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THE BEECH SCALE (*CRYPTOCOCCUS FAGISUGA*) IN
MICHIGAN: DISTRIBUTION, MODELS OF SPREAD AND
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THE BEECH SCALE (*CRYPTOCOCCUS FAGISUGA*) IN MICHIGAN:
DISTRIBUTION, MODELS OF SPREAD AND RELATION TO FOREST AND
WILDLIFE RESOURCES.

By

Nancy J. Schwalm

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ABSTRACT

THE BEECH SCALE (*CRYPTOCOCCUS FAGISUGA*) IN MICHIGAN: DISTRIBUTION, MODELS OF SPREAD AND RELEATION TO FOREST AND WILDLIFE RESOURCES.

By

Nancy J. Schwalm

The state of Michigan was surveyed from 2004-2006 to locate beech scale infestations and to collect baseline data of forest and wildlife resources of those study sites. Results of this survey demonstrated that beech scale was more widely distributed than previously thought. Beech scale was distributed in the Upper Peninsula in a single contiguous population, and encompassed nearly all of the distribution of American beech. In the Lower Peninsula, beech scale was distributed across several disjoint populations, and was found on several islands within the Great Lakes. The spread of beech scale was represented using an inverse modeling procedure. Results of these models showed that spread rates in the Upper Peninsula were higher than in the Lower Peninsula, and that spread rates depended on land cover types. Spread rates were modeled as a diffusion-like process, and were substantially lower than previous estimates based on large-scale jumps in distribution. To date, infestation with beech scale has shown little evidence of impact on forest wildlife resources, but as *Nectria* fungal infestations spread leading to beech bark disease, more widespread impacts are expected.

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TABLE OF CONTENTS

LIST OF TABLES.....	v
---------------------	---

LIST OF FIGURES.....	vii
----------------------	-----

CHAPTER 1

DISTRIBUTION OF BEECH SCALE INSECTS IN MICHIGAN: ASSOCIATION WITH FOREST AND WILDLIFE RESOURCES

Introduction.....	1
Invasive Species.....	3
American beech.....	5
Beech bark disease.....	7
Advancing front: beech scale.....	8
Beech scale biology.....	9
Killing front: <i>Nectria</i> fungi.....	14
<i>Nectria</i> taxonomy.....	16
Aftermath forest.....	19
Wildlife.....	21
Rate of Spread.....	23

CHAPTER 2.....26

MODELING THE SPATIAL SPREAD OF THE BEECH SCALE INSECT (CRYPTOCOCCUS FAGISUGA) IN MICHIGAN.

Abstract.....	26
Introduction.....	28
American beech and its importance to wildlife.....	30
Beech Scale.....	31
Methods	
Study Design: Site Selection.....	32
Study Design: Plot-level measurements.....	33
Study Design: Individual tree measurements.....	34
Statistical and spatial analysis methods.....	36
Results.....	38
Distribution of beech scale.....	39
Forest Resources.....	40
Wildlife Resources.....	42
Discussion	
Distribution of beech scale.....	44
Forest Resources.....	45
Wildlife Resources.....	48
Management Implications.....	54

CHAPTER 3
MODELING THE SPATIAL SPREAD OF THE BEECH SCALE (CRYPTOCOCCUS
FAGISUGA) IN MICHIGAN.

Abstract.....75
Introduction.....77
Methods
 Study Area.....82
 Model description and structure.....84
 Model parameters.....87
 Model selection procedures.....90
 Model assumptions and limitations.....92
Results
 Distribution of beech scale infestations.....93
 Model performance: Simple diffusion model.....95
 Model performance: Complex model.....96
Discussion
 Distribution of beech scale infestations.....98
 Model performance.....102
Management implications.....105

APPENDICES
 Appendix A Site Coordinates.....122
 Appendix B Model Parameters.....141
 Appendix C IF MAP Classifications.....142

BIBLIOGRAPHY.....146

LIST OF TABLES

Table 2-1. Satellite populations of beech scale infestations in Michigan.....	57
Table 2-2. Common name and number of trees by species associated with beech within study sites. Trees are arranged in descending order according to their abundance within study sites.....	58
Table 2-3. Results from an ANOVA to compare basal area for American beech and the seven most abundant other species across beech scale infestation classes. N is the number of individual trees examined across sites (n=737). Basal area is reported in m ² /hectare.....	59
Table 2-4. Number and percentage of beech trees per diameter class corresponding with the level of beech scale infestation. Each diameter class is recorded in centimeters and is represented in the table by the median number in its range of dbh measurements (i.e., dbh class “5” represents trees that are 1-9 cm dbh).....	60
Table 2-5. Frequency of occurrence for beech snap, tar spots, crown dieback and cankers across levels of beech scale infestation.....	61
Table 2-6. Mean number of beech snags (n=44) and non-beech snags (n=3,886) per site across levels of beech scale infestation. Basal area is reported in m ² /ha.....	61
Table 2-7. Common name and number of tree species examined within study sites. Number of cavity trees and percentage of total cavity trees arranged by species and presented in descending order of abundance.....	62
Table 2.8. Non-beech trees were divided up into 14 diameter at breast height (dbh) classes. Each dbh-class is represented in the table by the median number in its range of measurements (i.e., dbh-class “5” represents trees that are 1-9 cm dbh).....	63
Table 2-9. Chi-square table of cavity tree abundance across levels of beech scale infestation.....	64

Table 2-10. Chi-square table of beech cavity tree abundance across levels of beech scale infestation.....	64
---	----

Table 2-11. Volume of coarse woody debris (± 1 SE) and associated level of beech scale infestation. There were 453 sites in the absent category, 100 in the light and 71 in the moderate categories respectively.....	65
--	----

Table 2-12. Frequency of occurrence of coarse woody debris pieces in each decay class and corresponding beech scale infestation level.....	65
--	----

Table 3-1. Satellite infestations separated into beech scale infestation class and approximate size of the area infested as of 2006. Area was calculated using the area feature in ArcGIS.....	108
--	-----

Table 3-2. Contingency table of model errors for each of the models.....	108
--	-----

LIST OF FIGURES

Figure 1-1. Distribution of the American beech in North America (U.S. Geological Survey, 1999).....	25
Figure 2-1. Adaptive sampling design for designing the advancing front. The star represents the midpoint between a known infested site and a known uninfested site.....	66
Figure 2-2. Site layout with five plots; center, north, east, south, and west all 100 m apart. Each site also has two 100 m coarse woody debris transects between the center and north plot and the center and west plot.....	66
Figure 2-3. Photos used to standardize levels of beech scale infestation. Photo on the far left represents beech scale classification “trace”, middle photo represents “patchy” and right photo defines “whitewashed” (Photos taken by Nancy Schwalm, May 2004).....	67
Figure 2-4. Frequency of sites plotted against mean scale to determine beech scale infestation classes. Mean scale was determined by aggregating all plot-level data across a site to obtain averages per site.....	67
Figure 2-5. Map of Michigan, USA with study sites coded as uninfested (<i>open white circles</i>) or infested (<i>closed black circles</i>) or no beech sites (<i>triangles</i>).....	68
Figure 2-6. Map of Michigan, USA with beech study sites grouped into eleven distinct satellite populations.....	69
Figure 2-7a. Map of the Ludington and Silver Lake satellite populations enlarged to show the detail of sites coded according to their beech scale infestation level. Map created by Daniel Wieferich on March 30, 2007.....	70
Figure 2-7b. Map of the Upper Peninsula satellite population enlarged to show the detail of sites coded according to their beech scale infestation level. Map created by Daniel Wieferich on March 30, 2007.....	71

Figure 2-8. Mean beech basal area (± 1 SE) across level of beech scale infestation.....72

Figure 2-9. Mean beech diameter at breast height (dbh) (± 1 SE) across levels of beech scale infestation.....72

Figure 2-10. Percent of beech trees infested with beech scale as a function of tree diameter at breast height (dbh).....73

Figure 2-11. Frequency of beech trees within each beech scale infestation class across diameter at breast height (dbh) classes. Diameter at breast height classes represent the median number in a range of dbh measurements (i.e., dbh class “5” = dbh measurements 1-9 cm, “15” = 10-19 cm...”115” = 110-109 cm). Beech scale infestation classes are coded as “HV” for heavy infestation, “MD” for moderate infestation, “LT”, for light infestation and “AB” for uninfested.....73

Figure 2-12. Percent of beech trees within each beech scale infestation class across diameter at breast height (dbh) class. Beech scale infestation classes were coded as “LT” for lightly infested, “MD” for moderately infested, and “HV” for heavily infested.....74

Figure 3-1. Three types of rang-versus-time curves. Range expansion patterns commonly have an establishment phase (arrow), expansion phase (solid line), and saturation phase (dashed line), successively. The expansion phase is classified into three types. Type 1 shows linear expansion. Type 2 exhibits biphasic expansion, with an initial slow slope followed by a steep linear slop. In type 3, the rate of expansion continually increases with time (Shigesada and Kawasaki 1997).....109

Figure 3-2. Adaptive sampling design for designing the advancing front. The star represents the midpoint between a known infested site and a known uninfested site....109

Figure 3-3. Photos used to standardize levels of beech scale infestation. Photo on the far left represents beech scale classification “trace”, middle photo represents “patchy” and right photo defines “whitewashed” (Photos taken by Nancy Schwalm, May 2004).....110

Figure 3-4. Frequency of sites plotted against mean scale to determine beech scale infestation classes. Mean scale was determined by aggregating all plot-level data across a site to obtain averages per site.....110

Figure 3-5. Map of Michigan, USA with a layer of forest types grouped to locate beech. Beech was typically found within northern hardwood or deciduous forest cover types. Typically beech was not abundant in the oak association, coniferous or non-forested forest types. Data was extracted from IF_MAP data 2001, from MCGI website (www.mcgi.state.mi.us). Created by Daniel Wieferich on October 18th, 2006. Please note that this image is presented in color.....111

Figure 3-6. Map of Michigan, USA with study sites coded as uninfested (*open white circles*) or infested (*closed black circles*) or no beech sites (*small triangles*).....112

Figure 3-7. Map of Michigan, USA with beech study sites grouped into eleven distinct satellite populations.....113

Figure 3-8a. Modeled errors for the Upper Peninsula simple diffusion model mapped to show the location of model error. White dots in blue background illustrate individual model errors (SSE = 24) where the model predicted scale infestation in areas that were absent of infestations. The model accurately predicted absence of infestation in areas where it was absent (SSE = 0). Created by Daniel Wieferich on 12/14/2006. Please note that this image is presented in color.....114

Figure 3-8b. Model of Lower Peninsula simple diffusion model: red dots in black background illustrate individual errors (SSE = 21) where the model predicted scale infestation in areas that were absent of infestations. White dots on blue background illustrate a predicted absence of infestation in areas where it was present (SSE = 16). Created by Daniel Wieferich on 12/14/2006. Please note that this image is presented in color.....115

Figure 3-8c. Model of the Upper Peninsula land cover based model: red dots in black background illustrate individual errors (SSE = 5) where the model predicted scale infestation in areas that were absent of infestations. White dots on blue background illustrate a predicted absence of infestation in areas where it was present (SSE = 3). Created by Daniel Wieferich on 03/21/2007. Please note that this image is presented in color.....116

Figure 3-8d. Model of the Lower Peninsula land cover based model: red dots in black background illustrate individual errors ($SSE = 14$) where the model predicted scale infestation in areas that were absent of infestations. White dots on blue background illustrate a predicted absence of infestation in areas where it was present ($SSE = 14$). Created by Daniel Wieferich on 03/21/2007. Please note that this image is presented in color.....117

Figure 3-9a. Sum of squared errors plotted against spread rate parameter values.....118

Figure 3-9b. Sum of squared errors plotted against spread rate parameter values.....118

Figure 3-9c. Sum of squared errors plotted against spread rate parameter values.....119

Figure 3-9d. Sum of squared errors plotted against spread rate parameter values.....119

Figure 3-9e. Sum of squared errors plotted against spread rate parameter values.....120

Introduction

Non-native forest pests and pathogens have had an increasingly profound impact on the structure, dynamics, and ecosystem processes of forests in the past century (Kizlinski et al. 2002; Liebhold et al. 1995). Dominant species in North American forests such as the American chestnut (*Castanea dentata* [Marshall] Brokh.), American elm (*Ulmus americana* L.), eastern hemlock (*Tsuga canadensis* [L.] Carriere), and American beech (*Fagus grandifolia* Ehrh.) have suffered diebacks from exotic pests (Costello 1995; Liebhold et al. 1995; Orwig 2002). This study focuses on the beech scale insect (*Cryptococcus fagisuga* Lind.) (Homoptera: Coccidae) which is a non-native invasive insect and the precursor to beech bark disease (BBD). Beech bark disease has been part of North America's forest ecosystems since 1890, spreading into the northeastern United States from Canada around 1931 (Ehrlich 1934; Brower 1949; Houston 1975; Houston and Valentine 1988). Beech scale was first documented in Michigan in 1990. Because of the relatively recent arrival of beech scale to Michigan, and because Michigan is bounded by water, it provides a unique opportunity to study the spread of beech scale infestations and to better understand the impacts of this nonindigenous insect pest on our forests.

To understand rates and patterns of beech scale spread in Michigan, we must determine the beech scale distribution for the entire state. This is the crucial first step in BBD management because the arrival of scale inevitably leads to BBD, followed by tree death. There has never been an extensive statewide survey to document beech scale distribution in Michigan. This project provides the most comprehensive information about beech scale distribution across the Upper and Lower Peninsula's of Michigan, in

addition to documenting forest characteristics and species composition for stands containing beech. The information gathered during this study provides a baseline of the current state of the surveyed stands so that we may better understand changes initiated by BBD. Results will help forest health specialists; silviculturists and property owners prioritize areas for survey, management and public outreach activities. Finally this project will enhance our general understanding of how beech scale, a nonindigenous forest pest spreads and increases in density, “knowledge that has become increasingly important as we grapple with newly discovered exotic forest insect and pathogen pests” (National Research Council 2002).

Invasive Species

Invasions by exotic insects and pathogens are one of the most important threats to the stability and productivity of forest ecosystems around the world (Liebhold et al. 1995; Vitousak et al. 1996; Pimentel et al. 2000). Invasive species were ranked second, following habitat degradation, in the list of greatest threats to biodiversity in North America (Vitousak et al. 1996; Mooney and Hobbs 2000; USFWS 2006). Increasing international travel and globalization of trade provide pathways for the transport of nonindigenous species and have negated natural barriers such as oceans, rivers, and mountain ranges that originally deterred spread of nonindigenous species (Davis 2003). All regions of the world have been impacted by invasive species (Pimentel et al. 2000) and huge losses in the agricultural, forestry, livestock and fisheries industries have been documented. Economic losses and expenditures resulting from the introduction of invasive species in the United States were estimated at \$97 billion in 1991 and estimated costs in 2006 were \$138 billion (USFWS 2006).

Insects and pathogens were viewed historically as two of the most important damaging agents of forests (Hepting and Jemison 1958). The invasion of diseases such as chestnut blight (*Cryphonectria parasitica* [Murrill] Barr), practically eliminated all the American chestnut (*Castanea dentate*) from northeastern forests in the early 20th century (National Research Council 2002). The American chestnut tree comprised more than one-quarter of the canopy trees in eastern forests. The loss of this species may have initially appeared to have staggering effects on the ecosystems (Roane et al. 1986); however, species such as oak (*Quercus* spp.), hickory (*Carya* spp.), black cherry (*Prunus serotina*) and red maple (*Acer rubrum*) replaced chestnut in the canopy providing similar

ecosystem function (Yahner 1995; Youngs 2000). The invasive white pine blister rust (*Cronartium ribicola*) attacks five-needled pines including the whitebark pine (*Pinus albicaulis*). Whitebark pine, a keystone species of upper subalpine ecosystems, produces seeds that are an important source of food for a number of birds and mammals including nutcrackers, squirrels, and bears (Tomback et al. 2001). The above are two of many examples that illustrate how invasive species can dramatically alter ecosystems, impact wildlife species, and affect human economies. The ecological changes resulting from invasive pests, typically set off a cascading chain of events leading to ecosystem changes (Gibbs and Wainhouse 1986; National Research Council 2002). Consequences of forest invasive species include cumulative stresses on the host plant and alteration of the populations of other native species; effects that can extend to other trophic levels (National Research Council 2002). This study focuses on the distribution and spread of one of two invasive species that together cause beech bark disease (BBD), a disease impacting our beech forests in the eastern United States and the communities of wildlife that depend upon them.

American beech

American beech (hereafter referred to as beech) belongs to the family *Fagaceae* and is the only native species of the *Fagus* genus in North America. Beech is a slow-growing, common, deciduous tree that attains ages of 300 to 400 years. Beech is valued for its wood and as a source of food and habitat for wildlife. The fine-grained wood is used for flooring, furniture, and baskets because it is excellent for turning, steam bending, and veneer, it burns well and is easily treated with preservatives (Tubbs and Houston 1990; Barker et al. 1997). Beech wood is favored for fuel because of its high density and good burning qualities (Barker et al. 1997). Beech trees are aesthetically pleasing and are often valued by private property owners for their unique appearance in landscape settings.

Although beech is now confined to the eastern United States (except for the Mexican population) it once extended as far west as California and probably flourished over most of North America before the last glacial period. The current range of beech extends from Maine to northwest Florida, and west to eastern Wisconsin and Texas, Michigan is at the northern and western edge of beech range (Figure 1-1).

Beech grows on a variety of soil types, but grows best on deep, rich, well-drained moist soils and cool, shady, moist locations on fertile bottomlands and uplands (Rushmore 1961). The largest beech trees are found in the alluvial bottom lands of the Ohio and Mississippi River valleys and along the western slopes of the southern Appalachian Mountains. Beech is found at low elevations in the North and relatively high elevations in the southern Appalachians. Local soil and climatic factors probably determine whether beech grows at higher elevations (Tubbs and Houston 1990).

American beech trees are a major component of three northern forest cover types and a minor component of 17 other cover types (Tubbs and Houston 1990). Principle associates are sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), American basswood (*Tilia americana*), black cherry (*Prunus serotina*), southern magnolia (*Magnolia grandiflora*), eastern white pine (*Pinus strobes*), several hickory species (*Carya* spp.) and oak species (*Quercus* spp.) (Halls 1977; Tubbs and Houston 1990). As a co-dominant species within the maple-beech-birch forest type, beech influences many physical and biotic properties of the forest, including maintenance of canopy closure and understory light and moisture regimes (Storer et al. 2004).

Beech bark disease

Beech bark disease is caused by an etiological complex consisting of a sap-feeding beech scale insect, the focus of this study, and one of three fungi that kill phloem and cambium in the genus *Nectria*. Beech bark disease has been divided into three major phases. The leading edge of beech scale infestation is known as the advancing front. The leading edge of the *Nectria* fungal invasion following the advancing front is known as the killing front. The aftermath forest is the final result of BBD and is characterized by dead and declining overstory beech (Shigo 1972; MacKenzie 2004). These phases were originally proposed by Shigo (1972) and have been widely adopted since then (MacKenzie 2004).

Advancing front: beech scale

The first stage of BBD begins when beech becomes infested, for the first time, with beech scale (Wainhouse and Deeble 1980; Houston and O'Brien 1983). Beech scale probe the living tissues of the outer bark, extracting protoplasmic materials and causing the death of punctured cells. Beech scale arrived in North America from Europe, sometime in the mid-to-late 1800's on a ship carrying European beech tree (*Fagus sylvatica* L.) seedlings into the Canadian port of Halifax, Nova Scotia (Ehrlich 1934; Houston and O'Brien 1983). In 1890, some of the imported trees were found to be infested with "felted beech coccus," which was identified as *C. fagi* Baer, later renamed *C. fagisuga*, the beech scale (Ehrlich 1934). Thirty years later, beech trees in forests surrounding Halifax began dying and John Ehrlich, then a Ph.D. candidate at Harvard, began to study, describe, and name the disease (Houston 2004).

By the early 1930's, beech scale had spread throughout the Maritime Provinces and into Maine. Most of New England and areas of New York were affected by scale in the 1960's, areas of Pennsylvania in the 1970's, and a major infestation was discovered in West Virginia in 1981 (Houston and Lonsdale 1979; Houston 1994). Beech scale and BBD were discovered in the 1990's in localized areas of Ontario, Virginia, and Ohio (Houston 1994). Beech scale infestations were first documented in northwestern Lower Peninsula of Michigan in Ludington State Park, Mason County and the east-central Upper Peninsula in Bass Lake State Forest Campground, Luce County in 2000. Anecdotal records and data collected from affected stands suggest that beech scale was present in Ludington State Park as early as 1991 (O'Brien et al. 2001).

Beech scale biology

The beech scale is a small insect, 0.5-1.0 mm in length, reddish-brown eyes, a stylet about 2 mm long, rudimentary antennae and legs, and numerous minute glands (Shigo 1972). The species reproduces parthenogenetically, but is univoltine. Ehrlich (1934) and Houston and O'Brien (1983) reported an average of 50 eggs per female, whereas Wainhouse and Gate (1988) state a maximum observed fecundity of 43, with the average realized fecundity of 4-16 eggs per female. The yellowish-colored eggs are laid between July and November, depending upon temperature. Eggs hatch 20-25 days later to become first-instar, mobile crawlers (Shigo 1972; Wainhouse 1980; Houston 1994). Crawlers emerge from the eggs with well-developed legs and antennae (Borror and White 1970; Shigo 1972). Crawlers remain stationary under the females, migrate to cracks in the bark, establish themselves on other trees after being disseminated by various agents, or die (Shigo 1972). Mortality of crawlers was estimated to be about 86% but comparatively few (<1%) were washed off the bark during rainfall, contrary to previous assumptions (Wainhouse and Gate 1988). The crawler stage is the only mobile stage in the beech scale life cycle where it can successfully disperse (Wainhouse 1980).

Crawlers settle into cracks or in areas where the bark is rough, usually on the bole or large branches of the host tree. After settling, the crawler becomes stationary, forces its stylet into the bark, becomes a second-instar nymph without legs and produces a white-waxy filamentous secretion which completely surrounds its body. The waxy covering protects the scales from environmental hazards such as unfavorable weather conditions and natural enemies (Speight 1981). The insect hibernates in the second-instar

stage and molts in the spring to become an adult female and remains sessile for the rest of its life (Borror and White 1970; Shigo 1972).

Environmental and biological controls play a relatively small part in beech scale population dynamics. Air temperatures of -37° C (-35° F) are lethal to scales not protected by snow (Houston and O'Brien 1983). No parasitoids of beech scale have been found in Europe or North America despite repeated searches (Wainhouse and Gate 1988). A number of native predators are known to feed on scale and are effective in reducing scale populations on individual trees; however, their influence on the course of the disease is of little consequence (Houston 2004). A large red velvet mite (*Allothrombium mitchelli* Davis) was found to feed on beech scales in the Great Smoky Mountains National Park (Wiggins 2001). Among Coleoptera, Coccinellidae may be effective at reducing local populations of scale. The most common enemy is a native coccinellid, the twice-stabbed ladybird beetle (*Chilocorus stigma* Say). A cecidomyid fly (*Lestodiplosis* sp.) is also common, but generally prefers trees with moderate to heavy scale populations (Wainhouse and Gate 1988); both adults and larvae feed on scale (Houston 1997). Gall gnats (Diptera: Cecidomyiidae, *Lestodiplosis* spp.) may also be effective in reducing beech scale populations, especially at high densities (Storer et al. 2004). The effect of these predators on the scale population is considered negligible, but they may serve an important function as long-range vectors for the fungi (Shigo 1962).

Beech scales eventually infest all beech trees with individual stands but certain trees appear to be resistant (Ehrlich 1934; Shigo 1962; Houston 1983). In the northeastern forests, this may amount to less than one percent of American beech trees (Houston and Houston 1994, 2000). Resistant trees can occur as individuals, but often

are found in groups (Houston 1983) due to stump sprouting of parent trees. Individual beech trees vary in their susceptibility to the scale insect based on genetic differences (Speight 1981). Resistant beech tree bark contains significantly less total nitrogen than that of susceptible trees (Wargo 1988). Low nitrogen concentration is known to limit establishment and growth of sucking insects (Dadd and Mittler 1965). Tree resistance to attack may be related to the suitability of the bark for crawler settlement. Scales require crevices in the bark that may not be present on trees < 25 years old because their bark may be too smooth (Speight 1981). Other trees may be resistant or partially resistant to beech scale establishment through physical or chemical attributes or genetic differences. “Clean” trees are especially evident in some aftermath forests where their smooth, uncantered boles stand in sharp contrast to the highly marred stems of their susceptible neighbors (Houston 2004). These trees were originally thought to be resistant because the scale had no place to gain a “foothold” and lacked protection from the weather and enemies. In Pennsylvania, scale traps were used to determine if beech scale will colonize a tagged resistant tree if given a place to “hide” underneath the trap. These traps consist of a piece of composite board with foam underneath tied to a resistant tree by a rope. These traps provide suitable cover for beech scale on an otherwise very smooth-barked tree. Challenge trials showed the trees were resistant to beech scale even if the scales are given artificial protection (Houston 1982, 1983).

Dispersal of beech scale occurs only if crawlers or eggs settle on a suitable host. Characteristics such as small size, a flat body shape and abundant setae favor passive dispersal. Eggs and crawlers are transported passively in airstreams, where a small proportion of the population is wafted upward and dispersed above the canopy

(Wainhouse 1980). However, at least 90-99% of wind-dispersed crawlers are thought to travel no more than 10 m (Wainhouse 1980; Wainhouse and Gate 1988). There is little doubt that beech scale is also moved within stands by other insects (e.g., ladybird beetles), mammals (e.g., squirrels, raccoons) and birds (e.g., nuthatches, creepers, woodpeckers, titmice) and probably between stands and regions by birds and people (Houston 2004). The infestations in Michigan, West Virginia, and Ohio, for example, appear to be centered on campgrounds or scenic areas, suggesting beech scales were transported by humans perhaps via firewood.

