AB y	3.1 ± 1.8 A y	0 ± 0 A x	3.2 ± 3.1 B y
High	10.2 ± 4.9 B z	14.9 ± 5.5 B z	3.3 ± 1.8 B y	0 ± 0 A x
Initial Scale Infestation Level***				
Absent	2.8 ± 1.2 A y	1.9 ± 0.9 A y	0.1 ± 0.1 B x	1.9 ± 1.9 A xy
Light	21.3 ± 10.8 B z	4.4 ± 2.2 A y	0 ± 0 A x	0 ± 0 A x
Heavy	5.5 ± 2.0 A y	21.8 ± 6.3 B z	3.5 ± 2.1 C y	0.2 ± 0.2 A x
Peninsula				
Lower	3.3 ± 1.5 A z	5.5 ± 2.2 A z	0.8 ± 0.4 A y	0 ± 0 A x
Upper	9.7 ± 4.1 B y	6.2 ± 2.3 A y	0.7 ± 0.7 A x	2.2 ± 2.2 B xy

* Decay classes recorded as 0 (fresh material with intact bark and no obvious decay), 1 (bark starting to fall off, or the bark may be absent, but the inner sapwood was still solid), 2 (some decay; under impact, small wood chips break off, but the center remained firm), 3 (decaying; maintained original shape, but under impact loses form) or 4 (decayed; no structural integrity).

** Beech basal area recorded as low (<9 m^2/ha), moderate (9-18 m^2/ha) or high (>18 m^2/ha).

*** Initial scale infestation level recorded as absent (no infested trees), light (less than 50% of beech trees infested), or heavy (greater than 50% of beech trees infested).

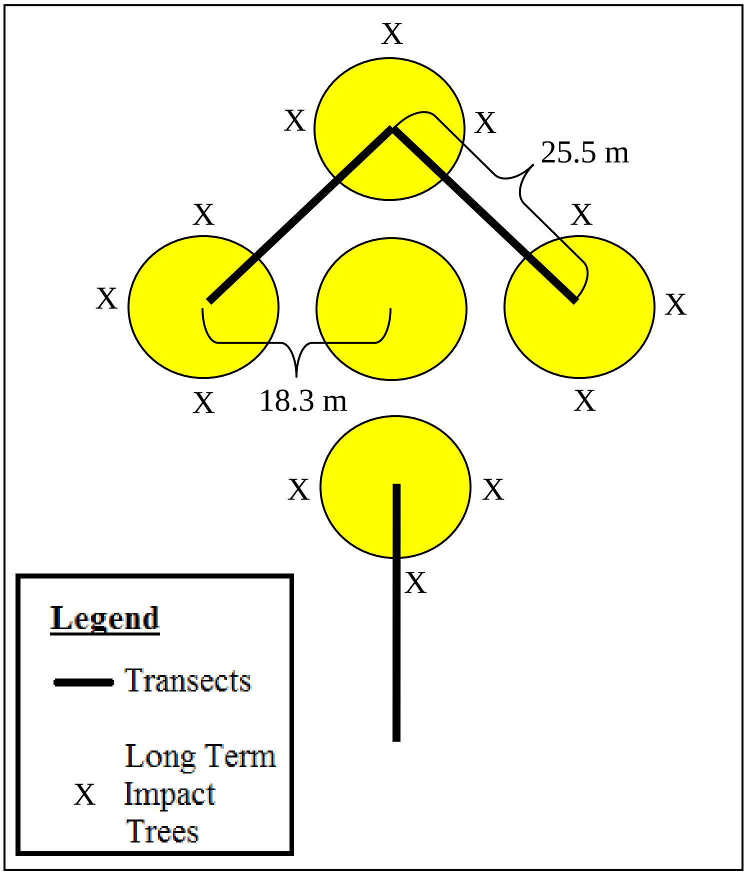

Figure 3.1: Location of transects for coarse woody material (CWM) survey and long term impact trees within each plot.