Long-term monitoring of beech scale establishment and rate of spread has important implications for public outreach efforts, design of pest surveys and silvicultural activities. If beech scale spreads primarily by passive dispersal in wind, the rate of spread should be somewhat predictable. However if spread is primarily by humans, spread rates may be harder to predict, and control of this dispersal method may involve public outreach activities designed to educate the public. Historic spread rates of beech scale in North America have been estimated to be 6-16 km per year (Houston et al. 1979; Wainhouse 1980; LaChance 1983; Towers 1983; Wainhouse and Gate 1988; Morin et al. 2004). These estimates include both natural and artificial dispersal. People moving firewood, ornamental trees or logs, crawlers on clothing or pets, and vehicles bearing eggs and crawlers are other potential modes of dispersal that leads to a different pattern of spread. Such artificial dispersal can result in establishment of satellite populations and accelerated spread rates when they eventually coalesce (Shigesada and Kawasaki 1997). If artificial dispersal is common, public outreach efforts can be focused on campers or visitors to recreation sites. Policies designed to restrict infested log or nursery stock

movements can be implemented. Such data could help support policies that limit transportation of firewood into public parks or campgrounds. By understanding spread rates, forest managers will be able to focus their management strategies along the leading edge of the advancing front. Any understanding of how exotics behave as they invade a new area will provide insights for foresters and wildlife biologists on how to manage their resources and for preventing similar invasions in the future (Lewin 1987). An improved understanding of these impacts may be useful in policy decisions relating to exotic species introductions and to the restoration of beech forests (Storer et al. 2004).

Killing Front: *Nectria* fungi

The second stage of BBD or killing front refers to stands where both beech scale populations and infection by *Nectria* are high, with associated tree mortality (Shigo 1972). *Nectria* infection begins when groups of dead cells, killed by beech scales, leads to tearing of the periderm, which enables the *Nectria* fungi to initiate infection (Ehrlich 1934; Speight 1981). Once past the barrier of phellem (i.e., cork cells that make up the first layer of the periderm), *Nectria* is able to advance through the living tissues of bark, cortex, phloem, cambium, and sapwood. Death of the infected tissues interferes with normal conduction and storage in the trunk and results in a progressive killing of the tree. Tree death results when the fungal lesions have coalesced sufficiently to block transport of materials to the crown of the tree. As infestation progresses, the foliage and twigs dry and die, whole branches cease to leaf out, and large areas of bark on the trunk crack, usually loosen from the wood, and eventually fall. On younger trees infection is less abundant because the fungus apparently advances less readily (Ehrlich 1934). It is the fungal infection and subsequent death of the cambium that leads to growth loss, internal defect, decay, and tree death (Burns and Houston 1987). Dead bark will crack and fissure as the tree grows providing additional refuges for the scale and points of entry for *Nectria*. Some trees may linger for several years, eventually succumbing to *Nectria*.

Areas devoid of beech scale or patches of black “wool”, indicative of dead scales, are evidence of places killed by *Nectria*. Beech scales cannot live on dead tissue; and as the tissues die a black fungus grows over them (Shigo 1972). *Nectria* may infect large areas on some trees, completely girdling them. The leaves that come out in the spring do not mature, giving the crowns an open appearance. The leaves turn yellow and usually

remain on the tree during the summer season. The chlorotic crowns are typical of trees dying from water deficiency (Shigo 1972).

The killing front, infection by *Nectria* fungi, typically follows the advancing front 1-4 years following a heavy buildup of scale (Houston, 1996). This estimate is based on historic records in the northeastern United States and whether this rate is consistent in newly infested areas such as Michigan is unknown because there has never been a *Nectria* distribution study conducted. Modes of transportation and fungal spread rates are even less understood than those of beech scales. Wind and rain are documented as agents of transportation for ascomycetes (Twery and Patterson 1984), responsible for infecting new trees with *Nectria* fungi. Insect vectors may also aid the spread of *Nectria* spores. Ladybird beetles (*Chilocorus stigma* Say) and Ambrosia beetles (*Scolytidae*, *Platypodidae*) are strong fliers; they go from tree to tree in search of food, often coming into contact with perithecia and sporodochia of *Nectria* in their search (Shigo 1962). Shigo (1964) isolated *Nectria* species from twice-stabbed ladybird beetles and postulated that this beetle may serve as a long-range vector for *Nectria* species (Cotter 1977).

Nectria taxonomy

Spaulding et al. (1936) recognized that more than one species of *Nectria* was causing cankers on American beech trees in North America following attack by beech scale. Historical understanding of BBD in North America involved three different *Nectria* fungi; two are native and one is introduced. Several taxa of *Nectria* infect the bark of beech trees in both North America and Europe and it is not always clear whether the tree is infected by an introduced or native species (Mahoney et al. 1999). Studies of *Neonectria* population genetics revealed the native var. *faginata* is more closely related to the Europe variety (Mahoney et al. 1999), leading to the hypothesis that it was introduced, probably about the same time as beech scale (Houston 1994, 2004). While the actual origin of *N. var. faginata* remains unknown, Plante et al. (2002) concurred with Mahoney et al. (1999) that *N. coccinea* var. *faginata* found in the eastern part of North America may have been introduced.

Nonindigenous *N. coccinea* var. *faginata* A. is the main species found in New England, northern New York, and the Maritime Provinces. The native *N. galligena* A. and *N. ochroleuca* A. are found in western Pennsylvania, West Virginia, and Michigan (Houston and Mahoney 1987; Wainhouse and Gate 1988; Houston 1994; MacKenzie 2004). *Nectria galligena* is typically the first species of fungus to infect beech trees because it is already present in the forests on non-beech hosts. The nonindigenous *N. coccinea* var. *faginata* quickly replaces the native *N. galligena*, as it spreads across the country following the advancing front (Witter et al. 2004). In Europe, *N. coccinea* is the only fungus associated with BBD (Wainhouse and Gate 1988). The fungi causing beech bark canker (e.g., BBD) have recently been transferred from genus *Nectria* to the genus

Neonectria Wollenw (Castlebury et al. 2006). The genus *Nectria* (*Hypocreales*, *Nectriaceae*) was described by Wollenweber (1917) based on *Nectria ramulariae* but was essentially ignored until Rossman et al. (1999) recognized this genus for species segregated from *Nectria*. Fungi associated with BBD will be referred throughout this thesis as *Neonectria*.

Our current understanding of BBD pathogens is at least two species of *Neonectria* are associated with BBD in North America. The most common is *Neonectria faginata*. The second species is *Neonectria ditissima*, which was previously referred to as *Neonectria galligena*. For many years the fungus causing beech bark disease in North America was recognized as *Nectria coccinea* var. *faginata* (Mahoney et al. 1999). Castlebury et al. (2006) indicate that *Neonectria faginata* should be recognized as a distinct species from *Neonectria coccinea*. At present, *Neonectria faginata* is known only on *Fagus* in North America and *Neonectria coccinea sensu stricto* is known only on *Fagus* in Europe. Castlebury et al. (2006) reported that the isolates from American beech trees did not reveal any signs of *Neonectria coccinea* and concluded that it does not occur in North America. Most studies have indicated that *Neonectria ditissima* (as *Neonectria galligena*) is likely native to North America due to the large amount of genetic variation present in North American isolates. However, without a similar comparison of the genetic variation of European populations, it is not possible to draw conclusions concerning the origin of *Neonectria ditissima*; therefore it is not clear where *Neonectria ditissima* originated (Castlebury et al. 2006).

Though *Neonectria* may be present in the forest on other hardwood tree species, experiments have determined that it is only able to enter and infect beech trees on which

the insect has been present for at least a year (Ehrlich 1934). In the absence of large beech scale populations, pathogen spores are unable to penetrate healthy bark (Speight 1981). Once openings in the periderm are created, *Neonectria* spores enter the sapwood, and mycelia spread throughout the tree (Ehrlich 1934; Houston 1994). To become established, *Neonectria* spores must penetrate the cambium layer (Lortie 1964). Once inside the tissues of a tree *Neonectria* grows parasitically, destroying the storage and vascular systems of the trunk and branches (Ehrlich 1934). Eventually, the vascular system stops functioning properly, resulting in increased leaf yellowing and eventual death of the tree (Speight 1981). Secondary factors such as other insect pests and pathogens cause structure weakening and tree crowns often break off during high winds a condition referred to as “beech snap” (Houston and O’Brien 1994).

Aftermath forest

The final stage of BBD, the aftermath forest, is characterized by poor quality surviving trees, resistant trees, beech tree thickets consisting of small beech saplings and relatively low levels of active disease (Shigo 1972). Declining mature beech trees often produce dense root-sprouts that are genetically identical to parent trees and equally susceptible to BBD (Houston 1975). Root sprouts originating from diseased trees are generally stunted or deformed, contributing to the characteristic aftermath forest structure that has replaced much of the original beech component of the northeastern United States (Houston 1994; Houston and Valentine 1987; Ostrofsky and McCormack 1986). Dense thickets of beech sucker sprouts in the northeastern United States are sometimes referred to as “beech hell” (M. Ayers, Dartmouth College, pers. comm.). Dense understory vegetation can limit the regeneration of other species including sugar maple (Houston 1975; Twery and Patterson 1984; Houston and Valentine 1987; Hane 2003), thereby providing a competitive advantage for beech. Kearney (2006) did not find an increase in the overall abundance of beech seedlings, saplings, or recruits in Michigan forests.

Beech regeneration is also favored when browsing white-tailed deer (*Odocoileus virginianus*) severely limit the height growth of more palatable (i.e., non-beech) species (Kelty and Nyland 1981; Marquis and Grisez 1978; Tilghman 1989). In northwestern Pennsylvania, high deer densities (40-80 deer/sq mi) negatively affected the regeneration of other tree species, such as red maple and northern red oak (Tilghman 1989). Even if high populations of deer do not eliminate regeneration of tree seedlings, they may delay the time period normally required for regeneration (Marquis and Grisez 1978). Michigan and Pennsylvania are similar in forest composition and deer densities that the same effect

on regeneration is likely to occur in Michigan as well. These types of competition, through crowding and selective browsing may change the species composition of the aftermath forest to favor beech. Other studies state that as beech decline, other tree species will replace beech. Following BBD, eastern hemlock (*Tsuga canadensis*) and sugar maple (*Acer saccharum*) in the northeastern United States and red spruce (*Picea rubens*) or fir (*abies* spp.) in the southern Appalachians, eventually become the major component of the forest (Twery and Patterson 1984; Runkle 1990; Gavin and Peart 1993; Leak and Smith 1996). Kearney (2006) found that either sugar maple or red maple would dominate the forest structure following the killing front and subsequent dieback of beech in her study areas in Michigan.

Trees that are killed by BBD often are invaded by other insects and wood-decay fungi. Ambrosia beetles and horntails (*Hymenoptera: Siricidae*) bore into the canker areas, allowing other fungal agents to enter (Morin et al. 2001). *Hypoxylon*, a sapwood decay fungus, often invades a tree. The shoestring root rot fungus, *Armillaria mellea*, sometimes invades weakened trees and hastens death. “Beech snap” is an important management concern in recreational areas, campgrounds and on private property where property damage or injury to people, pets, or livestock can occur (McCullough et al. 2000).

Wildlife

Beech trees are used by many birds for nesting, roosting, perching, and insect foraging (Robb and Bookhout 1995). Mammals frequently use cavities in beech trees for shelter or dens (Tubbs and Houston 1990). Coarse woody debris, produced by mature beech trees when they lose branches or die, facilitates travel pathways for small mammals (Graves et al. 1988; Greenberg 2002). Mixed species forests containing beech are critical habitat for avian species such as the hairy woodpecker (*Picoides villosus*), brown creeper (*Certhia americana*), and solitary vireo (*Vireo solitarius*) (Thompson and Capen 1988).

The loss of a dominant, mast-producing tree species such as beech, and its replacement by non-mast-producing species such as hemlock, spruce, or fir, not only affects plant composition of forests, but may also negatively impact the animals that use these trees for habitat and food (Wiggins et al. 2004). Wildlife communities depend upon a variety of vegetation types and structures for food, habitat and space requirements. Trees and shrubs that retain their leaves or needles throughout the winter provide thermal cover for a variety of wildlife species. Young and immature beech trees characteristically hold their leaves throughout the winter, providing thermal cover for a variety of wildlife species. In colder, northern forests dominated by spruce-hardwoods, beech is the sole hard mast producer (Tubbs and Houston 1990) and one of the few remaining mast-producing trees at altitudes greater than 4,500 ft (Russell 1953; Whittaker 1956). Beechnuts can be substantial components of winter diets for a variety of species including; white-tailed deer, ruffed grouse (*Bonasa umbellus*), wild turkey (*Meleagris gallopavo*), northern bobwhite (*Colinus virginianus*), and black bear (*Ursus americanus*) (Glover 1949; Nixon et al. 1968; Gysel 1971; Halls 1977; Beeman and Pelton 1978),

especially in northern regions where oaks and hickories are rare (McDonald and Fuller 1994; McLaughlin et al. 1994). BBD may significantly reduce beech nut production by large trees (Costello 1992). Beechnuts are high in fat and are available when other plant foods such as fleshy fruits and foliage are not (Elowe and Dodge 1989). They are also high in calcium and moderate in crude protein and phosphorus (Halls 1977). Beechnuts have a protein content equivalent to corn (11% dry mass) and a fat content (17.3% dry mass) five times greater than that of corn (Elowe and Dodge 1989). The loss of this mast resource could impact numerous species of wildlife and potentially have cascading impacts on our forest ecosystems. While many studies (i.e., Costello 1992; Storer et al. 2004; Kearney et al. 2006) have quantified wildlife resources in relation to BBD, no quantitative observational study has concluded a decline in mast production, cavity trees, coarse woody debris, or wildlife abundance as a result of BBD. While many effects of BBD on wildlife species have been speculated, none is actually documented. This is a huge gap in our understanding of BBD and these impacts need to be quantified.

Rate of spread

While historical records document the advance of beech scale and BBD in some areas of northeastern North America (Houston et al. 1979), there have been few efforts to quantify the rate and pattern of spread in newly affected areas such as Michigan. In the Allegheny National Forest in Pennsylvania, BBD has been established since at least 1985. Forest health protection specialists conducted roadside surveys, recorded beech scale presence and beech mortality, then drew contour maps by hand to estimate temporal progression of the advancing and killing fronts from 1985-1996 (MacKenzie 2004). These maps provide a limited basis; however, for predicting how rapidly beech scale and BBD may spread.

Morin et al. (2004) used existing BBD distribution information and historic records of invasion years to estimate a spread rate for the entire northeastern region of the United States. Historical BBD spread rates were estimated from maps depicting the killing front as contour lines drawn on a map incorporating year's 1935, 1950, 1960, 1970, and 1975 (Houston 1994). Years 1990, 1999, 2000, 2001, 2002, and 2003, were compiled into geographic information systems (GIS) to illustrate the advance of the killing front (Morin et al. 2004). To calculate spread rates, minimum distance from each infested county back to the area initially infested was calculated in GIS. Average radial rate of spread was estimated by the slope of the linear regression model of the minimum distances as a function of the year of initial infestation using. The estimated spread rate from the regression analysis was then applied to the 2003 BBD distribution to generate a map representing its predicted spread through 2025 over a 1 km² raster GIS layer (Morin et al. 2004). These calculations consider all areas behind the killing front to be infested

and also incorporate long-distance (or jump) dispersal into their calculations. Morin et al. (2004) estimated that BBD spreads at a rate of 14 km/year across all land cover areas but did not differentiate between beech scale infestation and fungal infection, or various land cover types. Whether this rate of spread is applicable to Michigan, is not known. One critical difference between our study and Morin et al (2004) study is that we focus exclusively on beech scale distributions, and do not incorporate the killing front into our spread rate calculations. Our spread rates are based on beech scale spread rates which may not be the same rate as the *Neonectria* infestations. Stands may be heavily infested with scale without *Neonectria* infection for several years; it is unknown how long between fronts, particularly if a forest is isolated from the killing front.



Figure 1-1. Distribution of the American beech in North America (U.S. Geological Survey, 1999).

**Distribution of beech scale in Michigan:
Association with forest and wildlife resources.**

Abstract

A total of 871 sites across Michigan were surveyed from 2004-2006 to document the presence and level of beech scale (*Cryptococcus fagisuga* Lind.) infestation, identify the advancing front and assess forest and wildlife resources. Eleven distinct beech scale infestations were clustered into populations and were identified as covering an approximate area of 15,095 km². Results showed that beech scale was present in ten counties not previously known to be infected. Stand characteristics including overstory composition and basal area, in addition to wildlife resources such as coarse woody debris, cavity, and snag abundance were quantified for each site. Thirty-seven other tree species co-occurred with beech (*Fagisuga grandifolia* Ehrh.). Common associates included: sugar maple, red maple, northern red oak, ash species, aspen, white oak and eastern hemlock. Basal area of beech and trees other than beech were not significantly related to levels of beech scale infestation. Beech diameters were positively related to levels of beech scale infestation. Snag density was significantly higher in moderately infested sites than in other sites. The majority of cavity trees were beech, with non-beech trees comprising of <1% of total cavity trees. Beech cavity trees were present in 4% of sites and their abundance was not significantly different among levels of beech scale infestation. Coarse woody debris abundance and decay class differed significantly among levels of beech scale infestation. Sites not infested with beech scale had the highest abundance of coarse woody material. Volume of coarse woody debris was not significantly different among levels of beech scale infestation. Presence of beech snag,

crown dieback, and tar spots were significantly different across levels of beech scale infestation; however presence of beech cankers was not. Overall, the presence of beech snap, tar spots, crown dieback and beech cankers were highest in uninfested sites. Within infested sites, presence of beech snap, tar spots, crown dieback and beech cankers were highest in moderately infested sites. These data will be useful for long-term monitoring of beech scale distributions and changes in forest and wildlife resources as a result of beech scale invasions.

Introduction

Beech bark disease (BBD) is caused by an etiological complex consisting of a nonindigenous sap-feeding beech scale insect (*Cryptococcus fagisuga* Lind.) and a parasitic fungus in the genus *Neonectria*. Beech bark disease has been divided into three major phases. The leading edge of beech scale infestation is known as the advancing front. The leading edge of the *Neonectria* fungal invasion, following the advancing front, is known as the killing front. The aftermath forest is the final result of BBD and is characterized by dead and declining overstory American beech (*Fagisuga grandifolia* Ehrh. - hereafter referred to as beech) (Shigo 1972; MacKenzie 2004). This study focused on the advancing front because, as a precursor for BBD, the advancing front and areas not yet infested with beech scale provide opportunities to document forest conditions pre-disease and to monitor effects as BBD progresses.

Beech bark disease has been studied in the United States since the 1930's, beginning with John Erhlich's work in 1934. Research on BBD has addressed an array of topics including distribution (e.g., Brower 1949; Griffin et al. 2003), spread rate (e.g., Houston et al. 1979; Houston 1994; MacKenzie 2004; Morin et al. 2004), pathology (e.g., Wollenweber 1917; Mahoney et al. 1999; Rossman et al. 1999; Castlebury et al. 2006), effects on wildlife (e.g., Jakubas et al 2004; Storer et al 2004; Kearney 2006), effects on stand composition (e.g., Houston 1975 and 2001; Houston and Valentine 1987; Hane 2003; Runkle 2005). This study is unique from other BBD studies in Michigan (e.g., O'Brien et al. 2001; McCullough et al. 2002; Storer et al. 2004; Petrillo and Witter 2004; Kearney 2006) in that it delineated the advancing front distribution in Michigan and provides baseline information on forest conditions. We conducted an extensive statewide

survey, building off of existing BBD study sites in Michigan to document beech scale distribution.

This project provides comprehensive information about beech scale distribution across the Upper and Lower Peninsulas of Michigan, in addition to documenting forest and wildlife resources in stands containing beech. This information provides a baseline of the current state of the surveyed stands so that we may better understand changes initiated by BBD. Results will help forest health specialists, silviculturalists and property owners prioritize areas for survey, management or public outreach activities. Finally, this project will enhance our general understanding of how beech scale, a nonindigenous forest pest, spreads and increases in density, “knowledge that has become increasingly important as we grapple with newly discovered exotic forest insect and pathogen pests” (National Research Council 2002). The goals of this research were to map the distribution of beech scale infestation throughout the state of Michigan and to record stand characteristics such as coarse woody debris, cavities per species, snags, basal area of all species, and BBD symptoms to provide baseline information on forest conditions prior to disease. The objectives were to 1) to document the extent of the advancing front throughout Michigan by surveying sites in all counties containing beech and 2) quantify stand characteristics including overstory composition, basal area, coarse woody debris, cavities, snags, beech snap, tar spots, crown condition and cankers.

American beech and its importance to wildlife

American beech is a major component of three northern forest cover types and a minor component of seventeen other cover types throughout North America (Tubbs and Houston 1990). As a co-dominant tree within the maple-beech forest type, beech influences many physical and biotic properties of the forest, including maintenance of canopy closure and understory light and moisture regimes (Storer et al. 2004). Mammals frequently use cavities in beech trees for shelter or dens (Tubbs and Houston 1990). Like the once-prominent American chestnut tree (*Castanea dentata* (Marshall) Borkhausen), beech produces hard mast that is an important autumn food source for a large number of bird and mammal species (Faison 2004). Coarse woody debris produced by mature beech trees facilitates travel pathways for small mammals (Graves et al. 1988; Greenberg 2002). The loss of overstory beech could impact numerous species of wildlife and potentially have cascading impacts in forest ecosystems.

Beech scale

The beech scale is a univoltine parthenogenetic insect producing 4-50 yellowish-colored eggs per adult. Eggs hatch in 20-25 days to become first-instar, mobile crawlers (Shigo 1972; Wainhouse 1980; Houston 1994) that may remain stationary or migrate to new areas (Borror and White 1970; Shigo 1972). The crawler stage is the only mobile stage in the beech scale life cycle where it can successfully be dispersed (Wainhouse 1980).

The beech scale was accidentally introduced into North America, from Europe, on a ship carrying European beech tree (*Fagus sylvatica* L.) seedlings into the Canadian port of Halifax, Nova Scotia in 1890 (Ehrlich 1934; Houston and O'Brien 1983). By the early 1930's, beech scale had spread throughout the Maritime Provinces and into Maine. New England and areas of New York were infested by the 1960's. In the 1970's, Pennsylvania was infested and by the 1980's, West Virginia (Houston and Lonsdale 1979; Houston 1994). Ontario, Virginia, and Ohio reported beech scale infestations in the 1990's (Houston 1994). Infestations in Michigan were first officially documented in 2000, in northwestern Lower Peninsula's Ludington State Park (Mason County) and the east-central Upper Peninsula's Bass Lake State Forest Campground (Luce County), although anecdotal records indicated that beech scale was present in Ludington State Park as early as 1991 (O'Brien et al. 2001).

Methods

Study Design: Site Selection

In 2004, study sites were located by systematically searching areas beyond the boundaries of 62 research study sites established in 2002-2003 by Kearney (2006). To the extent possible, sites were arranged in concentric circles approximately 1 km apart to locate the advancing front. In 2005, additional sites were surveyed to further define the advancing front using an adaptive sampling design (2-2) based on known locations of uninfested and infested sites. Sites were established by locating beech trees midway between two established sites where there was a discontinuity in beech scale distribution, *i.e.*, between a site with no evidence of beech scale and a site with evidence of beech scale. Sequential bisections were created to define the advancing front.

Sampling to explore for disjunct populations (here termed satellite populations) was conducted by systematically dividing a quadrangular map of the state of Michigan (1:150,000) into a north and south hemisphere. Each hemisphere was then further divided into eight to ten subsections of approximately 104 sq km in which to search for stands containing beech. In 2006, sites were surveyed in areas that had not been previously visited and in cover types predicted to contain beech as a major component according to the USDA Forest Service Forest Inventory Analysis (FIA) data. All searches were limited to areas accessible by public or private roads. In 2005 and 2006, selected sites along the advancing front were revisited to monitor changes in levels of infestation.

Study Design: Plot-level measurements

At each site, I established five plots where data were collected. Data from each of the five plots were pooled and means were calculated to obtain site-level data. The five variable radius plots (Held 1983; Pierce and Running 1988) were established using a 10 BAF prism (Panama Angle Gauge) (Figure 2-2). The center plot was initially established, followed by four additional plots 100 m in each cardinal direction from the center plot (Figure 2-2). Location of each plot was recorded using a handheld GPS (Garmin International, Inc., Olathe, Kansas) unit. GPS coordinates were recorded to the nearest 0.001 degrees, but accuracy depended on canopy coverage and satellites available. Accuracy ranged from ± 3 m to ± 30 m. Plot-level data included basal area of **b**eech, basal area of all other tree species combined, number of snags, and evidence of **b**eech snap, porcupine damage, tar spots, crown condition, and cankers.

Study Design: Individual-tree measurements

Data recorded for individual trees and snags included species and dbh and number and size of cavities. Diameter at breast height was measured on each tree at 1.3 m above ground. To be conservative over the positive identification among species of ash, White ash (*Fraxinus americana* L), green ash (*Fraxinus pennsylvanica* Marsh.) and black ash (*Fraxinus nigra* Marsh) were combined into *Fraxinus* genus rather than recorded as individual species. Additionally, large-tooth aspen (*Populus grandidentata*) and quaking aspen (*Populus tremuloides*) were also combined into *Populus* genus rather than recorded as individual species. Snags were defined as any dead standing tree >8 cm dbh and >1.8 m tall (Thomas et al. 1979; Kruse 1990). Cavity trees were defined as trees with a nest, cavity, den or hollow that might shelter a hole-nesting species (Healey et al. 1989) that were in any live tree >1 m above the ground that provided overhead shelter from precipitation and did not have cracks or openings other than the entrance (Carey 1983). Cavities were recorded as small (<6 cm in circumference), large (>6 cm) or multiple (two or more cavities).

Beech were visually examined, from the ground, for beech scale. Scale abundance was recorded using a qualitative rating of 0-4 based on visual comparisons with standardized photographs (Figure 2-3). Beech scale abundance classes were recorded as: 0) absent, with no detectable scale presence; 1) trace, with only a few scattered scales; 2) patchy infestation, with one or more dense patches of scale; 3) whitewashed, with heavy infestation covering the majority of bole and limbs; and 4) dead/declining trees presumably resulting from BBD, usually covered with dead scales characteristic of “black wool” (Shigo 1976).