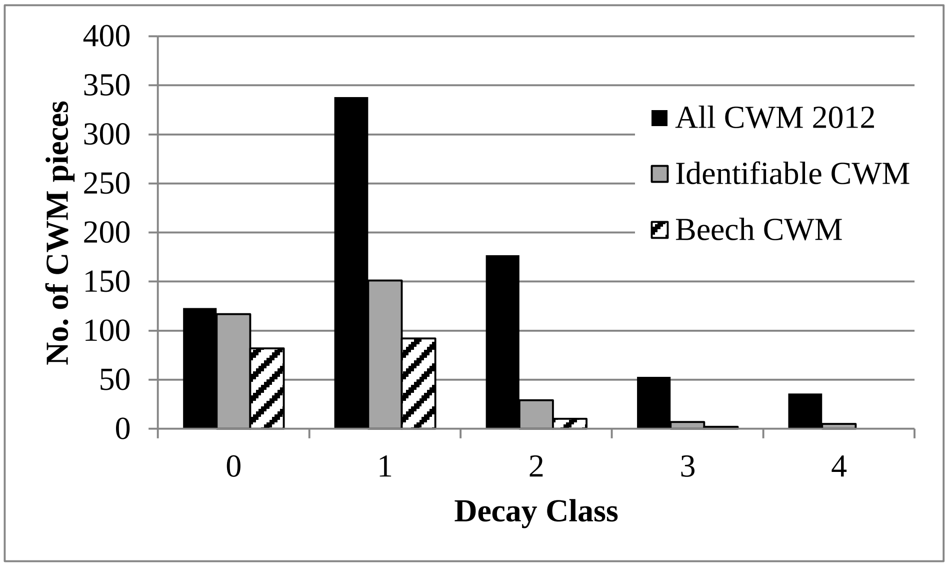

Figure 3.2: Total number of pieces of coarse woody material (CWM), identifiable CWM, and beech CWM recorded in 2012 grouped by decay class in 62 sites. Decay was classed as 0 (fresh material with intact bark and no obvious decay), 1 (bark starting to fall off, or the bark may be absent, but the inner sapwood was still solid), 2 (some decay; under impact, small wood chips break off, but the center remained firm), 3 (decaying; maintained original shape, but under impact loses form) or 4 (decayed; no structural integrity).

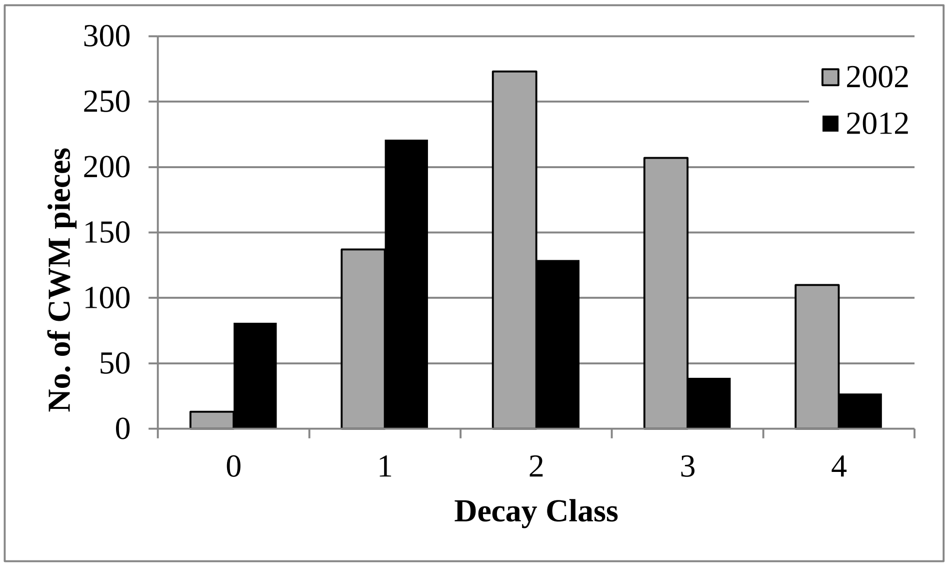

Figure 3.3: Total pieces of coarse woody material (CWM) encountered in the original 62 sites in 2002 and 2012 grouped by decay class. Decay classes recorded as 0 (fresh material with intact bark and no obvious decay), 1 (bark starting to fall off, or the bark may be absent, but the inner sapwood was still solid), 2 (some decay; under impact, small wood chips break off, but the center remained firm), 3 (decaying; maintained original shape, but under impact loses form) or 4 (decayed; no structural integrity).

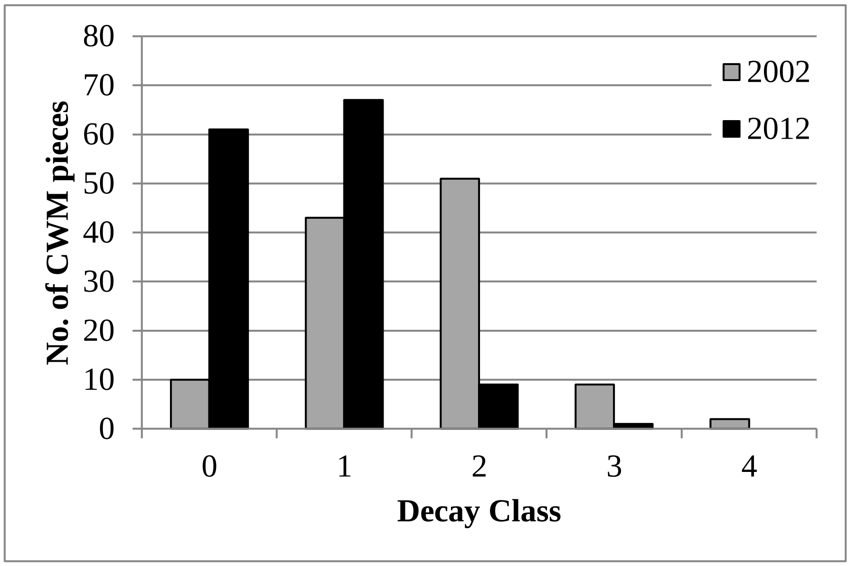

Figure 3.4: Abundance of American beech coarse woody material (CWM) recorded in 2002 and 2012 by decay class. Decay classes recorded as 0 (fresh material with intact bark and no obvious decay), 1 (bark starting to fall off, or the bark may be absent, but the inner sapwood was still solid), 2 (some decay; under impact, small wood chips break off, but the center remained firm), 3 (decaying; maintained original shape, but under impact loses form) or 4 (decayed; no structural integrity).

APPENDIX

DYNAMICS OF: *CRYPTOCOCCUS FAGISUGA* LIND., THE INSTIGATOR OF BEECH BARK DISEASE

INTRODUCTION

The nonindigenous, sap-feeding beech scale insect (*Cryptococcus fagisuga* Lind.) has continued to spread across much of the North American continent. This microscopic insect, only 0.5 mm in length, facilitates entry of the cambium-killing *Neonectria* fungi into American beech (*Fagus grandifolia*) trees. The complex of beech scale infestation and *Neonectria* infection is referred to as Beech Bark Disease (BBD) (Castlebury et al. 2006).

Native to western Asia and southeastern Europe, beech scale was transported to Nova Scotia, Canada around 1890 on imported nursery stock (Gwiazdowski et al. 2006). Beech scale had spread west to Ohio and parts of Tennessee and south to North Carolina by 1994. Today, BBD is present in slightly less than 50% of the native range of American beech in North America (Houston and O'Brien 1994, Morin 2007, Garnas 2011).

Beech scale is a univoltine, parthenogenic insect that lays an average of 50 eggs per adult (Ehrlich 1934, Wainhouse and Gate 1988). First instars, known as crawlers (Wainhouse 1980), must find a suitable location to feed, either on the beech tree where they hatched or following dispersal by wind (Felt 1933, Wainhouse 1980) or other vectors such as birds or other mobile wildlife that come in contact with eggs and/or crawlers (Ehrlich 1934, Houston 1994, Morin et al. 2007). When a suitable location is acquired, crawlers begin to feed, driving their 2 mm long stylets, or mouthparts, through the outer bark and piercing parenchyma cells. Once feeding begins, crawlers molt, losing their legs and become immobile (Shigo 1972). As beech scales feed, they secrete white wax which protects individual scales and causes heavily infested trees to appear to be coated with white 'wool' (Ehrlich 1934, Houston and O'Brien 1983)

After beech scales die, the small incisions in the bark allow *Neonectria* spores access to the cambium tissue (Ehrlich 1934, Castlebury et al. 2006). Two fungi are known to be associated with BBD; *Neonectria faginata* and *Neonectria ditissima* (Castlebury et al. 2006). The nonindigenous *N. faginata* attacks only the genus *Fagus* and is a variation of the European species *N. coccinea*. In contrast, *N. ditissima,* is a generalist that infects a variety of hardwoods in Europe and North America and is synonymous with *N. galligena* (Castlebury et al. 2006). The *Neonectria* fungi kills a small patch of cambium tissue. Patches coalesce over time, girdling large branches and even the trunk (Ehrlich 1934).

Three distinct phases are frequently used to describe beech bark disease (Shigo 1972, Houston and O'Brien 1983, Houston 1994). "The advancing front," denotes the first phase of BBD and represents areas that are infested with beech scale, but *Neonectria* is not present (Houston and O'Brien 1983). When *Neonectria* infects trees, the area shifts into the "the killing front." In this phase, approximately half of the beech trees over 25 cm in diameter at breast height (DBH) are expected to die (Houston 1994). Following substantial beech mortality, stands enter the third phase called "the aftermath forest." Here the disease persists, but beech overstory is typically replaced by other species (Shigo 1972, Houston 1994).