Additionally, all beech trees were visually examined from the ground to look for beech snap, crown dieback, beech cankers and tar spots. Beech snap refers to a beech crown that has “snapped off”, typically from the wind, after severe weakening of the stem due to pests or pathogens and only the bole remains upright. Crown dieback was recorded if >50% of a tree’s crown appeared dead or in severe decline. Beech cankers were recorded if there was evidence of necrosis on the bark of the stem. Tar spots were recorded if a black tar-like substance was evident on the stem.

Two coarse woody debris transects, each 100 m long and 2 m wide, were established between the center and north plot and the center and west plot (Figure 2-2). Coarse woody debris was defined as dead branches, stems and boles of trees, >10 cm in diameter, that had fallen and were at <45° angle to the ground. Diameter at the point of intersection and length was recorded for each individual piece. Volume of coarse woody debris was calculated as $(\text{length} \times \pi (\text{diameter}/2)^2)$ for each individual piece.

Statistical and spatial analysis methods

Although underlying data may not be normally distributed, means based on a large sample size are assumed to be normally distributed (Stewart-Oaten 1995). As such, we performed analysis on untransformed data to avoid potential problems with transformation bias (Hayes et al. 1995). All statistical analyses were performed using SAS (9.1; SAS Institute, Inc., Cary, North Carolina). Significance for all statistical tests were determined using an $\alpha=0.05$.

Summary statistics (e.g., total number of trees examined, number of species examined) are reported as total values for all sites. Most analyses were performed at the site-level by aggregating all plot-level data across a site to obtain averages per site. Plot-level comparisons may too easily be affected by local effects or random chance. This type of aggregation reduces variability within sites.

Sample size for each individual analysis varied and will be presented with each analysis in the results section. Some sites were examined for beech scale infestation only and stand-level data were not recorded. This type of sampling occurred in situations where we tried to delineate the advancing front and had to concentrate sites in a smaller area and in places where stand data could not be collected without sampling bias (e.g., residential areas, along roadsides, in campgrounds). These sites were used in defining the advancing front but were excluded from statistical analysis to avoid any sampling bias.

Mean beech scale abundance (i.e., level of infestation) was determined for all beech sites (n=739). Sites with no beech scale were categorized as beech scale infestation category "absent" (n=517). Infested sites were divided into three categories; "light" (n=123) included sites with mean beech scale abundance greater than zero but less

than one. “Moderate” sites (n=88) had a mean scale abundance greater than one but less than or equal to three. “Heavy” sites (n=11) had a mean scale abundance greater than three.

For basal area, beech dbh and snag analyses, simple descriptive statistics were used to characterize the abundance, mean and variance in the data. General linear models were used to test for differences among means (Searle 1987) of beech snap, tar spots, crown dieback and beech cankers. Frequency distributions and chi-square tests were calculated to assess associations among levels of beech scale infestation and presence of cavity trees. Fisher’s Exact Test was used to calculate p-values because chi-square assumptions would be violated due to a small number of expected positive occurrences (<5). Due to a small sample size of cavity trees in general, I did not examine associations between cavity size and beech scale infestation level.

All spatial data calculations were performed using ArcView GIS (3.2; ESRI, Redlands, California) to calculate area of and distances between satellite infestations. Satellite infestations were visually separated and grouped as distinct infested areas set apart from other infestations by uninfested beech or unsuitable habitat >10 km apart. Each satellite population was distinguished by its disjunct location in relation to other satellite populations and its distinctive core-to-periphery pattern of infestation. Typically a satellite infestation had a lighter-to-heavier gradient of infestation from the perimeter to the core respectively.

Results

A total of 871 sites were surveyed from 2004-2006. In total, 732 sites with beech trees and 139 sites devoid of beech were surveyed. In addition, 67 sites along the advancing front were re-visited to monitor spread in 2005 and 2006. Overall, 26% of all sites were infested. In the Upper Peninsula, the percentage of infested beech sites was higher, 47% (68 out of 144) were infested. In the Lower Peninsula, only 21% of beech sites were infested (125 out of 588).

Distribution of beech scale

Beech scale infestations occurred in 15 of the 63 counties (24%) where I surveyed sites with beech. Infestations were concentrated in the eastern Upper Peninsula and western Lower Peninsula (Figure 2-5). The distribution in the Upper Peninsula extends approximately 150 km east-west and approximately 75 km north-south. The beech scale infestation distribution in the Lower Peninsula extends approximately 250 km north-south and 150 km east-west (Figure 2-5). Beech scale infestations in the Upper Peninsula appear to be continuous while the Lower Peninsula, ten discontinuous areas of infestation, or satellite populations were identified (Figure 2- 6). Combined, these satellite populations cover approximately 15,100 km² (Table 2-1). Each satellite population in the Lower Peninsula had a distinct pattern of infestation in which it appeared to be more heavily infested at the core and less infested towards its periphery (Figure 2-7). The Upper Peninsula population did not have a small distinguishable core area; rather it covers a much larger geographical area than the Lower Peninsula satellite populations. The Upper Peninsula has a large contiguous population covering more land area than the two largest Lower Peninsula satellite populations combined (Table 2-1).

Forest resources

Thirty-seven tree species co-occurred with beech within our study sites (Table 2-1). Sugar maple (*Acer saccharum* Marsh.) was the most abundant (1,741), followed by red maple (*Acer rubrum* Linnaeus) (321), northern red oak (*Quercus rubra* L.) (296), ash species (*Fraxinus* spp.) (202), aspen species (*Populus* spp.) (201), white oak (*Quercus alba* L.) (158) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) respectively (130) (Table 2-2). Mean basal areas were not different for the seven most commonly encountered species among levels of beech scale infestation (Table 2-3). Mean beech basal area was not statistically different among level of beech scale infestation ($F_{3, 707} = 1.50$; $p = 0.2144$) however, basal areas exhibited a pattern of increase as beech scale infestation level also showed a pattern of increase (Figure 2-8).

A total of 4,307 beech trees were examined and grouped into 12 diameter classes (Table 2-4). The dbh of infested beech trees ranged from 10-117 cm. Mean scale abundance significantly increased as beech dbh increased ($F_{3, 3683} = 1.79$; $p = <0.0001$) (Figure 2-9). Within infested sites, approximately 35% of beech trees <65 cm dbh had some level of beech scale infestation, whereas 35-55% of beech trees >65 cm dbh were infested with beech scale (Figure 2-10). As beech trees approached 100 cm dbh, the percentage of infested trees declined sharply (Figure 2-10), but very few trees of this size were examined (Figure 2-11). The majority of infested trees (64%) had a light level of infestation (924 out of 1447). A smaller proportion (35%) showed moderate levels of infestation (512 out of 1447) and very few trees (<1%) were heavily infested (11 out of 1447) (Figure 2-12).

Beech trees were evaluated for porcupine feeding, beech snap, tar spots, crown dieback, and cankers. No evidence of porcupine feeding on beech trees was found. Occurrence of beech snap, tar spots, crown dieback and cankers were low, averaging less than 3.5% of sites. Occurrence of beech snap, tar spots and crown dieback were statistically different among levels of beech scale infestation; beech snap ($p=0.0073$), tar spots ($p=0.0099$) and crown dieback ($p<0.0001$). Occurrence of beech cankers was not statistically different among levels of beech scale infestation ($p=0.0619$). Overall, presence of beech snap, tar spots, crown dieback and beech cankers were highest in uninfested sites. Within infested sites, presence of beech snap, tar spots, crown dieback and beech cankers were highest in moderately infested sites (Tables 5-8).

Wildlife resources

A total of 291 snags representing 22 different tree species were observed in 148 of 730 sites (Table 2-2). Snag density for all species other than beech was significantly related to levels of beech scale infestation ($F_{3, 727} = 3.91$; $p = 0.0087$; Table 2-6) and was highest in moderately infested sites (Table 2-6). The total number of beech snags was positively related to increasing levels of beech scale infestation ($F_{1, 727} = 3.07$; $p = 0.0272$; Table 2-6). Beech snag density was higher in moderately infested sites than in uninfested and lightly infested sites followed (Table 2-6).

Cavity trees, other than beech, totaled 33 trees out of 3,491 trees examined (0.95%). Only 11 species of trees other than beech had cavities. Sugar maple, which was very abundant in transects, had the most cavities ($n=17$) but only <1% of sugar maples examined had a cavity. Other tree species generally provided a small number of cavities, but white pine, black oak, aspen, yellow birch and red maple all had a higher percentage of trees with cavities than sugar maple (Table 2-7). Even though the proportion of trees with cavities increased with dbh, the number of cavity trees peaked in the 45 to 65 cm dbh size classes because of their greater abundance (Table 2-8). Cavity tree abundance was not different among levels of beech scale infestation, $X^2 (3, n= 3,524) = 3.3, p= 0.35$ (Table 2-9). Beech cavity tree abundance was also not different among levels of beech scale infestation, $X^2 (3, n= 5,131) = 6.63, p= 0.085$ (Table 2-10).

In total, 1,230 pieces of coarse woody debris were recorded along 119 transects. Abundance of coarse woody debris was significantly different among levels of beech scale infestation ($F_{2, 1111} = 7.79$; $p=0.0004$). Sites without beech scale had the greatest amount of coarse woody material, followed by moderately infested sites and lightly

infested sites (Table 2-12). Volume of coarse woody debris was not significantly different among levels of beech scale infestation ($F_{2, 119} = 0.24$; $p=0.7840$; Table 2-11).

Discussion

Distribution of beech scale

Beech scale is more widely distributed in Michigan than previous surveys revealed. Kearney (2006) reported that beech scale infestations were limited to a five-county area in 2002-2003 (Chippewa, Manistee, Mason, Luce, and Oceana counties) based upon surveys by Witter and Petrillo (2005). Michigan's advancing front is spreading into new areas, creating smaller satellite infestations outside the original five-county front. Satellite populations were not evenly distributed between the Peninsulas, with a more fragmented distribution in the Lower Peninsula.

Forest resources

Although many species occur in northern hardwood stands, the forest nearly always include sugar maple, white ash, red maple, beech and eastern hemlock and occasionally aspen and northern red oak (Eyre 1980; Tubbs and Houston 1990; Dickman and Leefers 2003). Primary associates with beech in our study sites were similar to other studies involving BBD in the United States (e.g., Forrester and Runkle 2000; Griffin et al 2003; Latty et al. 2003; Kearney 2006).

Few studies have reported forest conditions in relationship to beech scale infestation; most report their results in comparison to BBD. This study focused exclusively on the distribution of beech scale because trees infested with beech scale are likely to eventually become infected with BBD (Ehrlich 1934; Speight 1981; Griffin et al. 2003). Beech bark disease studies conducted in northeastern United States reported 80-90% mortality of mature beech as a result of BBD (Houston 1984; Krasny 1992; Leak 2006). Results from this study showed that in sites with beech scale, only 35-60% of beech trees were infested. Lacking comparable studies, we are unable to conclude how Michigan's level of infestation compares to that of other areas. This study reveals only a snapshot in time of beech infested with beech scale. The advancing front is likely too recent in Michigan to have infested all susceptible trees within our sites and the number of infested trees will increase.

Factors affecting population dynamics of beech scale are poorly documented. Past studies have suggested specific geographic, climatic or biological conditions such as extreme winter temperatures and heavy autumn rainfalls that can temporarily reduce beech scale populations (Houston and Valentine 1988). Erlich (1934) noted that climatic

limitations are undoubtedly important in restricting beech scale range where it has been present long enough to allow wide distribution as in Europe. At the time of this study, it appeared that Michigan forests were less infested than forests in the northeastern United States. Future studies are needed to determine if infestation rates remain the same as infection rates.

Results from this study did not reveal a significant relationship between beech basal area and basal area of the other seven most abundant tree species. I also found that mean beech basal area was not statistically different among stands with varying levels of beech scale infestation. This finding coincides with Griffin et al. (2003) and Kearney (2006) whom did not find a significant difference among beech scale infestation and density of beech in New York and Michigan, respectively. I did find that beech basal area was highest in moderately infested sites.

Factors that predispose a stand to beech scale infestation, and subsequently BBD, are uncertain. Ehrlich (1934) stated that the density of beech would “influence infestation only as they affect retention of moisture and protection against driving rains, hot sun and strong winds.” Similar to Ehrlich’s (1934) idea about beech basal area influencing moisture retention, Twery and Patterson (1984) hypothesized that the presence of eastern hemlock would enhance shading and moisture retention, conditions which have been correlated with beech scale colonization and survival. Studies have found an increase in eastern hemlock in response to the loss of beech due to BBD (Twery and Patterson 1984; Runkle 1990; Le Guerrier et al. 2003). Eastern hemlock was one of the most commonly occurring tree species in our sites, but there was no significant relationship between basal area of eastern hemlock and beech scale infestation.

Similarly, Griffin et al. (2003) did not find any significant relationship between hemlock basal area and BBD severity in New York.

We surveyed beech trees with diameters ranging 10-117 cm dbh and the larger trees consistently were more highly infested than the smaller diameter trees. This finding is consistent with the literature (e.g., Ehrlich 1934; Shigo 1963, 1964; Houston et al. 1979; Fernandez and Boyer 1988; Runkle 1990; Griffin et al. 2003) and is probably a result of more suitable habitat for scale on the bark of older beech. Small-diameter trees can still be infested (Ehrlich 1934), however, as was observed during this study.

Sites were examined for evidence of porcupine feeding on beech trees because studies in the Allegheny National Forest in Pennsylvania observed that porcupines fed on beech trees without scale that were surrounded by infested beech trees. The author theorized that these trees exhibited a resistance to beech scale (R. White, USDA Forest Service Allegheny National Forest, personal communication, April 17, 2005). We did not find any evidence of porcupine feeding on any beech trees, regardless of beech scale infestation.

There was no clear progression of increasing abundance of beech snap, tar spots, crown dieback and beech cankers from lightly infested to heavily infested sites. Results from this analysis showed that moderately infested sites had the most occurrences of beech snap, tar spots, crown dieback and beech cankers, but there were not enough trees in the heavily infested sites to show any strong relationship.

Wildlife resources

Snags are an important wildlife resource, used for a variety of taxa. They provide perches for singing, hunting, foraging, resting and roosting, as well as foraging sites for insect-eating birds, mammals, reptiles and amphibians (Miller 1994). In the northern hardwood forests where most of our study sites were located, over 40 species of birds and mammals use snags and dead portions of live trees for nest sites, dens, escape cover and winter shelters (Evans and Conner 1979; DeGraaf and Shigo 1985). Each forest community has different requirements in terms of the number, species and size of snags necessary to support all the cavity users associated with that community. Height, dbh, condition, tree species, location and abundance of snags have a direct impact on the wildlife species that utilize a stand (DeGraaf and Shigo 1985). Bunnell et al. (2002) suggested maintaining a target density of 2-3 large snags (30 cm dbh) and 10-20 smaller snags per hectare throughout the stand. During this study, density of snags was highest within moderately infested sites for both beech and non-beech species. This is likely explained because sites there had larger-diameter trees than uninfested or lightly infested sites. Beech scale is a relatively recent (< 20 years) invader to Michigan's forests and as the advancing front progresses into the killing front, changes in forest ecosystems will likely become more evident. Results from our study showed that increasing levels of scale were positively related to the number of snags. Following beech scale infestation, the killing front moves through a forest stand and will result in declining health and death of overstory beech, producing an increasing number of beech snags in the infested forest. This study provides a baseline data for determining how snag and snag-using wildlife may change as BBD progresses.

Cavity trees are trees that are living or partially living and possess a cavity large enough to serve as shelter for birds and mammals. Cavities are created by injury, disease, woodpeckers or loss of large limbs. The best cavity trees have healthy crowns that protect a cavity from the elements and provide multiple benefits to the occupant such as protection from predators and foraging opportunities including mast production (Miller 1994). Smaller cavities are utilized by species such as chickadees (*Poecile* spp.), nuthatches (*Sitta* spp.) and northern pygmy owls (*Glaucidium californicum*), while larger cavities are used by species such as pileated wood peckers (*Dryocopus pileatus*), wood ducks (*Aix sponsa*) and northern flickers (*Colaptes auratus*). Cavities were unevenly distributed among trees species (Table 2-7). Results from this study showed that of the non-beech trees, sugar maple had the most cavities, but was probably more a product of abundance than anything else. This result concurred with Kenefic and Nyland (2007) who also found that sugar maple accounted for about half of observed cavity trees.

Less than 1% of all trees within study sites were observed to have cavities. Only 3.8% of cavity trees were beech, which is much lower than similar studies in the Monongahela National Forest in West Virginia. Beech comprised of 36.7% of cavity trees in the Kahler and Anderson (2006) study in New York whereas Carey (1983) found 29% of cavity trees were beech. Initially, we thought that the low number of cavity trees could be explained by reduced visibility due to heavy crown cover because this study was conducted in May-August when crowns are fully developed and can block views of upper canopy cavities. We suspected that our number would increase in the fall after leaf senescence. Healy et al. (1989) and Kahler and Anderson (2006) however, estimated that

80% of hardwood cavities were detected from the ground using binoculars. I did not use binoculars, which may potentially explain the relatively few number of cavities recorded.

Beech accounted for the majority of cavity trees but, they represented slightly more than 1% of all beech trees surveyed. Other studies (e.g., Kearney 2006; Gysel 1961; Robb and Bookhout 1995) also found that beech trees had more cavities than any other species. Kahler and Anderson (2006) found that black locust (*Robinia pseudoacacia*) followed by beech, were significantly more likely to have cavities than all other species in their studies in the Monongahela National Forest. In my study stands, we only encountered one black locust tree (Table 2-2). Fan et al. (2003) also found beech to be highly susceptible to cavity formation during studies conducted in Illinois, Indiana and Missouri. They noted that beech were highly prone to damage and/or infection from a number of sources, in part because of the thin bark and high susceptibility to fire, logging damage and decay-causing fungi. Older trees are almost invariably hollow as a result of the presence of various heart rot fungi (Hicks 1998).

In the analysis, abundance of beech cavity trees was not significantly related to beech scale infestation class but, cavity trees were less common in uninfested sites than moderately infested sites. Heavily infested sites did not have any cavities but, there were only 11 of these sites. Kearney (2006) found that tree diameter was significantly related to number of cavities. If consistent, declines in mature beech from BBD will likely reduce the abundance of cavities available for wildlife. Our data suggest that middle-sized trees were observed to have the most number of cavities but few larger-diameter trees were examined.

Kahler and Anderson (2006) cautioned against assessing the value of the beech as a cavity tree resource because of BBD. When beech bark disease infects a forest for the first time, a high proportion of large, mature trees are killed (Tubbs and Houston 1990) and replaced by trees that are too small for cavity formation (Houston 1994). Perhaps initially BBD will increase cavity abundance; in the long-term beech may not be viable cavity resource. What will replace it as a cavity resource in the aftermath forests is unknown.

Dead wood lying on the forest floor is commonly referred to as coarse woody debris. It can take the form of fallen logs, broken branches or downed treetops. Coarse woody debris provides habitat elements useful for many species of amphibians, reptiles, birds and mammals that may be important to their survival and migration (Harmon et al., 1986). In an old-growth maple-beech forest, 89% of the bird species that were permanent residents and fall/winter visitors used coarse woody debris (Williams 1936). Twenty-eight birds, 18 mammals, 23 reptiles and amphibians and hundreds of invertebrates and fungi use coarse woody debris in temperate deciduous forests (e.g., New England forests) (DeGraaf and Rudis 1986; Keddy and Drummond 1996).

In the short-term, BBD has the potential to increase coarse woody debris which will positively influence wildlife habitat but, in the long-term, it may negatively influence wildlife habitat. Extensive volumes of literature describe the relationship between coarse woody debris and animals (e.g., Menzel et al. 1999; Stone et al. 1999; Butts and McComb 2000; Greenburg 2002; Bate et al. 2004). Each species of wildlife in each region requires a different volume and size of CWD. Of all habitat variables assessed, downed wood is the least consistently measured, and it is impossible to equate number of

pieces, volume, and percent cover to extract broad patterns (Bunnell and Huggard 1999). In a study of 12 forest stands in Virginia, CWD volume ranged from 4-24 m³ /ha (Fuhrman 2004). Kearney (2006) found CWD volumes in Michigan beech stands range from 2.5-235 m³ /ha. I found CWD volumes considerably higher (27-36 m³ /ha) than the Virginia study, but within the broad range of Michigan study. Many factors influence the distribution and abundance of CWD including wind throw, topography insects and diseases which can affect stands of trees and highly exaggerate patterns for an area (Harmon et al. 1986; Rubino and McCarthy 2003). Much research has been conducted on CWD in relationship to wildlife. Several sources suggest that greater mean CWD volumes are associated with more wildlife and that low CWD volumes can be limiting to wildlife (Harmon et al. 1986, Newton 1994, Carey and Johnson 1995), however, I was not able to find a quantitative estimate of CWD volumes for wildlife. Instead, wildlife studies in relationship to CWD focused on volume, abundance and decay class as related to wildlife populations. Hagan and Grove (1999) stated that “if forest ecologists don’t know how much CWD is needed to maintain biodiversity, how are foresters supposed to know?” Further study is need on this topic, especially in relation to BBD. Traditionally, BBD has led to short-term regional increases in coarse woody debris, thus the disease may play an important role that influences landscape scale wildlife habitat characteristics (McGee 2000; Morin et al.). As BBD progresses in Michigan, there should be an increasing amount of coarse woody debris as more beech die and fall to the forest floor. Dead tree crowns will snap and fall to the forest floor, increasing downed coarse woody debris and creating snags and openings in the canopy. Changes as a result of BBD will likely increase wildlife habitat initially by increasing the number of snags, volume of

coarse woody debris and number of cavities, but the long-term effects on wildlife populations are unknown. Further studies regarding these changes in relationship to various stages will be extremely important as we try to understand changes initiated by the BBD complex.

Management implications

New scale infestations can be difficult to detect and new satellite populations are established through many different means; humans, small mammals, birds, and wind currents. People moving firewood or other materials bearing viable crawlers is another potential mode of dispersal into new areas. While reviewing invasive species literature, the following examples provide insight into potential management considerations.

Andow et al. (1990) and Muirhead et al. (2003) found that long-distance dispersal accelerated spread rates of cereal leaf beetles (*Oulema melanopus*) and emerald ash borer (*Agrilus planipennis*) respectively, by providing opportunities for ‘nascent foci’ to develop, from which new populations or coalescing nodes can be founded. The cereal leaf beetle was observed to spread much faster than microscale data suggested, likely due to macroscale movements such as through air currents or human transport (Andow et al. 1990). Likewise, the emerald ash borer diffusive spread models were “unable to account for 17 of the 48 new populations in the Great Lakes during 2004” due to long-distance dispersal (Muirhead et al. 2003). This resulted in an artificially higher dispersal rate when establishing new satellite infestations. Artificial dispersal can result in establishment of satellite populations and accelerated spread rates when they eventually coalesce (Shigesada and Kawasaki 1997). By understanding likely spread rates, forest managers would have time to focus their management strategies along the advancing front and to adapt their management plans to incorporate impacts from the disease and to target property owners in the vicinity. Moody and Mack (1988) found the spread of exotic plants to be greatly accelerated through the growth of satellite foci which

“eventually exceed the range occupied by the spread of a main focus” and they stressed the importance of focusing on satellite populations in managing spread.

Focusing management efforts such as scale control, on satellite infestations would likely be the best strategy for controlling spread and thereby reducing the forest impacts. Taylor and Hastings (2004) suggested “eradication prioritization for isolate, low-density smooth cordgrass (*Spartina alterniflora*) colonies as opposed to high-density core populations owing to faster spread capabilities of the former.” Sharov et al. (2002) stated that eradication efforts “targeted at isolated satellite colonies along the invasion front dramatically reduced the overall rate of spread by the gypsy moth (*Lymantria dispar*) in North America. While controlling isolated satellite infestations appears to be the best management strategy for reducing the spread rate, it also is a major challenge. Locating beech scale is easy. Theoretically, new satellite infestations can be established from a variety of means including people moving firewood, bird or mammal migrations, wind or water currents, therefore making it difficult to not only detect, but to manage.

Despite our best efforts to control the spread of beech scale, this will likely not lead to a total eradication from our forests even if it was deemed a worthy endeavor and all the funding and personnel were in place. Federal and or state quarantines are a means to limit the transportation of infested material out of the quarantined area during the critical period of scale development i.e., the crawler stage but like all regulations, quarantines are not totally effective as they rely upon cooperation, enforcement and catching every single violation of the law. Additionally, quarantines do not regulate unintentional movement of crawlers or bird, mammal, wind or water movements. Rather, quarantines are a people-management tool designed to slow the transport of crawlers out

of a known infested area. These measures do not safeguard against total compliance by people, bird, animal or wind movements nor do they protect from transportation of infested material out of non-quarantined areas. In short, it is a management tool only as effective as the compliance that it receives and the data of known infestations.

The advancing front is the prelude to BBD and likely the best place to employ management activities. We have the knowledge of the beech scale distribution in Michigan therefore; we know where to expect BBD in the future. Additionally, we are identifying new areas of infestation as this long-studied disease enters into new areas such as Michigan. This knowledge can help us to manage this exotic forest pest in forested ecosystems.

Table 2-1. Satellite populations of beech scale infestations in Michigan.

Satellite name	Number of sites	Light Scale	Moderate Scale	Heavy Scale	Area infested (Km²)
Beaver Island	8	2	1	5	91
Bois Blanc Island	4	2	1	1	40
Benzie County	3	2	1	0	10
Cadillac	16	11	3	2	595
Emmet County	7	5	1	1	506
Fisherman's Point	1	0	0	1	60
Leelanau	2	2	0	0	174
Ludington	59	22	15	22	2,533
Mackinaw Island	37	24	9	4	6
Silver Lake	68	17	16	35	1,267
Upper Peninsula	3	2	1	0	9,823

Table 2-2. Common name and number of trees by species associated with beech within study sites. Trees are arranged in descending order according to their abundance within study sites.