Small fissures in the bark, developed by beech scale feeding habits, provide entry for *Neonectria* fungi and become more abundant as beech scale densities increase, leading to beech mortality (Koch 2007). In 2007, we began a unique effort to track beech scale density on 145 individual trees in 14 sites. Sites were visited and specific areas on the same trees were photographed three times a year. Changes in wax produced by beech scale were quantified using imaging software (Wieferich et al. 2013). Visual estimates of scale density were also recorded. Photos and visual estimates of scales were repeated in 2008 and again in 2010-2012 at similar times of the year. Changes in beech scale density on individual trees and among trees within stands were evaluated over time. I also recorded the aspect of the first beech scales on newly infested trees and DBH of the individual trees.

To date, most studies on beech scale rely on visual estimates of scale density based on the presence and amount of bark covered by white wax (Wiggins et al. 2004, Houston et al. 2005, Kearney et al. 2005, Kasson and Livingston 2011). These subjective estimates are qualitative and may vary among observers. Recently, digital photography has been used to monitor scale density over time and may be more effective in detecting small changes in scale abundance than visual estimates of wax (Teale et al. 2009, Wieferich et al. 2013). However, digital photos may not fully represent the entire tree and typically require more time to analyze than visual estimates (Teale et al. 2009, Wieferich et al 2013).

METHODS

Site Establishment

In 2007, one fixed-radius plot, eight m in diameter, was established in 14 sites across the distribution of beech scale in Lower Michigan by a former Michigan State University graduate student, Daniel Wieferich. Four sites were selected in forested land in Emmett County, three were in Ludington State Park in Mason County, and seven were west of Cadillac in Wexford County (Figure 4.1). Within all plots, any beech tree over 6 cm in diameter at breast height (DBH) was tagged to ensure it would be re-located on subsequent visits. Individual plots contained two to 22 beech trees, with a mean of 10.4 (±1.0) beech trees per plot. When plots had less than eight beech trees, beech trees in close proximity to the perimeter of the plot were tagged until eight trees were included. In one site, beech density was so low that only five trees could be tagged.

Site Re-visits

Following establishment in July 2007, plots were revisited in October 2007, in March, July and again in October 2008 by Wieferich et al. (2013). I returned to these same plots to continue the study in August 2010, March, July and October 2011 and again in March, July, and November 2012. Timing corresponded to peak beech scale populations (July), scale populations after reproduction and dispersal (October/November), and following any winter mortality (March).

Procedures

Digital photography methods and qualitative visual estimates were used to estimate beech scale density. Photos were taken at 0.9 m, 1.2 m, and 1.5 m aboveground on each tagged tree at azimuths randomly selected in 2007. Photos were taken using a fixed lens and a built-in stabilizer to ensure the camera was the same distance from the tree (30 cm) and to guarantee the same area of the trunk was photographed each time. Two photos were taken at each position on every visit. Shadows and bright sun rays within the photographed area were blocked with a clipboard to reduce contrast within the photo.

Scale density for the entire tree was also visually estimated on each visit using a reference card to help produce more consistent results. Scale was classed as class 0 (absent) if no beech scale was present, 1 (trace) if only a few waxy spots were seen, 2 (patchy) if large amounts of scale wax was present, but only in clusters, or 3 (whitewashed) if at least one side was completely covered in scale wax. Along with the photos and visual scale estimates, DBH was also measured annually in all trees.

Photo Analysis

After photos were taken, they were uploaded to a computer and sorted. The better of the two photos taken at each position on each tree was analyzed using the image analysis software ImageJ V1.43. Photos were imported into ImageJ as JPEG images, and then scanned for beech scale evidence (wax). Images with beech scale wax were then converted to 8-bit images. A binary threshold was applied to the 8-bit images to identify and estimate area of the patches of white wax. Thresholds were manually adjusted for each photo, depending on photo contrast, brightness, and quality. In a few cases, threshold adjustments did not effectively distinguish between white wax and bark. Those images were edited by blacking out light bark, until the white wax could be separated from the rest of the photo. For each photo, we calculated percentage of the bark covered by wax in the photographed area. The linear relationship $Y = 869.02x + 45.798$ where Y is the number of beech scales per cm^2 and x is the percentage of bark covered by wax in the photo (Wieferich et al. 2013) was used to estimate the number of beech scales in each photo .

Statistical Analysis

Statistical analyses were performed using SAS 9.2 statistical software (SAS Institute 2003). Beech scale densities were calculated using percent wax coverage and its linear relationship $Y = 869.02x + 45.798$. Normality was tested for all variables using the Shapiro-Wilk test and residual plots (Shapiro and Wilk 1965). Repeated measures ANOVA [proc mixed] was applied to evaluate variability in beech scale densities among sites, counties and between inland and coastal sites over time. A one way ANOVA was used to determine if beech scale densities differed among azimuths of beech trees and to assess radial growth of beech trees among sites, counties and between inland and coastal sites.

RESULTS

Visual Estimates of Scale Abundance

A total of 144 beech trees were marked in the 14 plots in 2007. DBH averaged 24.6 ± 1.2 cm and ranged from 6 to 86.4 cm in 2007. By 2012, average DBH was 26.2 ± 1.3 cm and ranged from 6 to 84.6 cm.

Initially in 2007, 36 beech were uninfested by beech scale, 62 were infested with trace amounts of wax, 28 were grouped as patchy, 16 as whitewashed and two were dying beech. By 2010, four beech trees had succumbed to BBD (Two in Wexford County and two in Mason County) and only 11 of the 140 beech trees were uninfested. In 2011, two more beech trees died in Wexford County, increasing the number of dead to six. Of the 138 live beech trees examined in 2012, all were infested, with 41 having a trace amount of beech scale, 33 were classified as patchy and the remaining 64 were whitewashed.

Visual Estimates Versus Digital Photo Assessments

Comparing the visual estimates to the calculated beech scales from the digital images on the 1692 tree samples, photos did not detect beech scale on 41 trees that were visually observed as infested. Number of beech scales were then calculated using the equation above developed by Wieferich et al. (2013) on infested trees. Beech trees visually estimated to have trace amounts of wax ranged from 2 to 1534 scales per cm^2 (Table 4.1). Trees that were patchy ranged from 5 to

523 scales per cm^2 and whitewashed trees ranged from 7 to 3858 scales per cm^2 (Table 4.2, Table 4.3).

Scale Population Assessments

Of the 144 beech trees, 102, 101, 106 and 105 photos were taken on the east, north, south and west azimuth of the tree, respectively. Beech scale densities did not differ on the trunk of each tree among azimuths ($W = 0.5225$; $df = 3, 402$; $p = 0.5916$) (Table 4.4). Beech scale densities did differ among sites ($F = 13.63$; $df = 13, 1678$; $p < 0.0001$) (Table 4.5) and counties (Mason, Wexford and Emmet County) ($F= 15.64$; $df = 2, 1689$; $p < 0.0001$) (Figure 4.2). Beech scale populations in two sites in Emmet County have increased considerably more than other twelve sites (Figure 4.3).

Table A.1: Average (± SE) beech scale (*Cryptococcus fagisuga*) abundance per cm^2 on beech trees classed as having a trace[1] (low) beech scale infestation grouped by time. Within groups, different letters indicate a significant ($\alpha \leq 0.05$) difference between scale abundance (A,B,C,D,E,F).

		***C. fagisuga* abundance per cm^2**		
Time	No. of trees	Minimum	Maximum	Average
Summer 2007	60	15	313	46 ± 7 BC
Fall 2007	59	16	306	54 ± 6 CD
Spring 2008	60	15	65	30 ± 3 A
Summer 2008	62	16	442	46 ± 7 BC
Fall 2008	74	16	78	43 ± 2 B
Summer 2010	56	31	291	72 ± 6 DE
Spring 2011	36	46	184	61 ± 5 D
Summer 2011	46	15	1,129	96 ± 26 EF
Fall 2011	40	36	1,644	168 ± 55 F
Spring 2012	41	47	471	80 ± 12 E
Summer 2012	33	46	78	54 ± 1 C
Fall 2012	41	46	161	65 ± 4 DE

[1] Trace - Only a few spots of beech scale wax were present.

Table A.2: Average (± SE) beech scale (*Cryptococcus fagisuga*) abundance per cm^2 on beech trees classed as having a patchy[1] (moderate) beech scale infestation grouped by time. Within groups, different letters indicate a significant ($\alpha \leq 0.05$) difference between scale abundance (A,B,C).