Species	Number of trees examined	Number of Snags
American beech	3,445	57
Sugar maple	1,741	47
Red maple	321	17
Red oak	296	8
Ash species	202	11
Aspen species	201	23
White oak	158	13
Eastern hemlock	130	12
Black cherry	114	7
Black oak	99	0
Unknown	91	26
White pine	76	17
Paper birch	70	19
Red pine	70	5
Yellow birch	70	9
American hophornbeam	60	2
Northern white cedar	36	4
Jack pine	25	1
Elm species	16	3
Fir species	16	2
Spruce species	15	0
Basswood	14	0
Eastern cottonwood	12	4
Balsam fir	9	0
Black walnut	8	1
Unknown oak species	5	0
River birch	5	1
Tulip poplar	5	0
Stripped maple	4	0
Ironwood	3	0
Sycamore	3	0
Black birch	2	0
Box elder	2	0
Hickory species	2	0
Sassafras	2	0
Apple	1	0
Black locust	1	0
Choke cherry	1	0
Total	7,331	289

Table 2-3. Results from an ANOVA to compare basal area for American beech and the seven most abundant other species across beech scale infestation classes. N is the number of individual trees examined across sites (n=737). Basal area is reported in m²/hectare.

Tree species	N	Absent n=517 sites Basal area Mean ± SE	Light n=123 sites Basal area Mean ± SE	Moderate n=88 sites Basal area Mean ± SE	Heavy n=11 sites Basal area Mean ± SE	p-value
American beech	2,435	6.01 ± 0.06	6.22 ± 0.51	7.42 ± 0.64	7.64 ± 3.26	0.2144
Sugar maple	2,069	6.36 ± 0.25	5.69 ± 0.67	5.83 ± 0.06	1.15 ± 4.13	0.4167
Red maple	393	1.08 ± 0.14	1.12 ± 0.34	1.17 ± 0.32	1.08 ± 0.14	0.1990
Northern red oak	316	0.92 ± 0.14	1.06 ± 0.32	0.69 ± 0.30	0	0.9026
Aspen species	236	0.55 ± 0.11	0.69 ± 0.28	0.37 ± 0.25	0	0.0811
Ash species	213	0.71 ± 0.09	0.83 ± 0.23	0.14 ± 0.23	0	0.8346
White oak	172	0.44 ± 0.07	0.44 ± 0.07	0.05 ± 0.18	0	0.2019
Eastern hemlock	154	0.46 ± 0.09	0.46 ± 0.09	0.83 ± 0.21	0	0.1703

* Denotes significance between uninfested and infested sites at $\alpha = 0.05$.

Table 2-4. Number and percentage of beech trees per diameter class corresponding with the level of beech scale infestation. Each diameter class is recorded in centimeters and is represented in the table by the median number in its range of dbh measurements (i.e., dbh class “5” represents trees that are 1-9 cm dbh).

Diameter Class	No Scale	Percent No Scale	Light Scale	Percent Light Scale	Moderate Scale	Percent Moderate Scale	Heavy Scale	Percent Heavy Scale	Total
5	163	71	43	19	24	10	0	0	230
15	445	68	142	22	66	10	2	>1	655
25	639	68	200	21	93	10	1	>1	933
35	614	63	219	23	131	14	4	>1	968
45	466	66	159	22	82	12	0	0	707
55	291	67	86	20	54	12	2	>1	433
65	127	70	30	16	24	13	1	>1	182
75	69	62	23	21	18	16	1	>1	111
85	27	54	11	22	12	24	0	0	50
95	9	43	8	38	4	19	0	0	21
105	5	50	3	30	2	20	0	0	10
115	4	67	0	0	2	33	0	0	6
125	1	100	0	0	0	0	0	0	1
Totals	2860	66	924	21	512	12	11	>1	4,307

Table 2-5. Frequency of occurrence for beech snap, tar spots, crown dieback and cankers across levels of beech scale infestation.

	No Scale	Light Scale Infestation	Moderate Scale Infestation	Heavy Scale Infestation	Total
Sites with beech snap	27	2	11	0	40
Sites without beech snap	426	98	60	3	587
Sites with tar spots	11	3	8	0	22
Sites without tar spots	442	97	63	3	605
Sites with crown dieback	20	2	12	2	36
Sites without crown dieback	433	98	59	1	591
Sites with cankers	1	0	2	0	3
Sites without cankers	452	100	69	3	624
Total sites examined	453	100	71	3	627

Table 2-6. Mean number of beech snags (n=44) and non-beech snags (n=3,886) per site across levels of beech scale infestation. Basal area is reported in m²/ha.

	Beech Basal area Mean ± SE	Non-beech Basal area Mean ± SE
Absent	0.16 ± 0.05	0.87 ± 0.09
Light	0.11 ± 0.07	0.23 ± 0.18
Moderate	0.41 ± 0.09	1.12 ± 1.12
Heavy	0	0

Table 2-7. Common name and number of tree species examined within study sites. Number of cavity trees and percentage of total cavity trees arranged by species and presented in descending order of abundance.

Species	Number of trees examined	Number of cavity trees	Percent of cavity trees
American beech	4,945	186	3.76
Sugar maple	1,741	17	0.98
Red maple	321	3	0.93
Red oak	296	2	0.68
Ash species	202	1	0.50
Aspen species	201	3	1.49
White oak	158	0	0.00
Eastern hemlock	130	0	0.00
Black cherry	114	1	0.88
Black oak	99	1	1.01
Unknown	91	2	2.20
White pine	76	2	2.63
Paper birch	70	0	0.00
Red pine	70	0	0.00
Yellow birch	70	1	1.43
American hophornbeam	60	0	0.00
Northern white cedar	36	0	0.00
Jack pine	25	0	0.00
Elm species	16	0	0.00
Fir species	16	0	0.00
Spruce species	15	0	0.00
Basswood	14	0	0.00
Eastern cottonwood	12	0	0.00
Balsam fir	9	0	0.00
Black walnut	8	0	0.00
Unknown oak species	5	0	0.00
River birch	5	0	0.00
Tulip poplar	5	0	0.00
Stripped maple	4	0	0.00
Ironwood	3	0	0.00
Sycamore	3	0	0.00
Black birch	2	0	0.00
Box elder	2	0	0.00
Hickory species	2	0	0.00
Sassafras	2	0	0.00
Apple	1	0	0.00
Black locust	1	0	0.00
Choke cherry	1	0	0.00

Table 2-8. Non-beech trees were divided up into 14 diameter at breast height (dbh) classes. Each dbh-class is represented in the table by the median number in its range of measurements (i.e., dbh-class “5” represents trees that are 1-9 cm dbh).

Diameter class (cm)	Number of trees	Number of cavity trees	Percent of cavity trees
5	73	0	0
15	443	2	0.45
25	1,034	3	0.29
35	854	2	0.23
45	539	6	1.11
55	288	8	2.78
65	154	5	3.25
75	56	1	1.79
85	28	2	7.14
95	10	1	10.00
105	5	1	20.00
115	5	2	40.00
135	1	0	0
145	1	0	0

Table 2-9. Chi-square table of cavity tree abundance across levels of beech scale infestation.

	Absent	Light	Moderate	Heavy	Total
Cavity trees	27	1	5	0	33
Non-cavity trees	2,598	474	413	6	3,491
Total trees examined	2,625	475	418	6	3,524

Table 2-10. Chi-square table of beech cavity tree abundance across levels of beech scale infestation.

	Absent	Light	Moderate	Heavy	Total
Cavity trees	132	30	24	0	186
Non-cavity trees	3,099	1,162	673	11	4,945
Total	3,231	1,192	697	11	5,131

Table 2-11. Volume of coarse woody debris (± 1 SE) and associated level of beech scale infestation. There were 453 sites in the absent category, 100 in the light and 71 in the moderate categories respectively.

	Absent	Light	Moderate
Volume (m³) per hectare	36.25 $\pm$ 4.25	33 $\pm$ 10.5	27.25 $\pm$ 12.25
Mean number of pieces per hectare	10.18 $\pm$ 0.63	6.09 $\pm$ 1.85	13.73 $\pm$ 1.58
Mean diameter	9.65 $\pm$ 0.28	13.97 $\pm$ 1.15	9.05 $\pm$ 0.56
Mean length	13.67 $\pm$ 0.26	10.07 $\pm$ 1.03	13.54 $\pm$ 0.64
Total number of pieces per category	957	67	206

Table 2-12. Frequency of occurrence of coarse woody debris pieces in each decay class and corresponding beech scale infestation level.

Decay Class	Absent	Light	Moderate	Total number of pieces
1	110	7	38	155
2	343	23	73	439
3	294	26	52	372
4	159	5	30	194
5	51	6	13	70

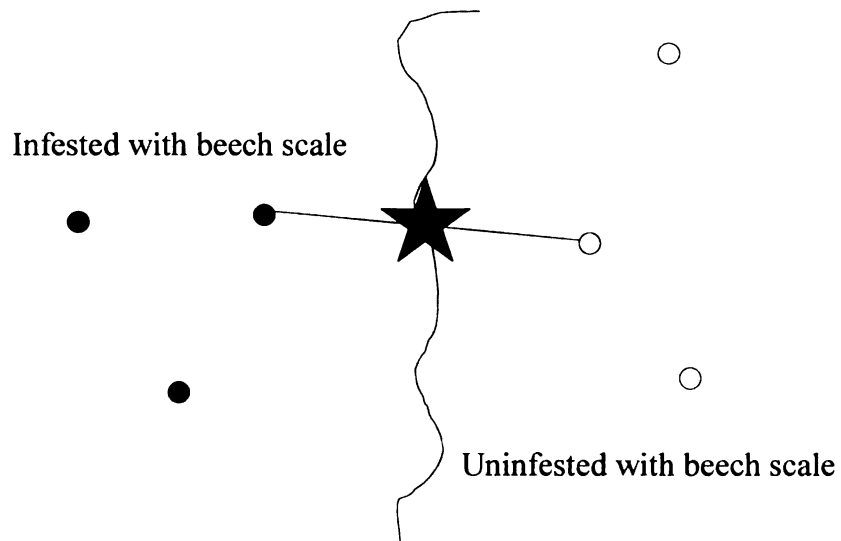


Figure 2-1. Adaptive sampling design for designing the advancing front. The star represents the midpoint between a known infested site and a known uninfested site.

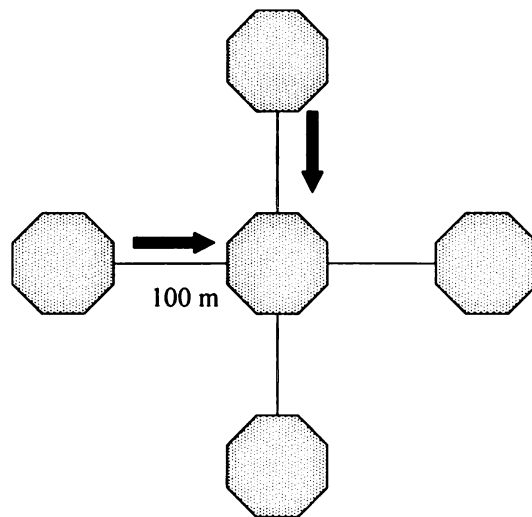


Figure 2-2. Site layout with five plots; center, north, east, south, and west each 100 m apart. Each site also has two 100 m coarse woody debris transects between the center and north plot and the center and west plot.



Figure 2-3. Photos used to standardize levels of beech scale infestation. Photo on the far left represents beech scale classification “trace”, middle photo represents “patchy” and right photo defines “whitewashed” (Photos taken by Nancy Schwalm, May 2004).

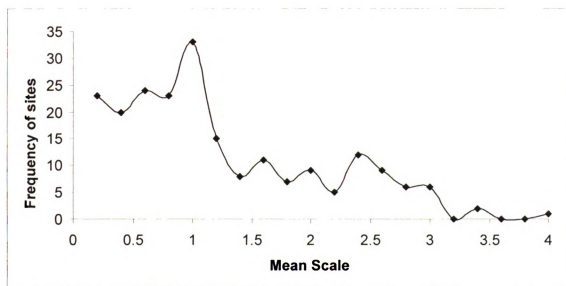


Figure 2-4. Frequency of sites plotted against mean scale to determine beech scale infestation classes. Mean scale was determined by aggregating all plot-level data across a site to obtain averages per site.

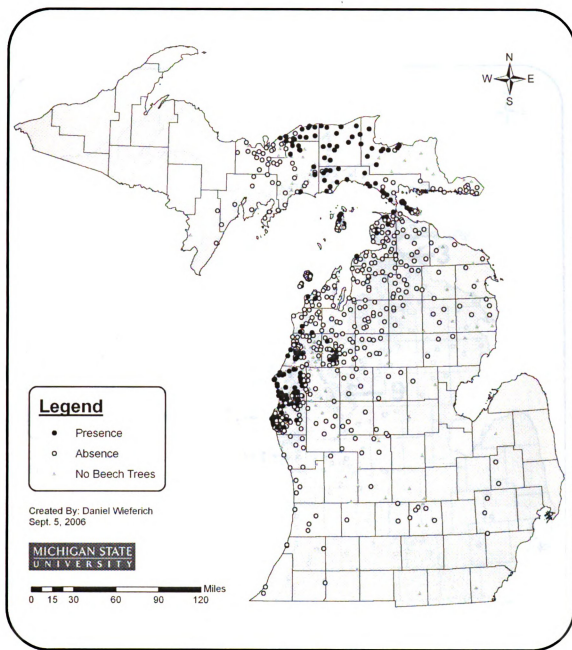


Figure 2-5. Map of Michigan, USA with study sites coded as uninfested (*open white circles*) or infested (*closed black circles*) or no beech sites (*triangles*).

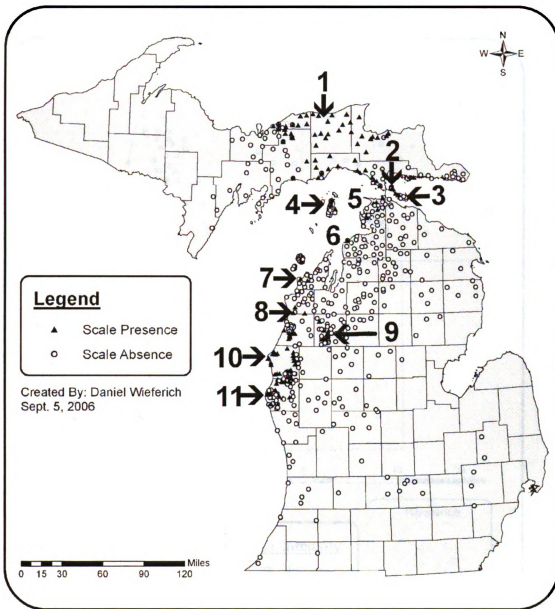


Figure 2-6. Map of Michigan, USA with beech study sites grouped into eleven distinct satellite populations designated as follows. 1-Upper Peninsula; 2-Mackinac Island; 3-Bois Blanc; 4-Beaver Island; 5-Emmet County; 6-Fishermen's Point; 7-Leelanau County; 8-Benzie County; 9-Cadillac; 10-Ludington; 11-Silver Lake.

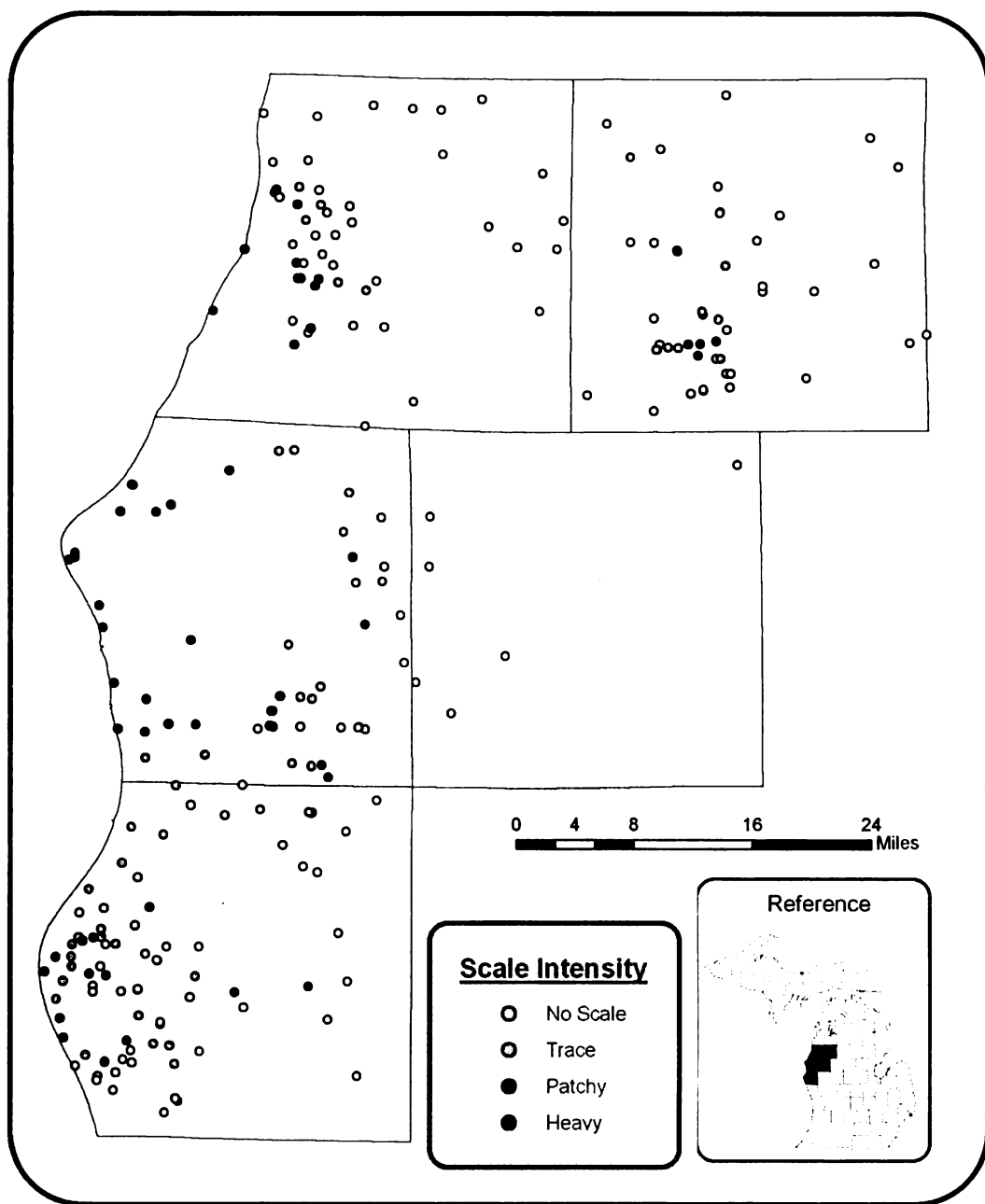


Figure 2-7a. Map of the Ludington and Silver Lake satellite populations enlarged to show the detail of sites coded according to their bee scale infestation level. Map created by Daniel Wieferich on March 30, 2007.

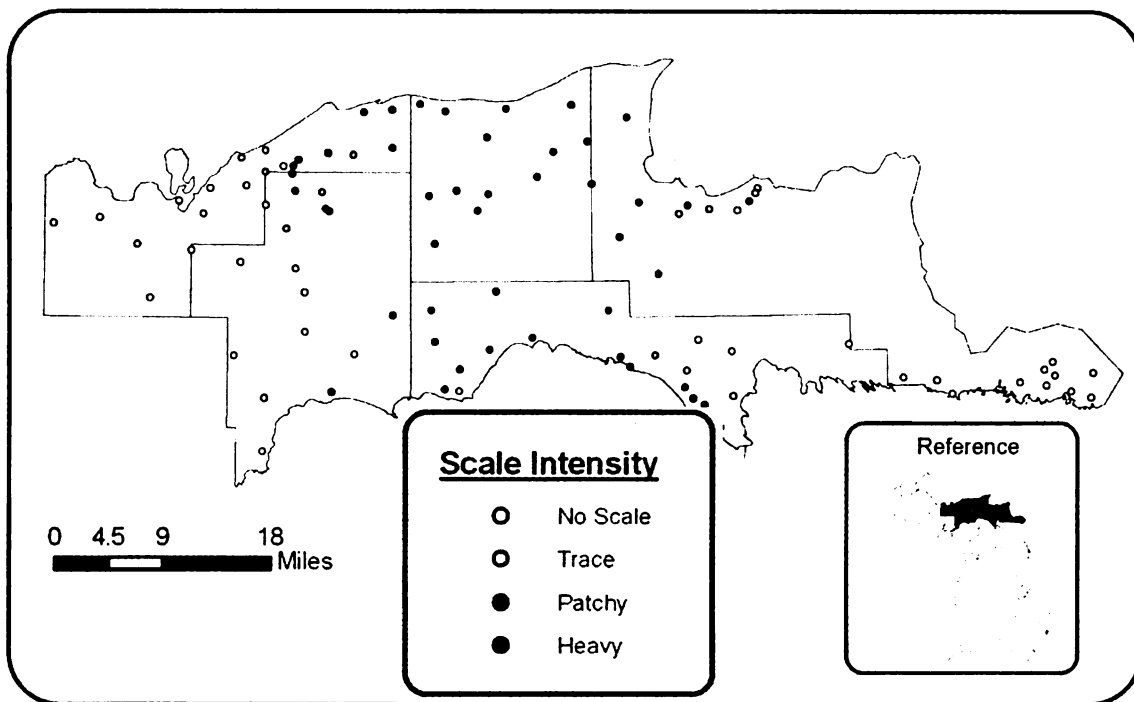


Figure 2-7b. Map of the Upper Peninsula satellite population enlarged to show the detail of sites coded according to their beech scale infestation level. Map created by Daniel Wieferich on March 30, 2007.

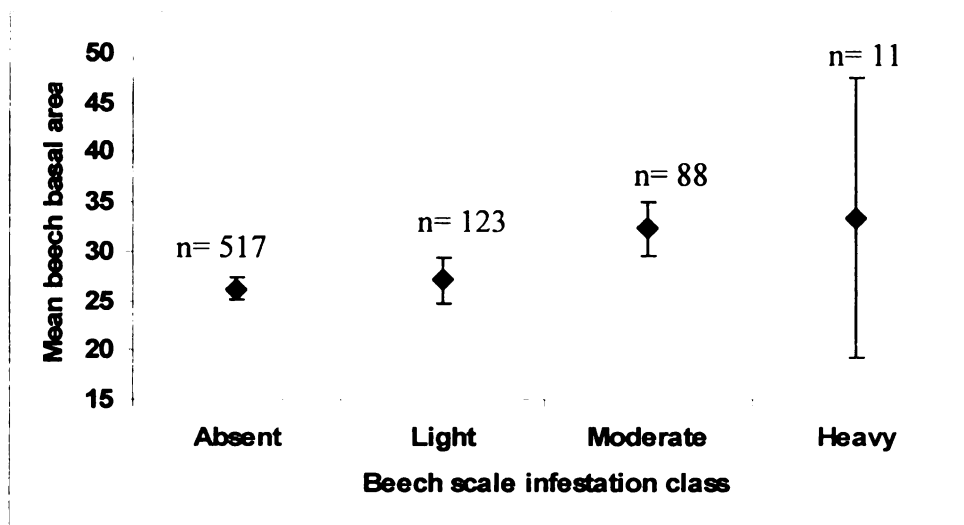


Figure 2-8. Mean beech basal area (± 1 SE) across level of beech scale infestation.

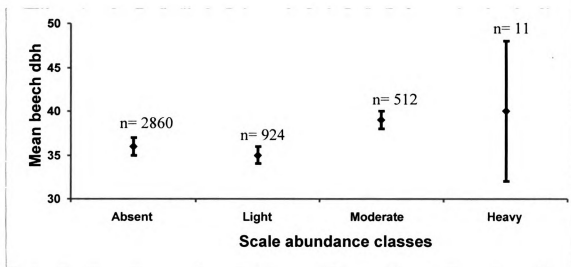


Figure 2-9. Mean beech diameter at breast height (dbh) (± 1 SE) across levels of beech scale infestation.

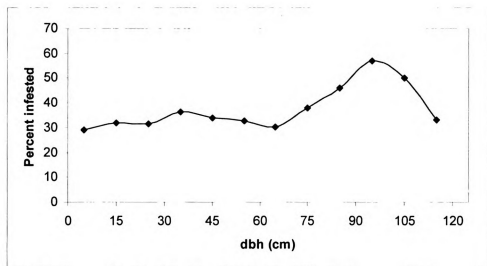


Figure 2-10. Percent of beech trees infested with beech scale as a function of tree diameter at breast height (dbh).

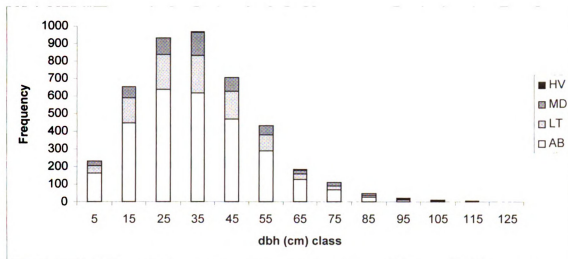


Figure 2-11. Frequency of beech trees within each beech scale infestation class across diameter at breast height (dbh) classes. Diameter at breast height classes represent the median number in a range of dbh measurements (i.e., dbh class “5” = dbh measurements 1-9 cm, “15” = 10-19 cm...”115” = 110-109 cm). Beech scale infestation classes are coded as “HV” for heavy infestation, “MD” for moderate infestation, “LT”, for light infestation and “AB” for uninfested.

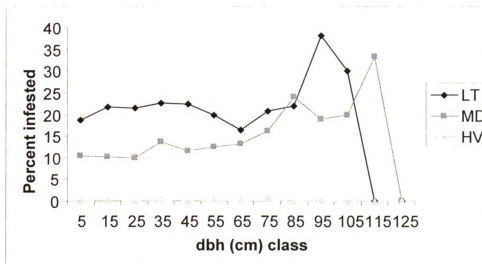


Figure 2-12. Percent of beech trees within each beech scale infestation class across diameter at breast height (dbh) class. Beech scale infestation classes were coded as “LT” for lightly infested, “MD” for moderately infested, and “HV” for heavily infested.