		***C. fagisuga* abundance per cm^2**		
Time	No. of trees	Minimum	Maximum	Average
Summer 2007	28	61	1,128	268 ± 47 B
Fall 2007	17	66	486	210 ± 33 B
Spring 2008	25	47	286	108 ± 14 A
Summer 2008	32	33	1,278	187 ± 52 B
Fall 2008	35	51	267	99 ± 10 A
Summer 2010	43	55	977	272 ± 34 B
Spring 2011	28	49	1,052	261 ± 49 B
Summer 2011	49	53	2,686	401± 69 C
Fall 2011	27	46	827	273 ± 39 B
Spring 2012	41	56	3,376	494 ± 92 CD
Summer 2012	30	52	2,473	564 ± 107 CD
Fall 2012	33	53	2,919	717 ± 142 D

[1]Patchy - Large clusters of beech scale were present.

Table A.3: Average (± SE) beech scale (*Cryptococcus fagisuga*) abundance per cm^2 on beech trees classed with a beech scale infestation level of whitewashed[1] grouped by time. Within groups, different letters indicate a significant ($\alpha \leq 0.05$) difference between scale abundance (A,B,C).

		***C. fagisuga* abundance per cm^2**		
Time	No. of trees	Minimum	Maximum	Average
Summer 2007	16	123	5,551	1,658 ± 414 CD
Fall 2007	19	55	6,223	1,692 ± 406 CD
Spring 2008	20	55	2,893	942 ± 154 BC
Summer 2008	16	75	1,732	382 ± 108 A
Fall 2008	18	101	2,637	653 ± 179 AB
Summer 2010	30	46	5,387	1,229 ± 250 C
Spring 2011	67	69	7,839	1,271 ± 198 C
Summer 2011	45	59	11,486	1,910 ± 316 D
Fall 2011	72	46	13,379	2,228 ± 322 D
Spring 2012	58	206	15,923	3,197 ± 480 E
Summer 2012	75	71	24,893	3,578 ± 534 E
Fall 2012	64	118	22,396	3,773 ± 581 E

[1]Whitewashed - At least one aspect of the beech tree was heavily covered in beech scale.

Table A.4: Average (±SE) beech scale (*Cryptococcus fagisuga*) abundance per cm^2 grouped by azimuth. Within azimuths, different letters indicate a significant ($\alpha \leq 0.05$) difference between beech scale densities (A,B,C,D).

Azimuth	**No. of Trees**	**No. of Scales per cm^2**
East	101	1,979 ± 429 A
North	98	2,317 ± 452 A
South	105	1,539 ± 346 A
West	102	1,867 ± 380 A

Table A.5: Average (±SE) beech scale (*Cryptococcus fagisuga*) abundance per cm^2 grouped by site. Within sites, different letters indicate a significant ($\alpha \leq 0.05$) difference between beech scale densities (A,B,C,D,E,F).

Site No.	**County**	**No. of Trees**	**No. of Scales per cm^2**
1	Emmet	10	1,550 ± 335 E
2	Emmet	12	2,051 ± 377 F
3	Emmet	10	450 ± 91 C
4	Emmet	4	120 ± 30 B
5	Mason	10	478 ± 48 C
6	Mason	9	485 ± 111 CD
7	Mason	8	667 ± 92 D
8	Wexford	22	62 ± 8 A
9	Wexford	7	59 ± 21 A
10	Wexford	7	1057 ± 217 E
11	Wexford	11	1131 ± 163 E
12	Wexford	9	146 ± 25 B
13	Wexford	11	1227 ± 173 E
14	Wexford	11	1359 ± 114 E