**Modeling the spatial spread of the beech scale
(*Cryptococcus fagisuga*) in Michigan.**

Abstract

The spread of invasive species is a growing concern for the ecological well being of forest ecosystems worldwide. Effectively managing invasive species includes the ability to predict how rapidly they will spread into new areas. Attempts have been made to model the spread of beech scale (*Cryptococcus fagisuga*) however; few efforts have been made to quantify the rate and pattern of spread in newly affected areas. Here I present an approach for modeling the spread of beech scale. I surveyed all counties in Michigan where the American beech (*Fagus grandifolia* Ehrh.) exists, to document the distribution of beech scale. I then utilized an inverse modeling approach to design a suite of dynamic models, entitled SCALESPREAD, to estimate spread rates for beech scale populations throughout Michigan. My initial model was based on a simple diffusion model with one parameter, spread rate. I also developed a model based on land cover type which had four parameters, spread rate for forest containing beech, deciduous non-beech forest, coniferous forest and other land cover types. I then used the observed distribution of beech scale to develop parameter estimates for spread rates in the Lower and Upper Peninsulas of Michigan. Results of the simple diffusion model suggested that beech scale spreads at a rate of 1.5 km/year in the Lower Peninsula and 4 km/year in the Upper Peninsula. The land cover based model for the Lower Peninsula indicated that beech scale spreads at a rate of 1.5 km/year in forests containing beech, 1 km/year in deciduous non-beech forest, 0.75 km/year in coniferous-dominated forest, and 1.5 km/year in other land cover types. The land cover based model for the Upper Peninsula

indicated that beech scale spreads at a rate of 5 km/year in beech forest, 2.5 km/year in deciduous non-beech forest, 2.5 km/year in coniferous forest, and 1 km/year in other land cover types. Although the simple diffusion model provided a reasonable fit to the data, the comparison of AIC_c values indicated that the land cover based model was significantly better than the simple diffusion model with an AIC_c value improvement of 81 and 38 for the Upper Peninsula and Lower Peninsula, respectively. These models provide the first estimate of dispersion rates for beech scale in Michigan.

Introduction

The spread of invasive species has a growing impact on the economic value and ecological well being of ecosystems worldwide. By one estimate, invasive species have staggering economic and environmental costs, approximately \$137 billion per year in the United States (Pimentel et al 2000). Invasions by exotic insects and diseases are one of the most important threats to the stability and productivity of forest ecosystems around the world (Liebhold et al. 1995; Vitousak et al. 1996; Pimentel et al. 2000). Over the last century, forests of eastern North America have suffered devastating effects by well-known invasive species and diseases such as the chestnut blight, gypsy moth (*Lymantria dispar* Linnaeus), hemlock wooly adelgid (*Adelges tsugae*), and beech bark disease (BBD) (Mattson 1997). Invasive species are also known to result in a multitude of community level effects, including changes in plant species richness, community structure, vegetation dynamics, and plant-animal interactions. Understanding insect community and population dynamics are crucial to understanding invasions, and there remains a great deal to know (National Research Council 2002).

This study focuses on the distribution and spread of beech scale (*Cryptococcus fagisuga* Lind), one of two nonindigenous organisms that together cause BBD. Beech bark disease is currently spreading across North America, endangering American beech (*Fagus grandifolia* Ehrh.) resources and the communities of wildlife that depend upon them. Beech bark disease is caused by an etiological complex consisting of the sap-feeding beech scale and a parasitic fungus in the genus *Neonectria*. Beech scale first arrived in North America, from Europe, sometime in the mid-to-late 1800's on a ship carrying European beech (*Fagus sylvatica* L.) seedlings into the Canadian port of

Halifax, Nova Scotia (Ehrlich 1934; Houston and O'Brien 1983). Since that time, the distribution of beech scale has expanded to include much of the distribution of American beech.

Beech bark disease has been divided into three major phases: the leading edge of beech scale infestation, known as the advancing front; the leading edge of the fungal invasion, known as the killing front; and finally, the loss of overstory beech from the forests, known as the aftermath forest. For early detection, locating the advancing front is particularly important, which is why it was the focus of my research.

While historical records document the advance of beech scale and BBD in some areas of northeastern North America (Houston et al. 1979), there have been few efforts to quantify the rate and pattern of spread in newly affected areas such as Michigan. In the Allegheny National Forest in Pennsylvania, BBD has been established since at least 1985. Forest health protection specialists conducted roadside surveys, recorded beech scale presence and beech mortality, then drew contour maps by hand to estimate temporal progression of the advancing and killing fronts from 1985-1996, where they predicted beech scale moved at 10 km/year (MacKenzie 2004). These maps provide a limited basis; however, for predicting how rapidly beech scale and BBD may spread.

Morin et al. (2004) used existing BBD distribution information and historic records of invasion years to estimate a spread rate for the entire northeastern region of the United States. Historical BBD spread rates were estimated from maps depicting the killing front as contour lines drawn on a map incorporating year's 1935, 1950, 1960, 1970, and 1975 (Houston 1994). Years 1990, 1999, 2000, 2001, 2002, and 2003, were compiled into geographic information systems (GIS) to illustrate the advance of the

killing front (Morin et al. 2004). To calculate spread rates, minimum distance from each infested county back to the area initially infested was calculated in GIS. Average radial rate of spread was estimated by the slope of the linear regression model of the minimum distances as a function of the year of initial infestation using. The estimated spread rate from the regression analysis was then applied to the 2003 BBD distribution to generate a map representing its predicted spread through 2025 over a 1 km² raster GIS layer (Morin et al. 2004). These calculations consider all areas behind the killing front to be infested and also incorporate long-distance (or jump) dispersal into their calculations. Morin et al. (2004) estimated that BBD spreads at a rate of 14 km/year across all land cover areas but did not differentiate between beech scale infestation and fungal infection, or various land cover types. Whether this rate of spread is applicable to Michigan, is not known. One critical difference between our study and Morin et al (2004) study is that we focused exclusively on beech scale distributions, and do not incorporate the killing front into our spread rate calculations. Our spread rates are based on beech scale spread rates which may not be the same rate as the *Neonectria* infestations. Stands may be heavily infested with scale without *Neonectria* infection for several years, particularly if a forest is isolated from the killing front.

People have long been interested in understanding and predicting spread rates of invasive species because of their potential impacts on humans, the environment, and global biodiversity (Muirhead et al. 2005). “Few events are as important in predicting the future role of a nonindigenous plant, arthropod, or pathogen as its attainment of the population size at which it rapidly adds members and spreads simultaneously into a new range” (Elton 1958). Life history, morphology, and behavioral traits related to dispersal

of newly established species obviously play important roles in determining the rate of range expansion, and knowledge of such characteristics would be useful in predicting the likelihood of an invasion (Hastings 1996). Once an immigrant population has arrived, it will become a successful invader only if the population is able to increase in abundance and spread from its point of entry. Population expansion typically consists of three steps: an initial establishment phase with little or no expansion, an expansion phase, during which the territory it inhabits is filled, and a saturation phase if there is a geographical limit to the available space (Shigesada and Kawasaki 1997) (Figure 3-1). Focusing on the expansion phase, the patterns are further divided into three categories. Type I, the range always expands linearly with time. Type II expansion phase involves a slow initial spread followed by linear expansion at a higher rate. Type III expansion phase occurs when spread rate is continually increasing with time, resulting in a convex curve (Shigesada and Kawasaki 1997). Beech scale follows a Type III expansion phase because it has a brief establishment phase where the population is not spreading into new areas, rather it is establishing itself. This is followed by exponential population growth where the reproduction is high and offspring begin to disperse. The final stage, the saturation phase, occurs when the expansion phase levels to an asymptote, presumably when the trees in a given area are no longer able to provide enough sustenance for the scale and the offspring are forced to diffuse into new areas or die.

The simplest mathematical representation of range expansion by an alien invader is a reaction-diffusion model, which combines exponential population growth with random (diffusive) spread (Skellam 1951). This model predicts a radial rate of spread that initially increases following establishment of the founding population, followed by a

period of constant radial range expansion until spread decelerates as the species saturates its potential range (Shigesada and Kawasaki 1997). Despite its simplicity, there has been remarkable congruence between this model's predictions and actual spread data from a variety of organisms (Levin 1989). It is from these basic principles that my model, SCALESPREAD, is derived.

Ideally, the model will be simple enough to provide a general framework for representing the spatial dynamics of scales in Michigan, yet be realistic enough to allow predictions of their rate of spatial spread and the result will provide a tool for forest managers to us to predict spread. There has not been an intensive statewide survey for documenting beech scale distribution in Michigan, nor has an analysis of spread rate been conducted. This project is the first to provide beech scale distribution information for the entire state of Michigan while also documenting forest characteristics and species composition. This information provides baseline data on the current state of the forests so that changes initiated by scale infestation may be better understood and appropriate management strategies can be developed. This project will enhance the general understanding of how this nonindigenous forest pest becomes established and spreads, "knowledge that has become increasingly important as we grapple with newly discovered exotic forest insect and pathogen pests" (National Research Council 2002). In this research, my objectives were: 1) to document beech scale distribution throughout Michigan by surveying sites in all counties containing beech; 2) to construct a hierarchy of dynamic models representing potential factors affecting spread rate; and 3) to compare the modeled spread rates with estimates from other areas such as the Allegheny National Forest in Pennsylvania.

Methods

Study area

From 2004-2006 the state of Michigan was intensely surveyed to locate beech scale infestations, covering all counties with beech, based upon Michigan's Department of Natural Resources Integrated Forest Monitoring, Assessment, and Prescription (IFMAP) project. In 2004, sites were located by systematical searching areas from the edge of 62 research sites established in 2002-2003 by Kearney (2006). To the extent possible, sites were arranged in concentric circles approximately 1 km apart to locate the advancing front. In 2005, sites were surveyed to further define the advancing front using an adaptive sampling design (Figure 3-2) based on known locations of uninfested and infested sites. Sites were established by locating beech stands approximately midway between two established sites where there was a discontinuity in beech scale distribution (i.e., between a site with no evidence of beech scale and a site with evidence of beech scale). Sequential bisections were created to identify the advancing front. Sampling to explore for disjunct populations (here termed satellite populations) was conducted by systematically dividing quadrangular maps (1:150,000) into a north and south hemisphere. Each hemisphere was then further divided into eight to ten subsections of approximately 104 square kilometers in which to search for stands containing beech. In 2006, sites were surveyed in areas that had not been previously surveyed and in cover types known to contain beech as a major component according to the USDA Forest Service Forest Inventory Analysis data. All searches were limited to areas accessible by public or private roads. In 2005 and 2006, selected sites along the advancing front were revisited to monitor changes in levels of infestation.

Within each site, beech trees were examined for scale, and scale abundance was recorded using a qualitative rating of 0-4 based on visual comparisons using standard photographs (Figure 3-3). Beech scale abundance was classified as: 0) absent, with no detectable scale presence; 1) trace, with a few scattered scales; 2) patchy infestation, with one or more patches of scale; 3) whitewashed, with heavy infestation covering the bole and limbs; and 4) dead/declining trees, likely as a result of BBD. Mean beech scale abundance (i.e., level of infestation) was determined for each site (n=739 sites). There were 517 sites with no beech scale. The distribution of sites with mean beech scale abundance >0 (i.e., infested sites) were plotted to determine infestation categories (Figure 3-4). Infested sites were divided into three categories, light (n=123) were sites with mean beech scale abundance between 0 and 1.0. Moderately infested sites (n=88) had a mean beech scale abundance between 1.0 and 3.0. Heavily infested sites (n=11) had a mean beech scale abundance >3.

Model description and structure

I used an inverse modeling approach (e.g., Nibbelink and Carpenter 1998) that combines the power of dynamic modeling with the need to recognize stochasticity in the processes of pest dynamics. In this method, combinations of parameters spanning a range of plausible values were simulated and then parameter values that best fit the data were selected (Swartzman and Kaluzny 1987). This method is described as inverse modeling because the model itself is used to estimate the unknown parameters by fitting them to known output (Parker 1977). When model simulations were completed, the number of statistical errors were used to rate the fit of the parameter values set. The parameter values set that produced the best fit and had the least discrepancy between predicted and observed beech scale distribution was the final set retained.

Fundamental to this modeling approach is the idea that movement of the pest across the landscape is analogous to a diffusion process. The rate of movement (diffusion), however, may not be a fixed number but potentially could vary depending upon factors such as prevailing wind direction, density of beech trees, and other factors (Shigesada and Kawasaki 1997). In this particular application, the inverse modeling approach takes the philosophy that the rate of movement is not known, but the current distribution is known. Thus, a mathematical search is conducted across a range of movement rates to make predictions of distribution. The movement rate that produced the best statistical fit between the predicted distribution and the known distribution was then selected as the best parameter set for the model. The challenge of how best to incorporate landscape heterogeneity into the model was addressed in the land cover based model where each land cover type had an associated permeability parameter. I defined

the permeability parameter as the value assigned to how resistant the land cover type was to beech scale dispersion. Smaller values of permeability were indicative of land cover types where it was more conducive for beech scale to establish and spread (e.g., beech forest). Higher values of permeability indicated land cover types that were unlikely places for beech scale to establish and spread (e.g., coniferous forest).

I created a suite of models in Microsoft Excel to incorporate spatially explicit information about the location of satellite populations and the edge of the advancing fronts. Each model was laid out in a 100x100 km structure, with 0.5 km grid cells. This was large enough to incorporate several of our larger satellite populations in each of the Upper and Lower Peninsulas. Three of our smallest infestations, located in Leelanau, Benzie and Emmet County were not included in the model because they did not fit within the modeling space. Initially, I divided the modeling landscape into 1 km grid cells but found this level of aggregation to be too coarse for the detailed infestation data.

The models are grouped into two general categories, simple diffusion models and land cover based models. Both categories of models simulated the spread of beech scale for the Lower Peninsula and the Upper Peninsula. In the simple diffusion model, spread was represented as a fixed number of cells each year from infested cells in all directions regardless of the land cover type. In the land cover based model, spread varied according to a parameter specific to each land cover type. Land cover types were aggregated into four categories to avoid an overly complex land cover layer and to maintain a relatively small number of potential parameters. The four land cover types used in SCALESREAD were; beech (i.e., northern hardwood forest which contains the maple-beech forest type), deciduous non-beech, coniferous-dominated forest, and other (e.g.,

urban, agriculture, water). Cover types were determined using the IFMAP classification system (Appendix 2).

Model Parameters

The simple diffusion model included only one parameter to adjust, spread rate. This parameter allowed an infested cell to spread across a fixed number of adjacent cells, equally in all directions, into uninfested cells. The simple diffusion model included three parameters; spread rate, year of infestation and initial infestation location (i.e., start point cell). These parameters were adjusted to best match predicted distribution of each satellite population with the observed distribution. At each step of the modeling process, the parameter values were adjusted to reduce the number of modeled errors between the predicted distribution (i.e., modeled distribution) and the actual distribution (based on empirical data). The model fitting process was iterative to adjust the model to best represent the field observations. Parameters were systematically adjusted one at a time until the smallest error value was obtained. Thus, I attempted to recover all three unknown parameters simultaneously by adjusting the year of initial infestation, start point cell and spread rate.

The land cover based model had one parameter to control maximum spread rate for habitats suited to dispersal of beech scale, and had four additional parameters (here I refer to these as permeability parameters) that limit movement through cells relative to the beech scale rate of dispersal based on cover type. In this model, I assumed that beech scale would spread faster in beech cover types than other cover types, such as urban or agricultural areas. Therefore, beech forests would have a lower permeability (i.e., easier to penetrate) value than urban or agricultural areas. In the land cover based model, parameter values were selected for beech forest, deciduous non-beech forest, coniferous non-beech forest and other including urban, water, and agriculture. Using the principle of

parsimony in modeling, we chose to categorize wetlands, sparsely vegetated areas, agriculture areas, lowland forests, and open land into the category “other” rather than separate them into their own categories. Deciduous non-beech forests included oak association, aspen association, and other upland/mixed deciduous forests that did not list beech as an overstory species. Beech forests included the northern hardwood association. Coniferous forests were based upon the upland coniferous forest categories. These categories were based upon IFMAP description of classes according to IFMAP decision rules for forest classes used in statewide maps of Michigan (Appendix 2).

Year of infestation and initial start point were constrained by three factors. The first constraint was documentation of a year of known infestation. A letter written from the Michigan Department of Natural Resources documented beech scale on beech trees in Ludington State Park Campground in 1991. This constraint was incorporated into the modeling by not allowing the start year for the Ludington satellite population to be any later than 1990, thereby allowing at least one establishment year prior to discovery. Anecdotal records indicate that beech scale was reported in Bass Lake State Park Campground in the Upper Peninsula around this same time, although no written documentation lists a specific year. A second constraint was the empirical evidence of beech scale spread rates area limited by the actual distribution. Preliminary evaluations of beech scale spread using a literature value of 14 km/year (Morin et al. 2005), produced results inconsistent with observed distribution. In fact, using a start year of 1990 for Ludington State Park and a spread rate of 10 km/year would infest an area well beyond the current distribution. Based on this, spread rates were limited to 10 km/year or less.

The final constraint was that the initial infestation cell (and subsequent advancing front) had to fall within the boundaries of the observed distribution for each population.

Model selection procedure

This modeling approach assumes that while several model formulations may make biological sense, a single model formulation cannot be chosen a priori. Burnham and Anderson (2002) stressed three principles that regulate our ability to make inferences in the sciences 1) parsimony, 2) having several working hypotheses, and 3) strength of evidence. I strove to provide the most parsimonious model that would accurately describe beech scale spread throughout Michigan. SCALESPREAD was created as a series of models with different cell sizes and numbers of parameters to find the best model fit with the empirical data. I built a hierarchy of models with increasing complexity which allowed goodness of fit between model predictions and the data to guide us in the model choice (Burnham and Anderson 2002). The principle of several working hypothesis consists in testing a hypothesis from one experiment (e.g., start point, year of infestation, spread rate) then according to the results, formulating a new hypothesis to test with a new experiment (Chamberlin 1965).

Model fit was measured through comparison of errors comparing the modeled distribution to the known distribution. In this approach, errors could occur by having predicted infestation where none was observed or having a predicted absence of infestation where infestation was observed. These errors were recorded in 2x2 contingency tables for each of the four models.

For model selection, I computed the log-likelihood from the contingency table, and used Akaike's information criterion to determine which model was the most representative and parsimonious. I used the small sample Akaike's information criterion (AIC_c) because the overall sample size was relatively small for this type of modeling

(generally <40 sites per satellite population) (Burnham and Anderson 2002). As sample size increases, the last term of the AICc approaches zero, and the AICc tends to yield the same conclusions as the AIC (Burnham and Anderson 2002).

The AICc formula is:

$$AICc = AIC + \frac{2K(K+1)}{n-K-1}$$

where K is the number of estimated parameters and n is the sample size. The AIC_c takes both the residual variance and the number of parameters in the model into account and balances the errors of “underfitting” and “overfitting” the models. The lower the AIC_c value, the better fit the model. From the output of each model, maximum likelihood estimates of the variance were calculated as the residual sum of squares divided by the number of data (i.e., number of errors).

The log-likelihood of the model given the data reflects the overall fit of the model. For binomial data with correct and incorrect model prediction arranged in a contingency table, the log-likelihood can be estimated via the formula for the G-statistic as follows:

$$G = 2 \sum_i O_i \cdot \ln(O_i / E_i)$$

Where O_i is the frequency observed in a cell, $\sum$ is sigma (i.e., sum), $\ln$ denotes the natural logarithm (loge to the base of e) and E_i is the frequency expected on the null hypothesis.

Model Assumptions and Limitations

For many population models it is natural to assume that individuals disperse within a continuous spatial habitat (Hardin et al. 1990). In the simple diffusion models, spread depends upon the adjacent cells all being homogenously equally able to accept scale infestations and the scale has an equal probability of moving to adjacent cells. The models treat the landscape as homogenous, with respect to scale dispersion and movement is equally probable in all directions.

For many models of biological populations it is natural to assume that time advances discretely. This assumption corresponds to populations with seasonal life cycles or synchronized generations (Hardin et al. 1990). Beech scales are univoltine, which allows distinct periods of population growth on an annual basis.

Long-distance or artificial spread was not represented in SCALESREAD; instead I focused on natural diffusive dispersal in a contiguous area. SCALESREAD also did not include Michigan's islands to determine spread rates, but these data may be useful in the future. Additionally, the land cover based model is limited to a maximum move of seven cells (3.5 km/year) within a function because of the limitations to the programming environment; Microsoft Excel has a limit of seven embedded functions within a formula. Finally, the models are based on discrete grid cells whereas the actual distribution of beech is continuous. The edges of the discrete modeled distribution and the observed point data did not always match up well because nature is not hard-lined, however, this discrepancy is unavoidable in a computer environment but at a landscape scale, the errors were negligible.

Results

Distribution of beech scale infestations

A total of 871 sites were surveyed from 2004-2006. In total, 732 beech sites and 139 sites devoid of beech were surveyed. In addition, 67 sites along the advancing front were re-visited to monitor spread between study years. Overall, 26% of sites surveyed were infested. In the Upper Peninsula the percentage of infested sites was higher, 47% (68 out of 144) of beech sites were infested. In the Lower Peninsula, the percentage of infested sites was lower, 21% (125 out of 588).

Beech occurs in 63 counties in Michigan. Beech scale occurred in 15 of those counties congregated in the eastern Upper Peninsula and the western Lower Peninsula (Figure 3-6). The distribution across the Upper Peninsula was more lateral than vertical with the distribution extending approximately 150 km east-west and approximately 75 km north-south. The distribution across the Lower Peninsula was more vertical than lateral, with the distributions approximately 250 km north-south and approximately 150 km east-west (Figure 3-6). Infestation in the Upper Peninsula was more continuous than the Lower Peninsula, where the distribution was divided into eleven discontinuous areas of infestation or satellite populations (Figure 3-7). Satellite populations were distinguished by their disjoint location in relation to other populations of beech scale infestation and their distinctive core-to-periphery pattern of infestation. Distance between satellite populations ranged from 11 to 38 km apart. Michigan's total area of infestation covers approximately 15,095 km² (Table 3-1).

In 2005, nine uninfested sites (selected from 2004) along the advancing front were re-visited, of which only two became infested suggesting that beech scale spread

was <1 km during the 2004-2005 year. In 2006, 58 uninfested sites (selected from 2004-2005 sites) were re-visited along the advancing front. Of these re-visited sites, 18 became infested during the 2005-2006 year, demonstrating that scale is able to disperse 1 to 3 km annually.

Model performance: Simple diffusion model

The best fitting set of parameters in the simple diffusion model indicated that the overall spread rate averaged 4 km/year in the Upper Peninsula and 1.5 km/year for the Lower Peninsula. The simple diffusion model for the Upper Peninsula had a total of 24 errors; all of which were model over-predictions (i.e., the model projected beech scale infestations in uninfested areas) (Figure 3-8a). The simple diffusion model for the Lower Peninsula had a total of 37 errors; 21 of which were model over-predictions and 16 were model under-predictions (Figure 3-8b).

A contingency table was created for each of the models (Table 3-2). The log-likelihood associated with the Upper Peninsula was 12. This particular approximation of the likelihood was conservative because the model had an under-prediction value of zero and in the likelihood function you cannot take the log of zero. In place of the zero, I used 0.001 as the under-predicted value, which was near the asymptotic value for zero that could be used. The log-likelihood associated with the Lower Peninsula simple diffusion model was 44. AIC_c values were calculated for the each of the simple diffusion models, the Upper Peninsula model had an AIC_c value of -21 and the Lower Peninsula had a value of -86.

Model Performance: Complex model

The best fitting complex model parameters indicated that the overall spread rate averaged 5 km/year in the Upper Peninsula and 1.5 km/year for the Lower Peninsula. Spread rate was calculated for each land cover type. In the Upper Peninsula, the most permeable land cover type was “beech” which the model predicted allows a spread rate of 5 km/year. The second most permeable land cover types were “deciduous non-beech”, and “coniferous,” each with a spread rate of 2.5 km/year. The “other” cover type had a much lower permeability with a spread rate of 1 km/year. In the Lower Peninsula, the most permeable cover types were “beech” and “other”, each with a spread rate of 1.5 km/year. The second most permeable land cover types were “deciduous non-beech” and “coniferous” with spread rates of 1 km/year and .75 km/year respectively (Appendix 1). Sensitivity analysis was conducted by adjusting one parameter at a time and recording the error values to determine the least number of errors. Sum of squared error values were plotted against spread rates to visualize the sensitivity of error rates to changes in parameter estimates and to determine the parameter set that produced the least number of errors (i.e., the lowest point on the graph) (Figures 3-9a-e).

The complex model for the Upper Peninsula had a total of eight errors; five of which were model over-predictions (i.e., the model projects beech scale infestations in uninfested areas) and three were model under-predictions (Figure 3-8c). The complex model for the Lower Peninsula had a total of 28 errors; 14 of which were model over-predictions and 14 were model under-predictions (Figure 3-8d). Contingency tables were created for each of the simple diffusion models (Table 3-2). The log-likelihood associated with the Upper Peninsula was 51. The log-likelihood associated with the

Lower Peninsula simple diffusion model was 67. The Upper Peninsula model had an AIC_c value of -93 and the Lower Peninsula had a value of -125.

Discussion

Distribution of beech scale infestations

The distribution of beech scale infestations in Michigan was divided into 11 satellite populations. Satellite populations were not evenly distributed between the Upper Peninsula and the Lower Peninsula. The Upper Peninsula had one only satellite population however it is the largest, covering more land area than the two largest Lower Peninsula satellite populations combined. The Lower Peninsula had ten satellite populations of varying sizes. Each satellite population appeared to be more heavily infested at the core and become progressively less infested towards its periphery, suggesting an advancing front that is moving away from the center of infestation.

To accurately map the advancing front, more sites were required in the Lower Peninsula to delineate the many disjointed satellite populations. Fewer sites were required to accurately map the advancing front in the Upper Peninsula because of the continuous nature of the single large infestation. The Upper Peninsula has a larger percent infested site than the Lower Peninsula which may be the result of more continuous stands of maple-beech forest. Forest stands with a high density (e.g., 160 sq. ft. of basal area/acre) of mature beech are considered to be a major source of dispersion (Le Guerrier et al. 2003). In contrast, the beech scale distribution in the Lower Peninsula is not as extensive. Substantial areas of beech in the northern Lower Peninsula remain uninfested. In the Lower Peninsula, beech scale infestations extended from Oceana County in the south, to Emmet County in the north. Beech scale infestations are bounded on the west by Lake Michigan and extend eastward to Wexford County covering a

considerably smaller extent (<50%) of the available beech range than in the Upper Peninsula.

There are widely-varying annual fluctuations in the distance that beech scale may spread annually. There were no observed changes in infestation of sites along the advancing front from 2003-2004. Twenty-five percent of uninfested sites along the advancing front became infested 2004-2005, whereas 41% of uninfested sites became infested from 2005-2006. This suggests that beech scale spread is variable from year-to-year and small-timescale snapshots may not accurately portray scale spread rates. Further study on annual beech scale spread will be needed to quantify these fluctuations in spread rates to help our understanding of beech scale spread throughout Michigan. Contributing factors such as precipitation, mast cycles, or other factors may need to be studied in relationship to beech scale movement. Studies are needed to quantify the role of various factors-such as wind, birds, natural migrations, human-mediated actions-that contribute to long-distance transport of individual species” (National Research Council 2002).

Migrating birds, wildlife or humans are also likely causes of long-distance dispersal. In studying biological invasions it was found that human-mediated dispersal transports a significant number of individuals to distances farther from the source than they could disperse naturally and that many disjoint populations could not be explained by diffusive spread (Muirhead et al. 2006; Herbert and Cristescu 2002). In this study, we found a number of disjoint populations in the Lower Peninsula, located in areas where humans often transport firewood, albeit at a low frequency in some areas. Analogous to a wildfire, beech scale spreads from the main infestation and produces smaller “spot fires”

(smaller disjunct infestations) that appear outside the perimeter of the main infestation. This type of spread is likely not passive dispersal because the areas between infestations are often uninfested beech forests, suggesting that beech scale jumped those areas. Passive beech scale dispersal is limited to a very small area (<1 m) surrounding the infested trees. Few larvae ($<1\%$) become trapped in airstreams above the canopy and potentially disperse (Houston et al. 1979). The main infestation eventually engulfs these “spot fires” and the infestation grows geometrically larger into one major infestation. The process is repeated, with more “spot fires” preceding the main front of infestation thereby leading to a larger and faster-moving advancing front.

I examined five islands in Michigan; three of which, Bois Blanc, Mackinac and Beaver Islands, were infested and two, North and South Manitou Islands, were not. As these islands are separated from mainland Michigan by water, short distance dispersal consistent with what I observed on the mainland can be ruled out. Beech scale would have to utilize long-distance dispersal mechanisms to pass over such vast areas of unsuitable habitat. Some of the potential long-distance dispersal agents might include birds and humans. Interestingly, the three infested islands have year-around human residents and open access via ferry for human goods. The two uninfested islands do not have year around human residents and have a limited number of visitors and restricted human goods. North and South Manitou Islands are managed by the National Park Service and have a restricted number of “low impact” campers per day. This dichotomy suggests that humans, and not birds, are the predominant agent in long-distance dispersal to these islands. This also suggests that birds may be a less important agent in long-

distance dispersal on the mainland as well. Follow-up research would be important to monitor these islands through time.

Model Performance

The simple diffusion model performed very well despite having only a single spread rate parameter. Both the simple and complex models predicted the same spread rate for the Lower Peninsula. The only difference between the two model's predictions was regarding the spread rate for the Upper Peninsula. The simple diffusion model predicted a spread rate of 4 km/year and the complex model predicted a spread rate of 5 km/year.

The land cover based models reduced the total number of sum of squared errors from 61 to 36 which lead to a substantial reduction in the AIC_c value, despite the increase number of parameters. The simple diffusion model provided a reasonable fit to the data and if a parsimonious model is most desirable, would be an acceptable substitution for the more complex land cover based models. These models provide the first estimate of dispersion rates for beech scale in Michigan, and the first estimates of differences in dispersal rate as a function of land cover.

The Lower Peninsula has a more heterogeneous landscape than the Upper Peninsula (Figure 3-5). This heterogeneity may account for the presence of satellite populations in the Lower Peninsula as compared to the larger population in the Upper Peninsula where the forested landscape is not as fragmented. This is consistent with conclusions by the National Research Council that "Environmental heterogeneity, the patchiness of the environment, can also influence the rate of spread" (National Research Council 2002). This may also account for the differences in spread rates between the Upper and Lower Peninsulas. Overall spread rate was four times faster in the Upper Peninsula than in the Lower Peninsula. The continuous beech forest may allow beech

scales to move more easily throughout the landscape, thereby increasing the spatial spread at a more accelerated rate than in areas, such as the Lower Peninsula, where beech forest patches are surrounded by non-suitable habitat for beech scales to disperse through.

The pattern of scale infestation in the Upper Peninsula satellite population suggests that there may have been more than one point of infestation. Though I lack direct evidence of multiple initial points of infestation, I theorize that sometime after the original 1990 infestation, a second infestation started in the Upper Peninsula and has already coalesced with the original satellite population. My theory of more than one start point may explain some of the discrepancies in the modeling. Without supporting data (e.g., historical observations), I did not incorporate a second start point in either of the Upper Peninsula's models. This may also explain the higher spread rate estimated for the Upper Peninsula. Perhaps beech scale is not spreading faster in the Upper Peninsula, but the larger extent represents the impact of a several smaller satellite infestations coalescing into a larger population. It is interesting to note that my estimates for spread are considerably smaller than prior BBD spread estimates (6-16 km/year). This discrepancy may be due in part to what is actually being modeled. One significant difference in this study versus Morin et al. (2004) is that we did not consider the spread rate of the killing front which may be faster than the advancing front. Additionally, Michigan's beech scale infestation is relatively new and the satellite infestations were more easily recognized as individual infestations. Our modeling efforts calculated spread rate based upon these individual infestations rather than a conglomerate of all infestations. This distinction can have an effect on spread rate that gives the false impression of a faster spread rate. Historic BBD spread rates may have unknowingly incorporated several disjoint

infestations into one larger infestation and therefore appears that BBD has engulfed more landscape than occurred via local dispersive processes.

Management implications

Nonindigenous species are often rare during the establishment phase of their colonization and are typically not detected for several years; therefore it is difficult to know how long they persisted in a certain area (Carey 1996; National Research Council 2002). Cryptic behavior such as “hide and survive” techniques, small bodies, concealment within small crevices in bark and their ability to remain in a dormant stage increase an invasive insects chance of survival during transport to new areas and reduce the likelihood that it will be detected in its new environment (National Research Council 2002). Low population densities might be exacerbated in species, such as the beech scale, that can reproduce parthenogenetically and lack the limitations of a sexually-producing organism. Additionally, nonindigenous insects initially lack natural enemies which aides in their survivability. New populations must exceed a threshold density before it can easily be detected and this threshold will depend on traits or behavior of the organism, including the extent of the damage it causes (National Research Council 2002).

Inadvertent transportation of a nonindigenous organism by humans can establish new foci at substantially greater distances than would occur by natural dispersal mechanisms of the species. Such transportation has been shown to have substantially increased the spread rate of such species as the gypsy moth. Bird dispersal is another common mechanism for invasive spread in forest ecosystems (National Research Council 2002). Moody and Mack (1988) stressed the importance of focusing on satellite populations in controlling spread of invading plants because when two smaller populations eventually coalesce, they produce a single faster-spreading advancing front. In an invasive plant study, Taylor and Hastings (2004) suggested eradication efforts to

target isolated, low-density colonies as opposed to high-density core populations owing to faster spread capabilities of the former. Since the onset of this project, two of the major satellite populations in the Lower Peninsula, Ludington and Silver Lake, have coalesced into one larger population. Within even a few years time it may be increasingly difficult to distinguish one satellite population from another, especially in the Lower Peninsula.

If beech scale spreads primarily through passive dispersal (e.g., wind) the rate of spread should remain fairly predictable. However, if artificial spread, human-induced (e.g., movement of firewood) may be harder to predict, and control of this dispersal method may involve public outreach activities designed to educate the public and limit artificial spread. Such artificial dispersal can result in establishment of satellite populations and accelerated spread rates when they eventually coalesce (Shigesada and Kawasaki 1997). Long-term monitoring of the establishment and rate of beech scale spread, the precursor to BBD, has important implications for public outreach efforts, design of pest surveys and silvicultural activities. Public outreach efforts could focus on education or policies that limit the transportation of firewood out of infested areas. By understanding spread rates, forest managers and property owners have time to incorporate impacts of BBD into their management plans to mitigate losses of beech resources along the advancing front. General patterns can be recognized and may be useful for predicting invasions (National Research Council 2002).

Managers of natural landscapes are faced with decisions about how to control these species and or minimize their impacts on the natural resource on a limited budget. Very often the problem with invasive species is that they are so extensive in their range

that management actions are generally taken after a nonindigenous species has invaded, rather than preventative action (Neubert 2004). Decisions on how to best allocate resources to nonnative species management should be based on a risk analysis that evaluates the potential for long-term, negative effects on natural ecosystems, including populations of native species (Neubert 2004). I would suggest focusing management strategies on controlling the small satellite populations before they have the opportunity to coalesce into larger faster-moving fronts. Smaller populations are logistically easier to contain and treat before an area becomes too large. In a study on invasive plants, Mack (1985) concluded that the area occupied through the growth of satellite foci eventually exceeds the range occupied by the spread of a main focus. If the initial area of a single large focus and the initial collective area of many small foci are equal and all grow at the same constant rate, the small foci will collectively occupy space much faster than the single large focus.

Table 3-1. Satellite infestations separated into beech scale infestation class and approximate size of the area infested as of 2006. Area was calculated using the area feature in ArcGIS.

Satellite name	Estimated Start Year	Approximate area of infestation (km ²)
Beaver Island	*	91.23
Bois Blanc Island	*	40.25
Benzie County	*	448.67
Cadillac	2004	595.09
Emmet County	*	506.14
Fisherman's Point	2004	59.82
Leelanau	*	173.82
Ludington	1989	2,386.06
Mackinaw Island	*	6.17
Silver Lake	1997	964.84
Upper Peninsula	1989	9,823.06

* Indicates satellite populations that were not included in modeling.

Table 3-2. Contingency table of model errors for each of the models.

Observed Scale Occurrence		Modeled Scale Occurrence	
		Present	Absent
Upper Peninsula simple diffusion	Present	44	0
	Absent	24	6
Lower Peninsula simple diffusion	Present	50	21
	Absent	16	69
Upper Peninsula complex land cover	Present	39	3
	Absent	5	27
Lower Peninsula complex land cover	Present	52	14
	Absent	14	76

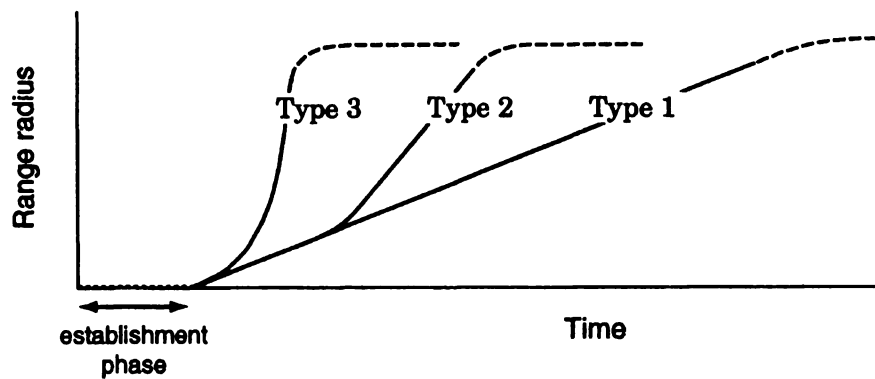


Figure 3-1. Three types of rang-versus-time curves. Range expansion patterns commonly have an establishment phase (arrow), expansion phase (solid line), and saturation phase (dashed line), successively. The expansion phase is classified into three types. Type 1 shows linear expansion. Type 2 exhibits biphasic expansion, with an initial slow slope followed by a steep linear slop. In type 3, the rate of expansion continually increases with time (Shigesada and Kawasaki 1997).

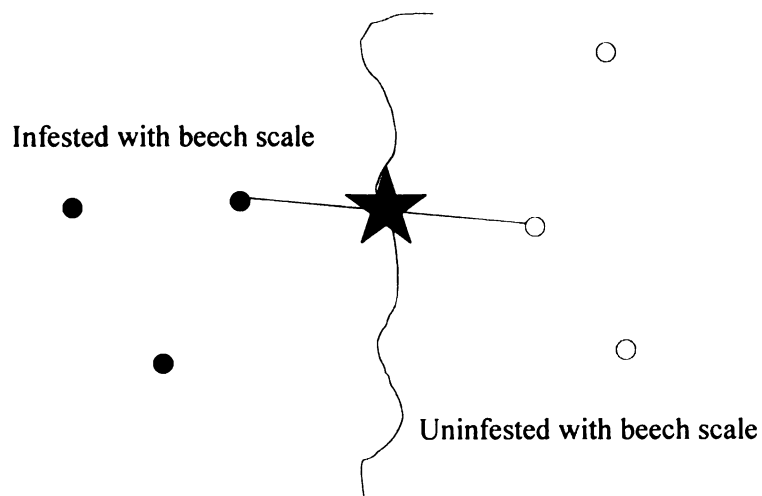


Figure 3-2. Adaptive sampling design for designing the advancing front. The star represents the midpoint between a known infested site and a known uninfested site.



Figure 3-3. Photos used to standardize levels of beech scale infestation. Photo on the far left represents beech scale classification “trace”, middle photo represents “patchy” and right photo defines “whitewashed” (Photos taken by Nancy Schwalm, May 2004).

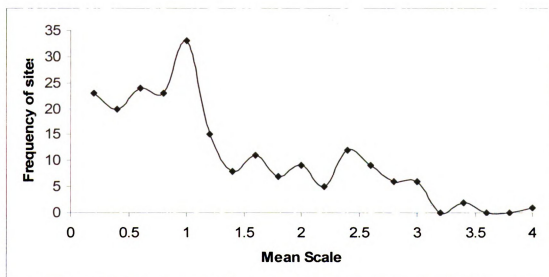


Figure 3-4. Frequency of sites plotted against mean scale to determine beech scale infestation classes. Mean scale was determined by aggregating all plot-level data across a site to obtain averages per site.

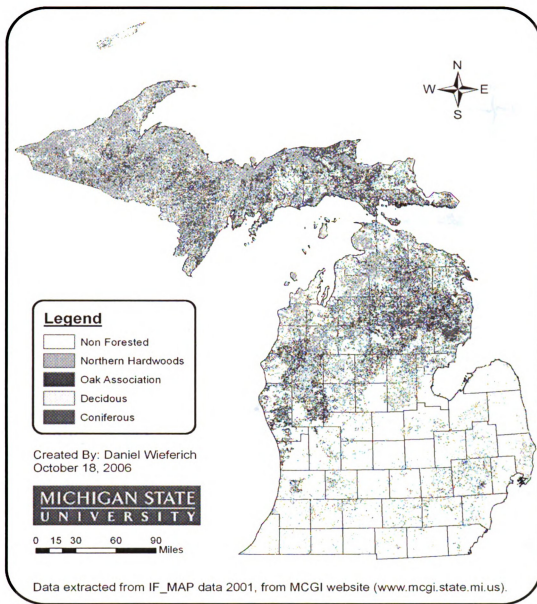


Figure 3-5. Map of Michigan, USA with a layer of forest types grouped to locate beech. Beech was typically found within northern hardwood or deciduous forest cover types. Typically beech was not abundant in the oak association, coniferous or non-forested forest types. Data was extracted from IF_MAP data 2001, from MCGI website (www.mcgi.state.mi.us). Map was created by Daniel Wieferich on October 18th, 2006. Please note that this image is presented in color.

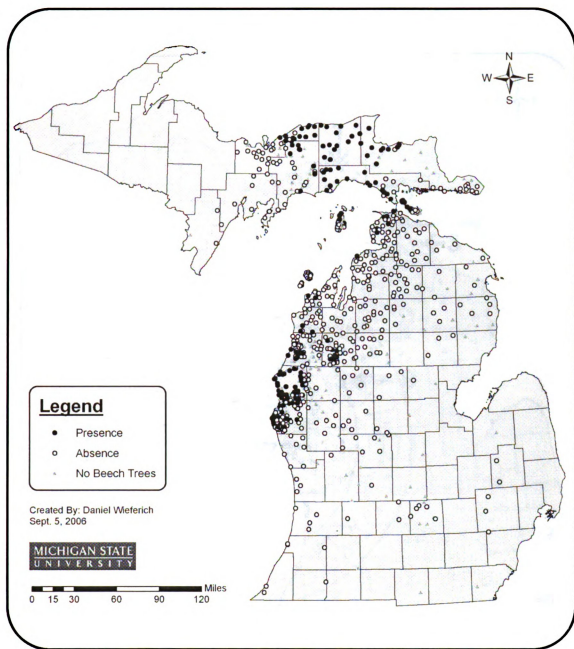


Figure 3-6. Map of Michigan, USA with study sites coded as uninfested (*open white circles*) or infested (*closed black circles*) or no beech sites (*small triangles*).

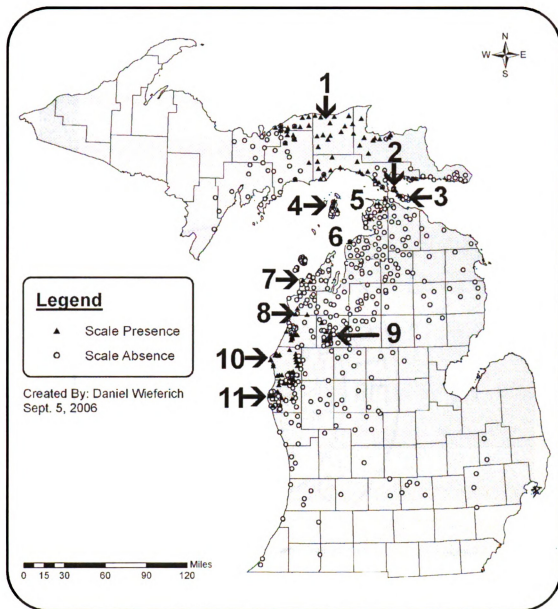


Figure 2-6. Map of Michigan, USA with beech study sites grouped into eleven distinct satellite populations designated as follows. 1-Upper Peninsula; 2-Mackinac Island; 3-Bois Blanc; 4-Beaver Island; 5-Emmet County; 6-Fishermen's Point; 7-Leelanau County; 8-Benzie County; 9-Cadillac; 10-Ludington; 11-Silver Lake.

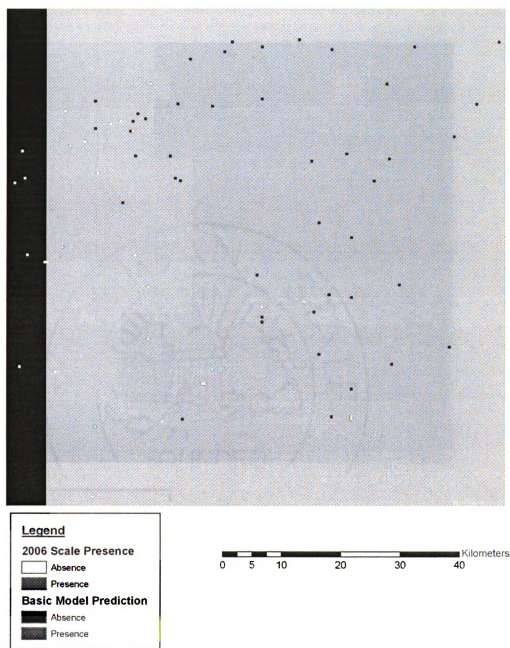


Figure 3-8a. Modeled errors for the Upper Peninsula simple diffusion model mapped to show the location of model error. White dots in blue background illustrate individual model errors ($SSE = 24$) where the model predicted scale infestation in areas that were absent of infestations. The model accurately predicted absence of infestation in areas where it was absent ($SSE = 0$). Created by Daniel Wieferich on 12/14/2006. Please note that this image is presented in color.

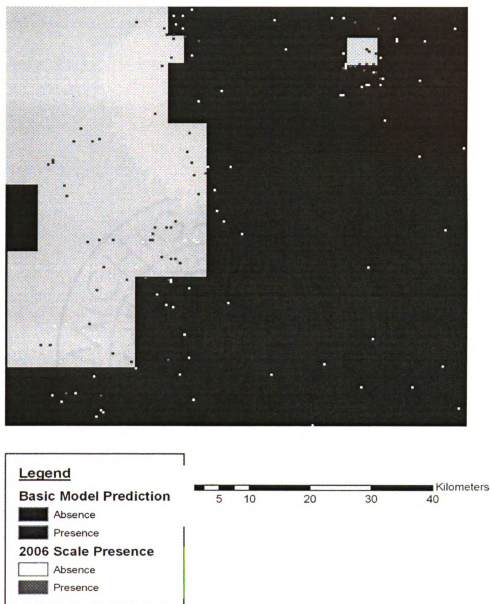


Figure 3-8b. Model of Lower Peninsula simple diffusion model: red dots in black background illustrate individual errors (SSE = 21) where the model predicted scale infestation in areas that were absent of infestations. White dots on blue background illustrate a predicted absence of infestation in areas where it was present (SSE = 16). Created by Daniel Wieferich on 12/14/2006. Please note that this image is presented in color.

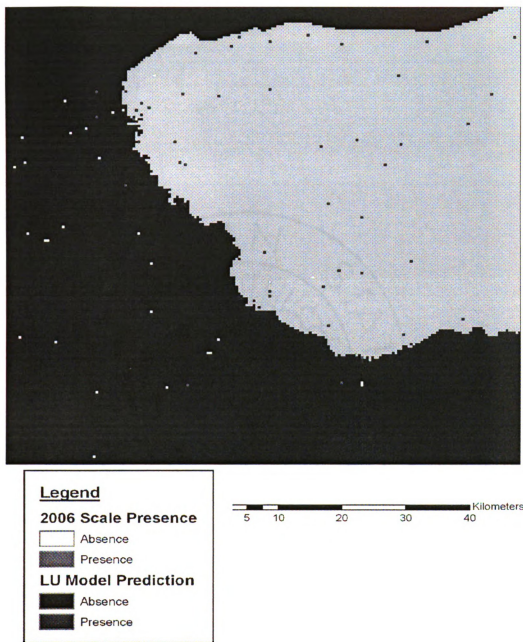


Figure 3-8c. Model of the Upper Peninsula land cover based model: red dots in black background illustrate individual errors ($SSE = 5$) where the model predicted scale infestation in areas that were absent of infestations. White dots on blue background illustrate a predicted absence of infestation in areas where it was present ($SSE = 3$). Created by Daniel Wieferich on 03/21/2007. Please note that this image is presented in color.

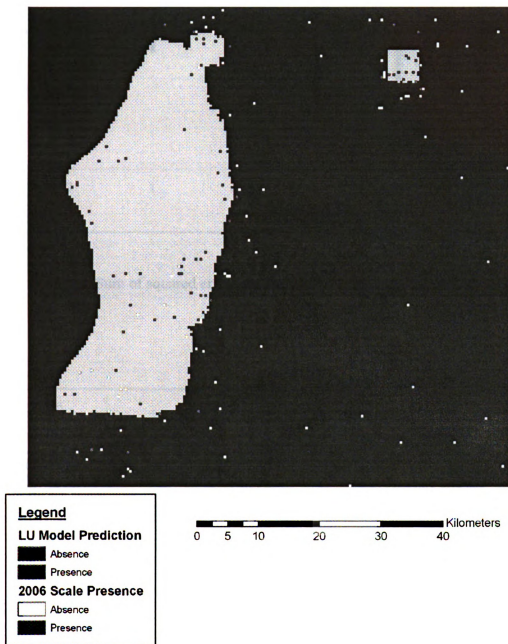


Figure 3-8d. Model of the Lower Peninsula land cover based model: red dots in black background illustrate individual errors ($SSE = 14$) where the model predicted scale infestation in areas that were absent of infestations. White dots on blue background illustrate a predicted absence of infestation in areas where it was present ($SSE = 14$).

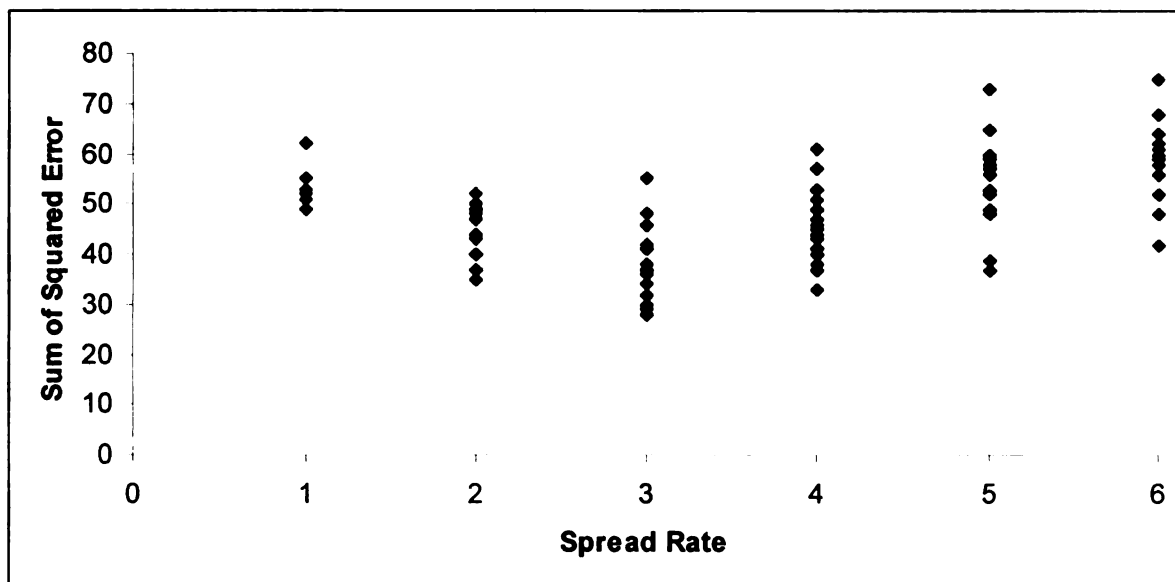


Figure 3-9a. Sum of squared errors plotted against spread rate parameter values.