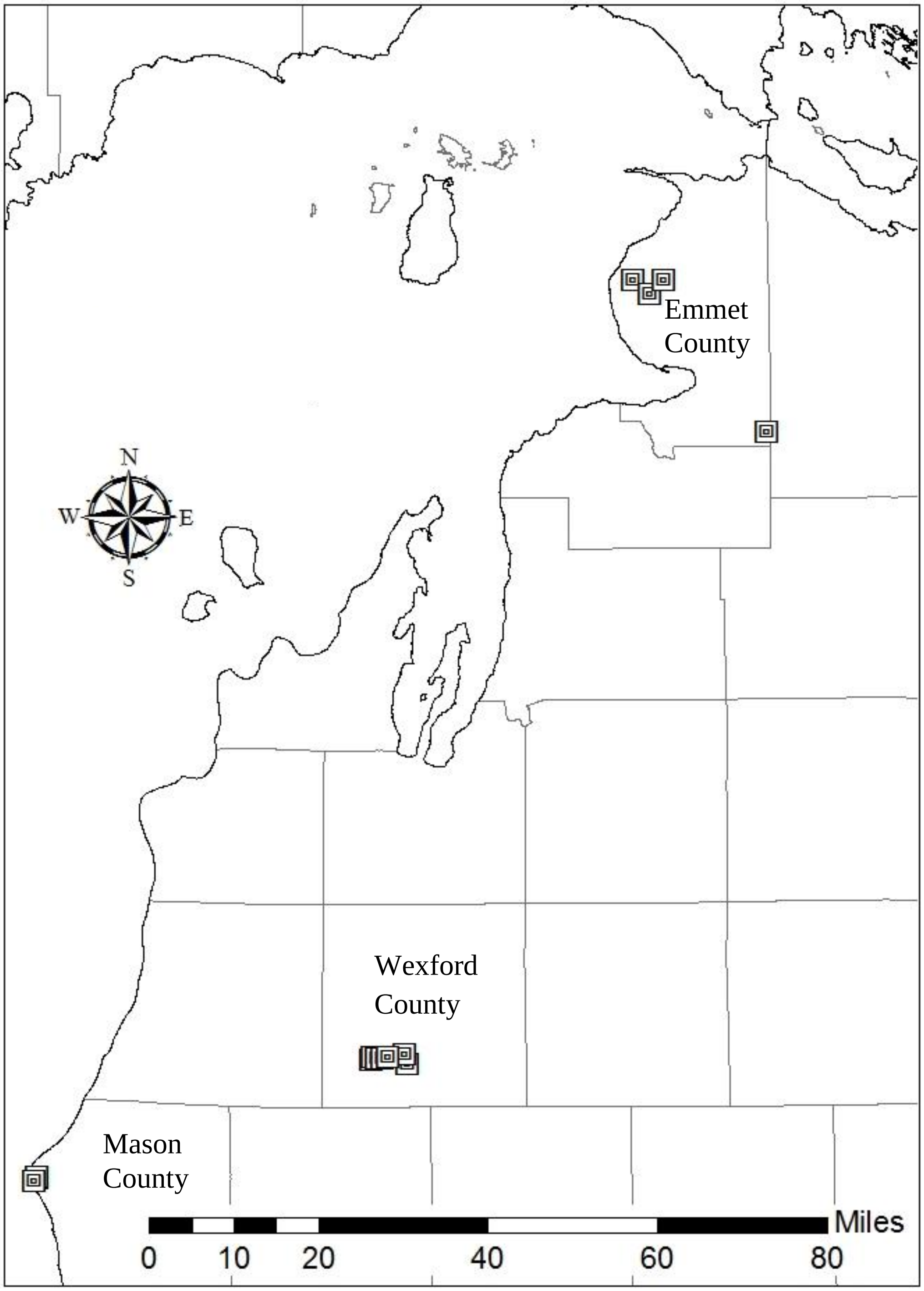

Figure A.1: Distribution of beech scale (*Cryptococcus fagisuga* Lind.) dynamic plots across the northwestern Lower Peninsula in Michigan.