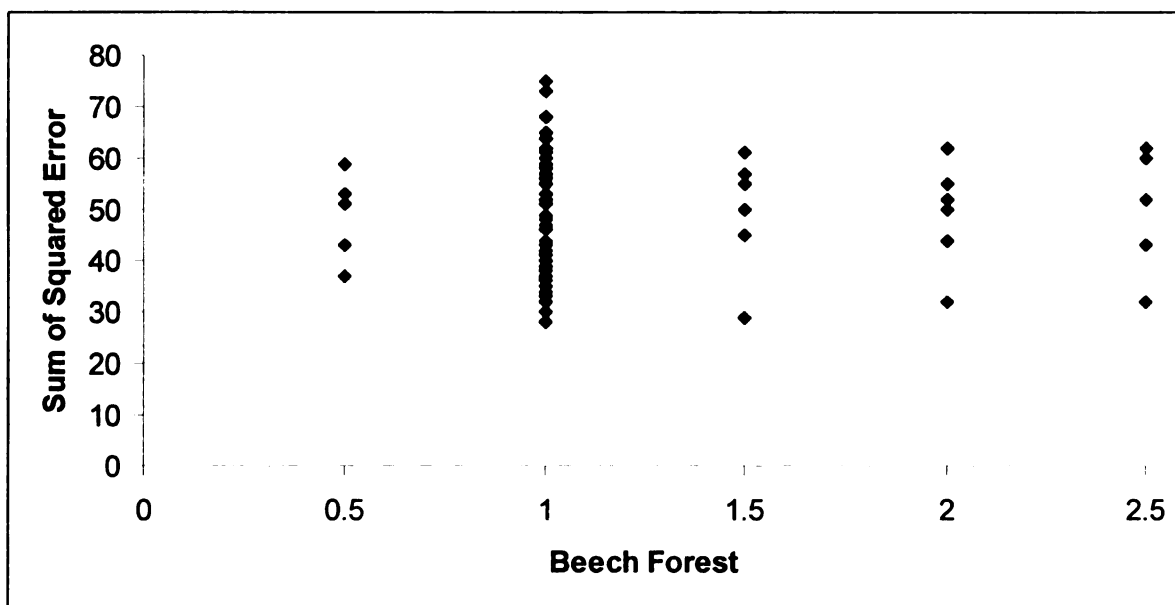


Figure 3-9b. Sum of squared errors plotted against spread rate parameter values.

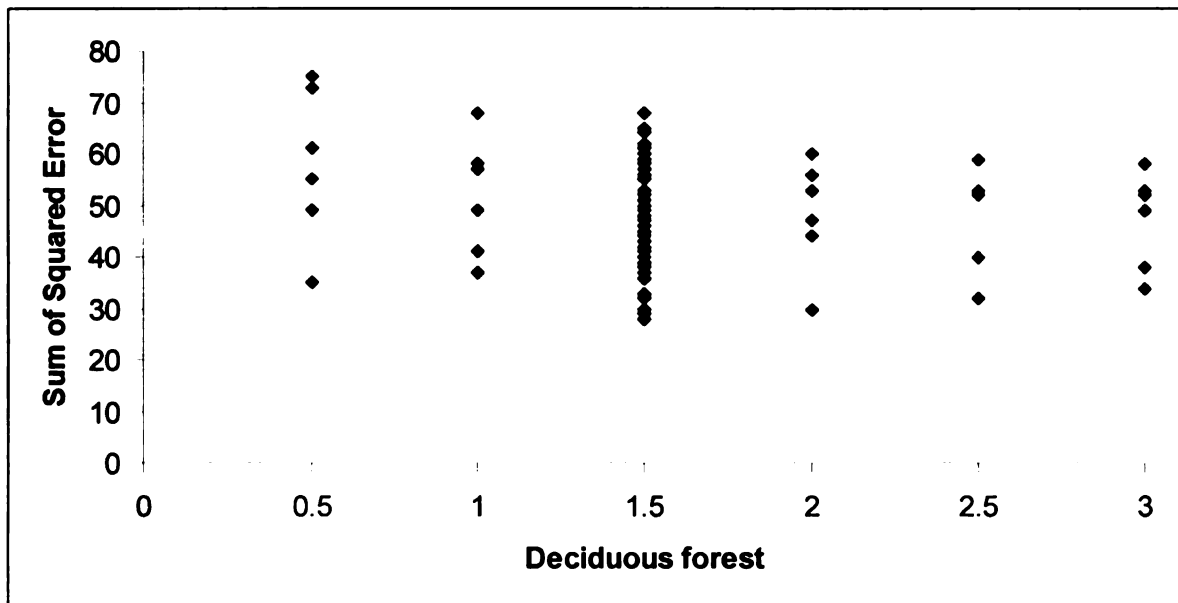


Figure 3-9c. Sum of squared errors plotted against spread rate parameter values.

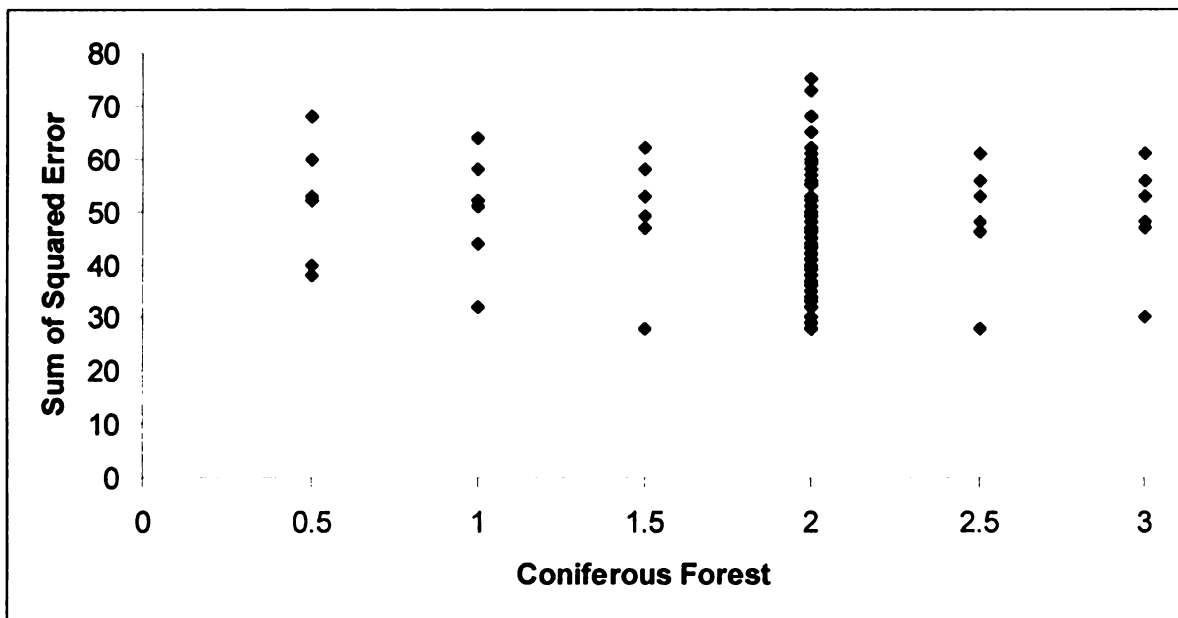


Figure 3-9d. Sum of squared errors plotted against spread rate parameter values.

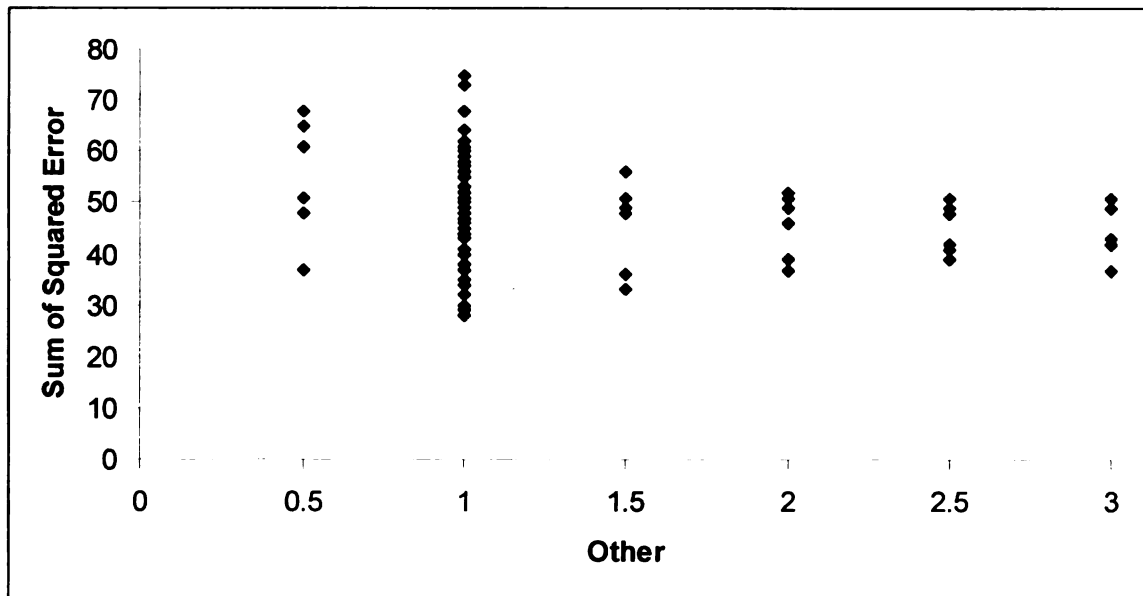


Figure 3-9e. Sum of squared errors plotted against spread rate parameter values.

APPENDICIES

County	Site	Latitude	Longitude	Date	Scale
ALCONA	1082	44.846483	-83.445100	5/30/2006	No Scale
ALCONA	1083	44.779750	-83.403950	5/30/2006	No Scale
ALCONA	1084	44.683800	-83.403650	5/30/2006	No Scale
ALCONA	1085	44.569750	-83.368150	5/30/2006	No Beech
ALCONA	1086	44.566800	-83.592017	5/30/2006	No Beech
ALCONA	1087	44.692800	-83.666033	5/30/2006	No Scale
ALCONA	1093	44.784500	-83.832050	5/30/2006	No Scale
ALGER	200	46.665983	-86.009600	8/10/2004	Patchy
ALGER	201	46.633900	-86.119517	8/10/2004	Trace
ALGER	202	46.606183	-86.215600	8/10/2004	No Beech
ALGER	203	46.588650	-86.222817	8/10/2004	No Scale
ALGER	204	46.526350	-86.232933	8/10/2004	Trace
ALGER	205	46.516050	-86.327633	8/11/2004	No Scale
ALGER	206	46.485133	-86.394683	8/11/2004	No Scale
ALGER	207	46.428433	-86.448917	8/11/2004	No Beech
ALGER	208	46.419300	-86.546400	8/11/2004	No Scale
ALGER	209	46.489367	-86.954217	8/12/2004	No Scale
ALGER	210	46.460750	-86.926150	8/12/2004	No Beech
ALGER	211	46.376800	-86.835800	8/12/2004	No Scale
ALGER	212	46.393467	-86.766133	8/12/2004	No Scale
ALGER	213	46.375550	-86.700533	8/12/2004	No Scale
ALGER	214	46.307833	-86.716617	8/12/2004	No Scale
ALGER	215	46.264133	-86.627550	8/12/2004	No Scale
ALGER	219	46.358050	-86.469700	8/13/2004	No Beech
ALGER	732	46.655183	-85.929017	7/12/2005	Whitewashed
ALGER	743	46.467267	-86.552500	7/6/2005	No Scale
ALGER	745	46.407150	-86.574450	7/6/2005	No Scale
ALGER	747	46.319500	-86.615700	7/6/2005	No Scale
ALGER	750	46.557283	-86.363767	7/6/2005	No Scale
ALGER	752	46.564083	-85.927800	7/12/2005	Whitewashed
ALGER	760	46.333350	-86.799167	7/25/2005	No Scale
ALGER	761	46.506917	-86.363483	7/7/2005	No Scale
ALGER	763	46.520783	-86.268700	7/7/2005	Patchy
ALGER	765	46.535583	-86.252533	7/7/2005	Whitewashed
ALGER	767	46.552383	-86.150400	7/7/2005	No Scale
ALGER	769	46.547500	-86.062600	7/7/2005	Trace
ALGER	1170	46.205850	-86.754167	6/27/2006	No Scale
ALGER	1172	46.436767	-86.658250	6/28/2006	No Scale
ALGER	1173	46.396000	-86.928233	6/28/2006	No Scale
ALGER	1174	46.381317	-87.086033	6/28/2006	No Scale
ALGER	1253	46.557233	-86.364117	7/24/2006	Trace
ALGER	1254	46.552283	-86.150383	7/25/2006	Whitewashed
ALGER	1255	46.520517	-86.303133	7/25/2006	No Scale
ALGER	1256	46.506783	-86.363483	7/25/2006	Trace
ALGER	1257	46.539867	-86.446233	7/25/2006	Trace
ALGER	1258	46.467233	-86.552517	7/25/2006	No Scale
ALGER	1259	46.474533	-86.428000	7/25/2006	No Scale

ALGER	748	46.649020	-86.027480	7/14/2005	Patchy
ALLEGAN	838	42.703050	-86.197217	8/8/2005	No Scale
ALLEGAN	1063	42.647167	-85.898567	5/25/2006	No Beech
ALLEGAN	1064	42.636000	-85.898767	5/25/2006	No Scale
ALLEGAN	1065	42.485067	-86.010467	5/26/2006	No Scale
ALLEGAN	1066	42.553000	-85.995700	5/26/2006	No Scale
ALPENA	1078	45.176150	-83.731100	5/29/2006	No Scale
ALPENA	1079	45.042117	-83.563283	5/29/2006	No Beech
ALPENA	1080	44.982733	-83.616967	5/29/2006	No Scale
ALPENA	1081	44.898583	-83.668150	5/29/2006	No Beech
ANTRIM	585	44.881833	-85.423033	6/15/2005	No Scale
ANTRIM	587	44.863150	-85.353250	6/15/2005	No Scale
ANTRIM	591	44.989833	-85.134683	6/15/2005	No Scale
ANTRIM	599	44.961200	-85.134650	6/15/2005	No Scale
ANTRIM	618	45.064567	-84.907433	6/20/2005	No Scale
ANTRIM	663	45.168500	-85.226467	6/22/2005	No Scale
ANTRIM	666	45.049900	-85.153950	6/22/2005	No Scale
ANTRIM	668	45.090683	-85.138650	6/22/2005	No Scale
ANTRIM	671	45.182200	-85.376550	6/22/2005	No Scale
ANTRIM	673	45.075667	-85.361200	6/22/2005	No Scale
ANTRIM	675	45.159350	-85.299850	6/22/2005	No Scale
ANTRIM	677	45.048683	-85.299383	6/22/2005	No Scale
ANTRIM	679	45.029750	-85.217217	6/22/2005	No Scale
ANTRIM	681	45.103017	-85.144617	6/22/2005	No Scale
BARRY	1067	42.594717	-85.465600	5/26/2006	No Scale
BAY	1194	43.668550	-83.908917	7/6/2006	No Beech
BENZIE	535	44.535767	-86.105417	6/8/2005	No Scale
BENZIE	536	44.590067	-86.102367	6/8/2005	Trace
BENZIE	537	44.683267	-86.113633	6/8/2005	No Scale
BENZIE	538	44.720683	-86.062250	6/8/2005	No Scale
BENZIE	539	44.764000	-86.074600	6/8/2005	No Scale
BENZIE	545	44.757517	-85.999050	6/9/2005	No Scale
BENZIE	547	44.718183	-85.885667	6/9/2005	No Scale
BENZIE	548	44.644917	-85.979617	6/9/2005	No Scale
BENZIE	549	44.680067	-85.957933	6/9/2005	No Scale
BENZIE	550	44.617150	-85.909067	6/9/2005	No Scale
BENZIE	551	44.617533	-86.046283	6/9/2005	No Scale
BENZIE	552	44.695850	-86.230717	6/9/2005	No Scale
BENZIE	553	44.531017	-86.129967	6/9/2005	Trace
BENZIE	554	44.525450	-85.958850	6/9/2005	Patchy
BENZIE	569	44.547333	-85.818517	6/14/2005	No Scale
BENZIE	573	44.678117	-85.841933	6/14/2005	No Scale
BENZIE	575	44.739933	-85.858383	6/14/2005	No Scale
BERRIEN	832	41.839433	-86.625583	8/8/2005	No Scale
BERRIEN	834	41.904450	-86.601800	8/8/2005	No Scale
CASS	1190	41.948700	-85.769467	7/5/2006	No Scale
CHARLEVOIX	614	45.186717	-84.751350	6/20/2005	No Scale
CHARLEVOIX	616	45.146717	-84.935217	6/20/2005	No Scale

CHARLEVOIX	623	45.277800	-84.935633	6/20/2005	No Scale
CHARLEVOIX	652	45.349517	-85.166383	6/21/2005	No Scale
CHARLEVOIX	654	45.310900	-85.178083	6/21/2005	No Scale
CHARLEVOIX	656	45.312250	-85.058583	6/21/2005	No Scale
CHARLEVOIX	658	45.241900	-85.042883	6/21/2005	No Scale
CHARLEVOIX	660	45.237300	-85.093317	6/21/2005	No Scale
CHARLEVOIX	662	45.171817	-85.130967	6/21/2005	No Scale
CHARLEVOIX	664	45.128200	-85.040050	6/22/2005	No Scale
CHARLEVOIX	665	45.215550	-85.201717	6/22/2005	No Scale
CHARLEVOIX	665	45.214933	-85.201867	6/22/2005	No Scale
CHARLEVOIX	667	45.279283	-85.254583	6/22/2005	No Scale
CHARLEVOIX	669	45.255567	-85.321833	6/22/2005	No Scale
CHARLEVOIX	762	45.747867	-85.539133	7/26/2005	Dead/Declining
CHARLEVOIX	764	45.734033	-85.556917	7/26/2005	No Scale
CHARLEVOIX	766	45.725367	-85.564267	7/26/2005	Whitewashed
CHARLEVOIX	768	45.687983	-85.559117	7/26/2005	No Scale
CHARLEVOIX	770	45.646733	-85.491433	7/27/2005	Patchy
CHARLEVOIX	772	45.606000	-85.496317	7/27/2005	No Scale
CHARLEVOIX	774	45.575517	-85.570633	7/27/2005	No Scale
CHARLEVOIX	776	45.659700	-85.553750	7/27/2005	No Scale
CHARLEVOIX	778	45.659283	-85.579433	7/27/2005	No Scale
CHARLEVOIX	780	45.647350	-85.583083	7/27/2005	No Scale
CHARLEVOIX	782	45.608700	-85.592383	7/27/2005	No Scale
CHARLEVOIX	784	45.584650	-85.596467	7/27/2005	No Scale
CHARLEVOIX	1096	45.273820	-84.737970	5/31/2006	No Scale
CHARLEVOIX	1236	45.307667	-85.306633	7/17/2006	No Scale
CHARLEVOIX	1237	45.307367	-85.311067	7/17/2006	Whitewashed
CHARLEVOIX	1238	45.646617	-85.491300	7/18/2006	Whitewashed
CHARLEVOIX	1239	45.614517	-85.491367	7/18/2006	Whitewashed
CHARLEVOIX	1240	45.606300	-85.496500	7/18/2006	No Scale
CHARLEVOIX	1241	45.575433	-85.570600	7/18/2006	No Scale
CHARLEVOIX	1242	45.584017	-85.596567	7/18/2006	No Scale
CHARLEVOIX	1243	45.608233	-85.592250	7/18/2006	No Scale
CHARLEVOIX	1244	45.647767	-85.582933	7/18/2006	No Scale
CHARLEVOIX	1245	45.659483	-85.579267	7/18/2006	No Scale
CHARLEVOIX	1246	45.687783	-85.558800	7/18/2006	Trace
CHARLEVOIX	1247	45.749783	-85.539033	7/18/2006	Dead/Declining
CHARLEVOIX	1248	45.734183	-85.557067	7/18/2006	Trace
CHARLEVOIX	1249	45.694150	-85.502583	7/19/2006	No Beech
CHARLEVOIX	1250	45.609317	-85.513767	7/19/2006	No Beech
CHARLEVOIX	1251	45.633933	-85.569633	7/19/2006	No Scale
CHARLEVOIX	1252	45.655850	-85.527850	7/19/2006	No Beech
CHEBOYGAN	619	45.205200	-84.591100	6/20/2005	No Scale
CHEBOYGAN	621	45.244350	-84.666867	6/20/2005	No Scale
CHEBOYGAN	628	45.504983	-84.576183	6/21/2005	No Scale
CHEBOYGAN	630	45.550933	-84.715917	6/21/2005	No Scale
CHEBOYGAN	632	45.574917	-84.631650	6/21/2005	No Scale
CHEBOYGAN	634	45.691633	-84.728233	6/21/2005	No Scale

CHEBOYGAN	638	45.683233	-84.650650	6/21/2005	No Scale
CHEBOYGAN	640	45.664617	-84.638567	6/21/2005	No Scale
CHEBOYGAN	642	45.579550	-84.328167	6/21/2005	No Scale
CHEBOYGAN	644	45.538733	-84.396283	6/21/2005	No Scale
CHEBOYGAN	646	45.569167	-84.454183	6/21/2005	No Scale
CHEBOYGAN	648	45.318967	-84.508033	6/21/2005	No Scale
CHEBOYGAN	650	45.254217	-84.477317	6/21/2005	No Scale
CHEBOYGAN	683	45.435617	-84.470750	6/23/2005	No Scale
CHEBOYGAN	685	45.343850	-84.431900	6/23/2005	No Scale
CHEBOYGAN	691	45.274017	-84.307667	6/23/2005	No Scale
CHEBOYGAN	1273	45.744217	-84.670433	7/27/2006	No Scale
CHIPPEWA	775	46.431417	-85.076000	7/11/2005	Whitewashed
CHIPPEWA	777	46.634417	-85.115333	7/11/2005	Whitewashed
CHIPPEWA	793	46.349600	-85.144733	7/12/2005	Whitewashed
CHIPPEWA	797	46.261400	-85.012300	7/12/2005	Dead/Declining
CHIPPEWA	805	46.462167	-84.668767	7/12/2005	Trace
CHIPPEWA	1105	46.003570	-84.185810	6/5/2006	No Scale
CHIPPEWA	1106	45.961810	-84.021250	6/5/2006	No Scale
CHIPPEWA	1107	46.089440	-83.724680	6/6/2006	No Beech
CHIPPEWA	1108	46.072390	-83.618990	6/6/2006	No Beech
CHIPPEWA	1109	46.031190	-83.673410	6/6/2006	No Scale
CHIPPEWA	1110	46.013050	-83.703080	6/6/2006	No Scale
CHIPPEWA	1111	45.998700	-83.667490	6/6/2006	No Scale
CHIPPEWA	1112	45.943410	-83.545520	6/6/2006	No Scale
CHIPPEWA	1113	46.002410	-83.536660	6/6/2006	No Scale
CHIPPEWA	1114	45.959890	-83.611910	6/6/2006	No Scale
CHIPPEWA	1115	45.975230	-83.697280	6/6/2006	No Scale
CHIPPEWA	1116	45.984440	-83.787600	6/6/2006	No Scale
CHIPPEWA	1117	45.994590	-84.072580	6/7/2006	No Scale
CHIPPEWA	1118	46.158980	-84.175060	6/7/2006	No Beech
CHIPPEWA	1119	46.212850	-84.271260	6/7/2006	No Beech
CHIPPEWA	1120	46.375767	-84.353450	6/7/2006	No Beech
CHIPPEWA	1121	46.409633	-84.739117	6/7/2006	No Scale
CHIPPEWA	1122	46.431783	-84.697583	6/7/2006	Patchy
CHIPPEWA	1123	46.450733	-84.677290	6/7/2006	Trace
CHIPPEWA	1124	46.403683	-84.938933	6/7/2006	Trace
CHIPPEWA	1125	46.422850	-84.908770	6/7/2006	Patchy
CHIPPEWA	1126	46.413483	-84.835050	6/7/2006	Trace
CHIPPEWA	1127	46.302783	-84.591733	6/7/2006	No Beech
CHIPPEWA	1128	46.186783	-84.787083	6/7/2006	No Beech
CHIPPEWA	1186	46.331983	-84.974350	6/29/2006	No Beech
CLARE	697	44.069317	-84.869483	6/27/2005	No Scale
CLARE	699	44.106717	-84.692950	6/27/2005	No Scale
CLARE	1032	43.842717	-85.009867	5/23/2006	No Scale
CLINTON	140	42.812450	-84.389517	5/23/2005	No Beech
CLINTON	1000	42.914417	-84.590567	5/8/2006	No Beech
CRAWFORD	604	44.801367	-84.645800	6/16/2005	No Scale
CRAWFORD	605	44.680533	-84.646733	6/16/2005	No Beech