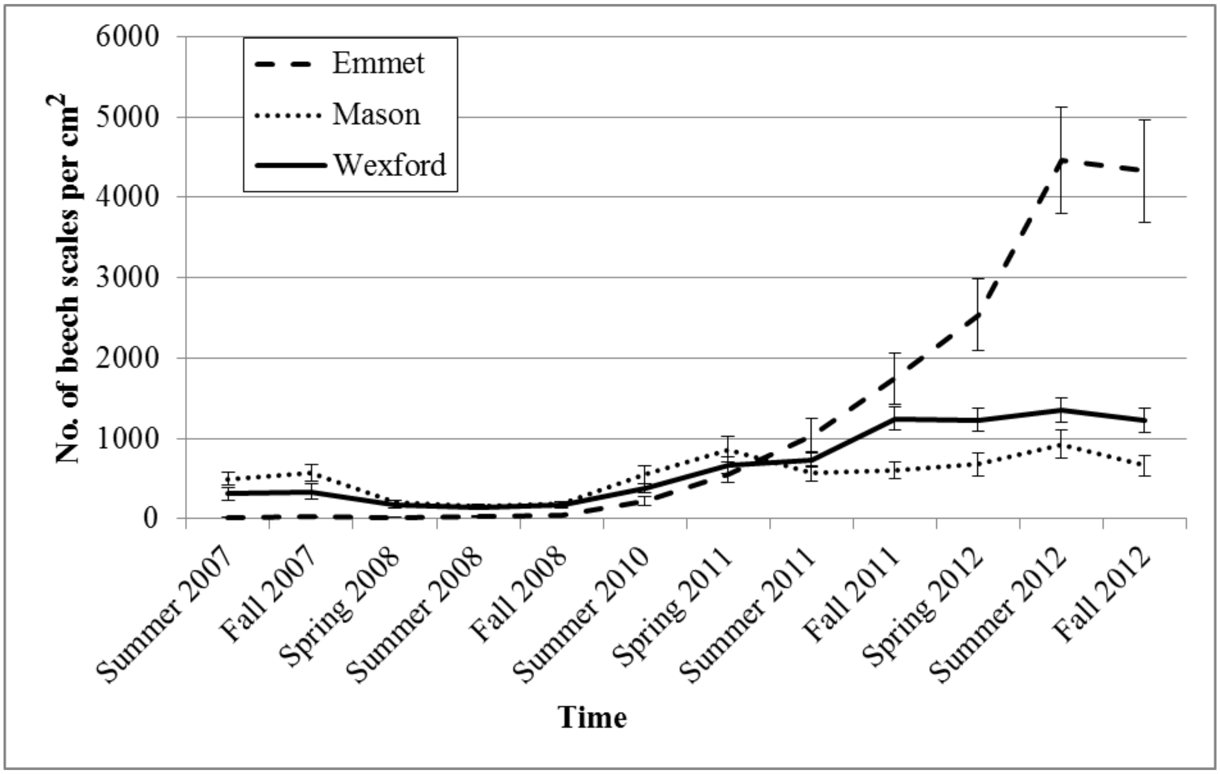

Figure A.2: Average (±SE) abundance of beech scale (*Cryptococcus fagisuga* Lind.) grouped by County from 2007 to 2012.

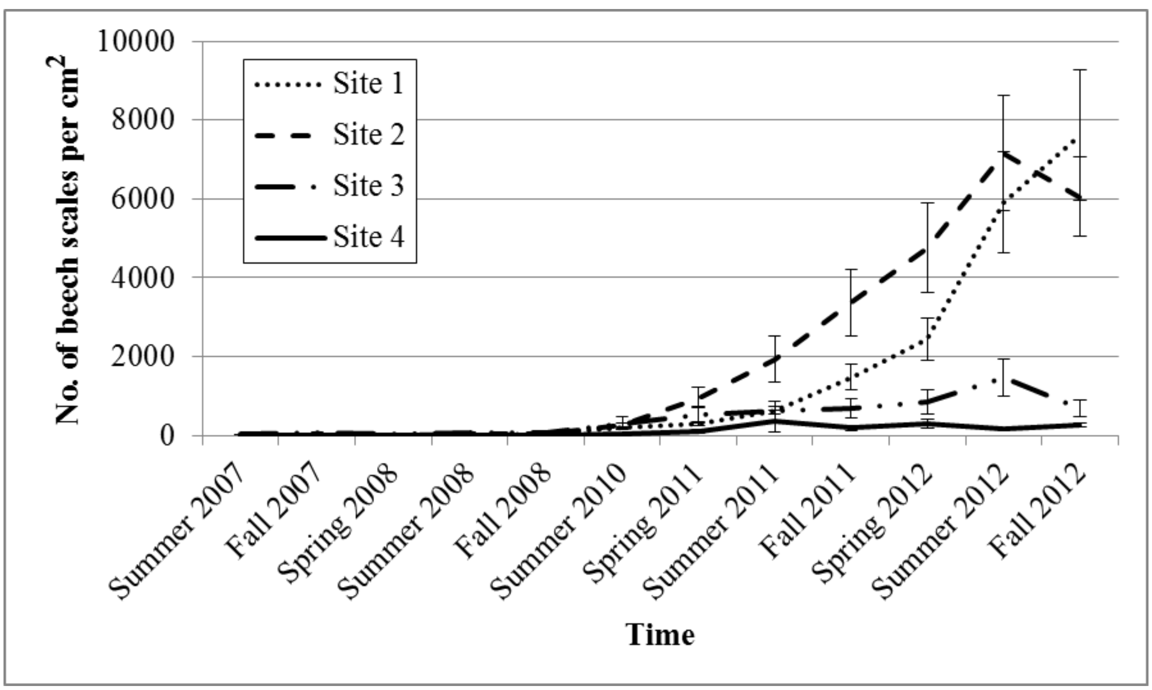

Figure A.3: Average (±SE) abundance of beech scale (*Cryptococcus fagisuga* Lind.) grouped by site from 2007 to 2012 in Emmet County.

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