CRAWFORD	607	44.753950	-84.777067	6/16/2005	No Scale
CRAWFORD	612	44.776867	-84.781083	6/16/2005	No Scale
CRAWFORD	617	44.598067	-84.765667	6/16/2005	No Scale
DELTA	714	45.767200	-86.599717	7/6/2005	No Scale
DELTA	716	45.700633	-86.663900	7/6/2005	No Scale
DELTA	718	45.785700	-86.469867	7/6/2005	No Scale
DELTA	749	46.157417	-86.635817	7/6/2005	No Scale
DELTA	751	46.073883	-86.557167	7/6/2005	No Scale
DELTA	753	45.788317	-86.863250	7/6/2005	No Scale
DELTA	755	46.036000	-86.857100	7/6/2005	No Scale
DELTA	756	45.625767	-87.303833	7/20/2005	No Scale
DELTA	757	46.134650	-86.837600	7/6/2005	No Scale
DELTA	758	45.840917	-87.111133	7/20/2005	No Scale
EATON	133	42.577867	-84.758250	5/19/2005	No Scale
EATON	134	42.759433	-84.759833	5/19/2005	No Scale
EMMET	625	45.352433	-84.816567	6/20/2005	No Scale
EMMET	627	45.326267	-84.741800	6/20/2005	No Scale
EMMET	629	45.441717	-84.766617	6/21/2005	No Scale
EMMET	631	45.516083	-84.762033	6/21/2005	No Scale
EMMET	633	45.628750	-84.792533	6/21/2005	No Scale
EMMET	635	45.719233	-84.772850	6/21/2005	No Scale
EMMET	637	45.766750	-84.769517	6/21/2005	Whitewashed
EMMET	641	45.650717	-85.014617	6/21/2005	No Scale
EMMET	643	45.606650	-85.085083	6/21/2005	No Scale
EMMET	645	45.551100	-85.016117	6/21/2005	No Scale
EMMET	647	45.550283	-84.935817	6/21/2005	No Scale
EMMET	649	45.613783	-84.929617	6/21/2005	No Scale
EMMET	651	45.636700	-84.849550	6/21/2005	Trace
EMMET	653	45.551250	-84.845683	6/22/2005	No Scale
EMMET	655	45.471133	-84.852250	6/22/2005	No Scale
EMMET	657	45.456783	-84.926967	6/22/2005	No Scale
EMMET	659	45.377000	-84.799567	6/22/2005	No Scale
EMMET	661	45.407783	-84.906317	6/22/2005	No Scale
EMMET	804	45.508017	-85.069417	8/4/2005	No Scale
EMMET	806	45.589067	-85.015433	8/4/2005	Trace
EMMET	826	45.458067	-85.066983	8/4/2005	No Scale
EMMET	828	45.680267	-84.892900	8/4/2005	No Scale
EMMET	830	45.655683	-84.774100	8/4/2005	No Scale
EMMET	1097	45.313160	-84.746820	5/31/2006	No Scale
EMMET	1098	45.310333	-84.882050	5/31/2006	No Scale
EMMET	1099	45.492980	-84.876680	5/31/2006	No Scale
EMMET	1100	45.547090	-84.855870	5/31/2006	No Scale
EMMET	1164	45.576433	-84.984733	6/22/2006	No Scale
EMMET	1165	45.575717	-85.057183	6/22/2006	No Scale
EMMET	1181	45.680667	-84.841267	6/29/2006	No Scale
EMMET	1182	45.707900	-84.910067	6/29/2006	Trace
EMMET	1183	45.716867	-84.868267	6/29/2006	Patchy
EMMET	1274	45.719550	-84.772133	7/27/2006	No Scale

EMMET	1275	45.694467	-84.887000	7/27/2006	Trace
EMMET	1276	45.680150	-84.893200	7/27/2006	No Scale
EMMET	1277	45.608840	-85.082960	7/27/2006	No Scale
EMMET	1278	45.549833	-85.015500	7/27/2006	Trace
GLADWIN	741	44.016500	-84.520550	6/30/2005	No Scale
GLADWIN	1135	43.979067	-84.209850	6/12/2006	No Beech
GRAND TRAVERSE	563	44.512217	-85.519717	6/14/2005	No Scale
GRAND TRAVERSE	567	44.546733	-85.677517	6/14/2005	No Scale
GRAND TRAVERSE	571	44.604517	-85.797917	6/14/2005	No Scale
GRAND TRAVERSE	577	44.668067	-85.675950	6/14/2005	No Scale
GRAND TRAVERSE	579	44.635517	-85.599000	6/14/2005	No Scale
GRAND TRAVERSE	581	44.627783	-85.556700	6/14/2005	No Scale
GRAND TRAVERSE	583	44.712433	-85.494300	6/14/2005	No Scale
GRAND TRAVERSE	586	44.763033	-85.403083	6/15/2005	No Scale
GRAND TRAVERSE	588	44.587800	-85.345683	6/15/2005	No Scale
GRATIOT	1134	43.251550	-84.409233	6/12/2006	No Beech
HILLSDALE	1192	41.833333	-84.473583	7/5/2006	No Beech
INGHAM	130	42.717733	-84.477117	5/19/2005	No Scale
INGHAM	131	42.689233	-84.511217	5/19/2005	No Scale
INGHAM	132	42.609200	-84.591217	5/19/2005	No Scale
INGHAM	135	42.530750	-84.471433	5/23/2005	No Beech
INGHAM	136	42.526700	-84.363667	5/23/2005	No Beech
INGHAM	137	42.596400	-84.279033	5/23/2005	No Beech
INGHAM	138	42.705367	-84.369233	5/23/2005	No Scale
INGHAM	139	42.755183	-84.407617	5/23/2005	No Beech
INGHAM	754	42.577817	-84.253950	7/12/2005	No Scale
IONIA	1187	42.820433	-84.927533	7/5/2006	No Beech
IONIA	1188	42.936250	-85.129617	7/5/2006	No Scale
IOSCO	1088	44.456300	-83.766350	5/30/2006	No Beech
ISABELLA	1030	43.481633	-84.909283	5/23/2006	No Scale
ISABELLA	1031	43.524583	-85.047200	5/23/2006	No Scale
KALAMAZOO	1191	42.086083	-85.327517	7/5/2006	No Beech
KALKASKA	589	44.857717	-85.189300	6/15/2005	No Scale
KALKASKA	590	44.526667	-85.316750	6/15/2005	No Scale
KALKASKA	592	44.583950	-85.177983	6/15/2005	No Scale
KALKASKA	593	44.839367	-85.050600	6/15/2005	No Scale
KALKASKA	594	44.641033	-85.143433	6/15/2005	No Scale
KALKASKA	595	44.792533	-85.193333	6/15/2005	No Scale
KALKASKA	596	44.654900	-85.196450	6/15/2005	No Scale
KALKASKA	597	44.782900	-85.268300	6/15/2005	No Scale

KALKASKA	598	44.670000	-85.154500	6/15/2005	No Scale
KALKASKA	600	44.698683	-85.073783	6/15/2005	No Scale
KALKASKA	601	44.728217	-85.071367	6/15/2005	No Scale
KALKASKA	602	44.572567	-85.211800	6/15/2005	No Scale
KALKASKA	603	44.728600	-85.072733	6/15/2005	No Scale
KALKASKA	609	44.770933	-84.884450	6/16/2005	No Scale
KALKASKA	611	44.713383	-84.976050	6/16/2005	No Scale
KALKASKA	613	44.635333	-84.914350	6/16/2005	No Scale
KALKASKA	615	44.539900	-84.955833	6/16/2005	No Scale
KENT	1054	43.252883	-85.697300	5/25/2006	No Scale
KENT	1068	42.785467	-85.408700	5/26/2006	No Beech
KENT	1069	42.948983	-85.311967	5/26/2006	No Beech
KENT	1070	43.043567	-85.484900	5/26/2006	No Beech
LAKE	94	43.948033	-85.997367	8/2/2004	No Beech
LAKE	95	43.944833	-85.901433	8/2/2004	No Beech
LAKE	96	43.944550	-85.911183	8/2/2004	No Scale
LAKE	113	44.147817	-85.987633	8/4/2004	No Beech
LAKE	122	44.081550	-86.014333	8/4/2004	No Scale
LAKE	124	43.918317	-86.033500	8/5/2004	No Scale
LAKE	690	44.132250	-85.594533	6/29/2005	No Scale
LAKE	1024	43.849867	-85.824667	5/10/2006	No Beech
LAKE	1025	43.923033	-85.764050	5/10/2006	No Beech
LAKE	1034	44.140500	-85.870500	5/24/2006	No Beech
LAKE	1036	44.032233	-86.015600	5/24/2006	No Scale
LAKE	1037	43.887683	-85.985167	5/24/2006	No Scale
LAKE	1038	43.823333	-85.970533	5/24/2006	No Beech
LAPEER	1196	43.166783	-83.378933	7/6/2006	No Scale
LAPEER	1197	42.942617	-83.346200	7/6/2006	No Scale
LEELANAU	540	44.845950	-86.035900	6/8/2005	No Scale
LEELANAU	541	44.897033	-86.020983	6/8/2005	Trace
LEELANAU	542	44.935383	-85.925250	6/8/2005	No Scale
LEELANAU	543	44.877067	-85.914717	6/8/2005	Trace
LEELANAU	544	44.842800	-85.969817	6/8/2005	No Scale
LEELANAU	546	44.807283	-85.957233	6/9/2005	No Scale
LEELANAU	562	44.810400	-85.855250	6/14/2005	No Scale
LEELANAU	564	44.878800	-85.853750	6/14/2005	No Scale
LEELANAU	566	44.922017	-85.864367	6/14/2005	No Scale
LEELANAU	568	44.891550	-85.744700	6/14/2005	No Scale
LEELANAU	570	44.982217	-85.726950	6/14/2005	No Scale
LEELANAU	572	44.994433	-85.759900	6/14/2005	No Scale
LEELANAU	574	44.980483	-85.776433	6/14/2005	No Scale
LEELANAU	576	44.958967	-85.796383	6/14/2005	No Scale
LEELANAU	578	45.006317	-85.633150	6/14/2005	No Scale
LEELANAU	580	45.102800	-85.643583	6/14/2005	No Scale
LEELANAU	582	44.887300	-85.674500	6/14/2005	No Scale
LEELANAU	584	44.802483	-85.652217	6/14/2005	No Scale
LEELANAU	786	45.003483	-86.134283	8/1/2005	No Scale
LEELANAU	788	45.108233	-85.985950	8/2/2005	No Scale

LEELANAU	790	45.119917	-86.053850	8/3/2005	No Scale
LEELANAU	792	45.138150	-86.047450	8/3/2005	No Scale
LEELANAU	794	45.142933	-86.019717	8/3/2005	No Scale
LEELANAU	796	45.129400	-86.014417	8/3/2005	No Scale
LEELANAU	798	45.122850	-85.989567	8/3/2005	No Scale
LEELANAU	800	45.002750	-86.139500	8/1/2005	No Scale
LEELANAU	802	45.005683	-86.112983	8/1/2005	No Scale
LEELANAU	808	45.116717	-85.980483	8/2/2005	No Scale
LEELANAU	810	45.097950	-86.006183	8/2/2005	No Scale
LEELANAU	812	45.111017	-86.059217	8/3/2005	No Scale
LEELANAU	814	45.098900	-86.047400	8/3/2005	No Scale
LEELANAU	816	45.080900	-86.029600	8/3/2005	No Scale
LEELANAU	818	45.073433	-86.007267	8/3/2005	No Scale
LEELANAU	820	45.080033	-85.989600	8/3/2005	No Scale
LEELANAU	822	45.090917	-85.989800	8/3/2005	No Scale
LEELANAU	824	45.103433	-85.985067	8/3/2005	No Scale
LEELANAU	1158	45.011700	-86.113883	6/20/2006	No Scale
LEELANAU	1159	45.019050	-86.113817	6/20/2006	No Scale
LEELANAU	1160	45.032717	-86.112600	6/20/2006	No Scale
LEELANAU	1161	45.034233	-86.112850	6/20/2006	No Beech
LEELANAU	1162	45.025533	-86.120717	6/20/2006	No Scale
LEELANAU	1163	44.998933	-86.139850	6/21/2006	No Scale
LEELANAU	1232	44.845650	-86.035883	7/17/2006	No Scale
LEELANAU	1233	44.842833	-85.969767	7/17/2006	No Scale
LEELANAU	1234	44.917550	-85.874900	7/17/2006	No Scale
LEELANAU	1235	44.922017	-85.864367	7/17/2006	No Scale
LUCE	241	46.310200	-85.694900	8/17/2004	Patchy
LUCE	726	46.589300	-85.600417	7/12/2005	Dead/Declining
LUCE	728	46.651683	-85.745033	7/12/2005	Dead/Declining
LUCE	730	46.669700	-85.831650	7/12/2005	Dead/Declining
LUCE	742	46.335917	-85.783100	7/12/2005	Dead/Declining
LUCE	744	46.462317	-85.707250	7/12/2005	Dead/Declining
LUCE	746	46.450583	-85.801350	7/13/2005	Whitewashed
LUCE	779	46.577883	-85.252400	7/11/2005	Dead/Declining
LUCE	781	46.553667	-85.370083	7/11/2005	Dead/Declining
LUCE	783	46.665633	-85.307633	7/11/2005	Whitewashed
LUCE	785	46.657200	-85.533733	7/11/2005	Patchy
LUCE	787	46.453967	-85.597267	7/11/2005	Whitewashed
LUCE	789	46.494767	-85.426883	7/12/2005	Dead/Declining
LUCE	791	46.414383	-85.634167	7/12/2005	Whitewashed
LUCE	795	46.477017	-85.239400	7/12/2005	Whitewashed
MACKINAC	242	46.194917	-85.818117	8/17/2004	No Scale
MACKINAC	243	46.205767	-85.754100	8/17/2004	Patchy
MACKINAC	244	46.203000	-85.697767	8/17/2004	Trace
MACKINAC	736	46.100767	-85.782933	7/12/2005	Whitewashed
MACKINAC	738	46.035550	-85.696767	7/12/2005	No Scale
MACKINAC	740	46.222383	-85.572000	7/12/2005	Whitewashed
MACKINAC	799	46.174450	-85.184867	7/12/2005	Whitewashed

MACKINAC	801	46.110483	-85.446550	7/12/2005	Whitewashed
MACKINAC	803	46.039317	-85.112283	7/12/2005	Patchy
MACKINAC	807	45.988333	-84.925633	7/14/2005	Dead/Declining
MACKINAC	809	45.892833	-84.806950	7/14/2005	No Scale
MACKINAC	811	45.966483	-84.761417	7/14/2005	No Scale
MACKINAC	1101	45.928920	-84.913390	6/5/2006	Whitewashed
MACKINAC	1102	45.928610	-84.912800	6/5/2006	No Scale
MACKINAC	1103	45.961900	-84.898250	6/5/2006	Patchy
MACKINAC	1104	46.085960	-84.369680	6/5/2006	No Scale
MACKINAC	1129	46.063067	-85.146600	6/8/2006	Dead/Declining
MACKINAC	1130	46.065950	-85.026667	6/8/2006	Trace
MACKINAC	1131	46.028433	-84.918850	6/8/2006	No Scale
MACKINAC	1132	46.102300	-84.879950	6/8/2006	No Scale
MACKINAC	1133	46.073600	-84.765533	6/8/2006	No Scale
MACKINAC	1136	45.855933	-84.605317	6/13/2006	No Beech
MACKINAC	1137	45.877600	-84.624067	6/13/2006	No Beech
MACKINAC	1138	45.879500	-84.629000	6/13/2006	No Scale
MACKINAC	1139	45.871100	-84.624183	6/13/2006	Whitewashed
MACKINAC	1140	45.874000	-84.635467	6/13/2006	No Scale
MACKINAC	1141	45.872917	-84.643650	6/13/2006	Trace
MACKINAC	1142	45.871467	-84.645267	6/13/2006	Patchy
MACKINAC	1143	45.870767	-84.646217	6/13/2006	Whitewashed
MACKINAC	1144	45.865550	-84.645033	6/13/2006	Whitewashed
MACKINAC	1145	45.858633	-84.637617	6/13/2006	No Scale
MACKINAC	1146	45.862783	-84.633467	6/13/2006	No Scale
MACKINAC	1147	45.861783	-84.625417	6/13/2006	Patchy
MACKINAC	1148	45.857733	-84.609950	6/13/2006	Trace
MACKINAC	1149	45.809000	-84.571017	6/14/2006	Dead/Declining
MACKINAC	1150	45.794467	-84.536400	6/14/2006	Trace
MACKINAC	1151	45.790550	-84.520783	6/14/2006	Patchy
MACKINAC	1152	45.770733	-84.513100	6/14/2006	Trace
MACKINAC	1153	45.752350	-84.493117	6/14/2006	No Scale
MACKINAC	1154	45.779017	-84.384667	6/14/2006	No Beech
MACKINAC	1155	45.743217	-84.385900	6/14/2006	No Beech
MACKINAC	1156	45.761883	-84.424383	6/14/2006	No Scale
MACKINAC	1157	45.772750	-84.451883	6/14/2006	No Scale
MACKINAC	1166	46.081817	-85.594483	6/26/2006	Patchy
MACKINAC	1167	45.983700	-85.700117	6/26/2006	No Scale
MACKINAC	1171	46.177167	-85.795233	6/27/2006	Whitewashed
MACKINAC	1180	45.945883	-84.859750	6/29/2006	Whitewashed
MACKINAC	1270	46.035033	-85.696800	7/26/2006	Patchy
MACKINAC	1271	45.987900	-85.749233	7/26/2006	Patchy
MACKINAC	1272	45.966717	-84.762600	7/27/2006	No Scale
MACKINAC	1279	45.892750	-84.806767	7/24/2006	Patchy
MANISTEE	67	44.184217	-86.117000	7/27/2004	No Beech
MANISTEE	68	44.172933	-86.207867	7/27/2004	No Beech
MANISTEE	69	44.175000	-86.256517	7/27/2004	No Beech
MANISTEE	70	44.284333	-86.310600	7/28/2004	Whitewashed

MANISTEE	71	44.274133	-86.202717	7/28/2004	No Scale
MANISTEE	72	44.268733	-86.077650	7/28/2004	No Scale
MANISTEE	73	44.270800	-85.944433	7/28/2004	No Beech
MANISTEE	74	44.321583	-85.961000	7/27/2004	No Beech
MANISTEE	75	44.314033	-86.088500	7/27/2004	No Scale
MANISTEE	98	44.316733	-86.196017	8/3/2004	Trace
MANISTEE	99	44.373633	-86.184883	8/3/2004	Trace
MANISTEE	100	44.371650	-86.071833	8/3/2004	No Beech
MANISTEE	101	44.375917	-85.975800	8/3/2004	No Beech
MANISTEE	102	44.367667	-85.933467	8/3/2004	No Scale
MANISTEE	103	44.373450	-85.831067	8/3/2004	No Scale
MANISTEE	104	44.419750	-85.859383	8/3/2004	No Scale
MANISTEE	105	44.426150	-85.919717	8/3/2004	No Beech
MANISTEE	106	44.426550	-85.927500	8/3/2004	No Beech
MANISTEE	107	44.483133	-85.999600	8/3/2004	No Scale
MANISTEE	108	44.493500	-85.943650	8/3/2004	No Scale
MANISTEE	109	44.484117	-86.038750	8/3/2004	No Scale
MANISTEE	110	44.487217	-86.092900	8/3/2004	No Scale
MANISTEE	111	44.476050	-86.169917	8/3/2004	No Scale
MANISTEE	112	44.432250	-86.181900	8/3/2004	No Scale
MANISTEE	114	44.168917	-85.905950	8/4/2004	No Beech
MANISTEE	116	44.252650	-85.860400	8/4/2004	No Beech
MANISTEE	118	44.345633	-85.839467	8/4/2004	No Scale
MANISTEE	119	44.223500	-85.910183	8/4/2004	No Beech
MANISTEE	120	44.228900	-86.013300	8/4/2004	No Beech
MANISTEE	121	44.222450	-86.216883	8/4/2004	No Beech
MANISTEE	123	44.269733	-86.120217	8/4/2004	No Scale
MANISTEE	182	44.347317	-85.894467	6/1/2005	No Scale
MANISTEE	183	44.438733	-85.997333	6/1/2005	No Scale
MANISTEE	184	44.479150	-86.243383	6/1/2005	No Scale
MANISTEE	185	44.430600	-86.230367	6/1/2005	No Scale
MANISTEE	186	44.403700	-86.225900	6/1/2005	Trace
MANISTEE	187	44.400950	-86.227433	6/1/2005	Whitewashed
MANISTEE	188	44.388983	-86.196467	6/1/2005	Patchy
MANISTEE	189	44.388550	-86.164800	6/1/2005	Trace
MANISTEE	190	44.403133	-86.167300	6/1/2005	No Scale
MANISTEE	191	44.406400	-86.194417	6/1/2005	Trace
MANISTEE	192	44.358933	-86.145117	6/1/2005	No Scale
MANISTEE	193	44.387633	-86.125017	6/1/2005	No Scale
MANISTEE	194	44.371417	-86.122367	6/1/2005	No Scale
MANISTEE	195	44.329767	-86.147667	6/1/2005	No Scale
MANISTEE	196	44.309117	-86.172700	6/1/2005	Whitewashed
MANISTEE	197	44.315767	-86.167733	6/2/2005	Patchy
MANISTEE	198	44.340083	-86.162250	6/2/2005	No Scale
MANISTEE	199	44.381283	-86.155850	6/2/2005	No Scale
MANISTEE	500	44.358517	-86.171950	6/2/2005	No Scale
MANISTEE	501	44.349650	-86.202467	6/2/2005	No Scale
MANISTEE	502	44.331483	-86.197933	6/2/2005	Patchy

MANISTEE	503	44.331267	-86.187900	6/2/2005	No Scale
MANISTEE	504	44.316833	-86.192117	6/2/2005	Whitewashed
MANISTEE	505	44.262683	-86.181617	6/2/2005	No Scale
MANISTEE	506	44.267067	-86.177350	6/2/2005	Trace
MANISTEE	530	44.250883	-86.200683	6/7/2005	Patchy
MANISTEE	531	44.170733	-86.103333	6/7/2005	No Scale
MANISTEE	532	44.312883	-86.141133	6/8/2005	Trace
MANISTEE	533	44.304967	-86.102350	6/8/2005	Trace
MANISTEE	534	44.344967	-86.268333	6/8/2005	Patchy
MANISTEE	847	44.396233	-86.221350	6/1/2005	No Scale
MANISTEE	1008	44.194767	-86.037100	5/9/2006	No Scale
MANISTEE	1009	44.267290	-86.178300	5/9/2006	Whitewashed
MANISTEE	1226	44.284070	-85.863730	7/13/2006	No Scale
MASON	61	43.916650	-86.442783	7/26/2004	Whitewashed
MASON	62	44.112050	-86.419450	7/27/2004	Patchy
MASON	63	44.131367	-86.333800	7/27/2004	No Beech
MASON	64	44.126567	-86.287650	7/27/2004	Patchy
MASON	65	44.146783	-86.200500	7/27/2004	Trace
MASON	66	44.144017	-86.102983	7/27/2004	No Beech
MASON	84	43.833017	-86.428300	8/1/2004	No Beech
MASON	85	43.871850	-86.436967	8/1/2004	Patchy
MASON	86	43.900933	-86.398483	8/1/2004	Whitewashed
MASON	88	43.843333	-86.399150	8/2/2004	Trace
MASON	89	43.847017	-86.319683	8/2/2004	Trace
MASON	90	43.825133	-86.259333	8/2/2004	No Beech
MASON	91	43.959383	-86.339200	8/2/2004	Patchy
MASON	92	43.955200	-86.207050	8/2/2004	Trace
MASON	93	43.945950	-86.077133	8/2/2004	No Beech
MASON	97	44.018867	-86.145083	8/2/2004	No Beech
MASON	127	44.116900	-86.374267	7/27/2004	No Beech
MASON	158	44.040050	-86.496317	5/26/2005	Whitewashed
MASON	159	43.993067	-86.463183	5/26/2005	Whitewashed
MASON	160	43.971350	-86.458350	5/26/2005	Whitewashed
MASON	161	43.944700	-86.398467	5/26/2005	No Beech
MASON	162	43.890650	-86.284883	5/26/2005	No Beech
MASON	163	43.876533	-86.331667	5/26/2005	Whitewashed
MASON	164	43.876667	-86.368283	5/26/2005	Patchy
MASON	165	43.868800	-86.399983	5/26/2005	Whitewashed
MASON	171	43.848150	-86.077333	5/31/2005	No Beech
MASON	172	43.871900	-86.102500	5/31/2005	No Scale
MASON	173	43.874083	-86.110733	5/31/2005	No Scale
MASON	174	43.873750	-86.135050	5/31/2005	No Scale
MASON	175	43.874683	-86.190933	5/31/2005	No Scale
MASON	176	43.875383	-86.231483	5/31/2005	Patchy
MASON	177	43.874333	-86.227717	5/31/2005	Patchy
MASON	178	43.889867	-86.229783	5/31/2005	No Scale
MASON	179	43.890050	-86.227817	5/31/2005	Patchy
MASON	180	43.904550	-86.218483	5/31/2005	Patchy

MASON	181	43.975367	-86.103317	5/31/2005	Patchy
MASON	511	43.872067	-86.248200	6/6/2005	No Scale
MASON	512	43.838850	-86.201450	6/6/2005	No Scale
MASON	513	43.835733	-86.175550	6/6/2005	No Scale
MASON	514	43.837000	-86.161683	6/6/2005	Whitewashed
MASON	517	43.911333	-86.153117	6/7/2005	No Beech
MASON	518	43.914067	-86.163433	6/7/2005	Trace
MASON	519	43.903767	-86.190683	6/7/2005	Trace
MASON	520	43.902117	-86.175050	6/7/2005	Trace
MASON	521	43.937650	-86.050033	6/7/2005	No Scale
MASON	522	43.984800	-86.054617	6/7/2005	No Scale
MASON	523	44.017817	-86.080133	6/7/2005	Trace
MASON	524	44.016317	-86.115900	6/7/2005	Trace
MASON	525	44.032250	-86.077217	6/7/2005	No Scale
MASON	526	44.041767	-86.120400	6/7/2005	Whitewashed
MASON	527	44.066317	-86.132400	6/7/2005	Trace
MASON	528	44.104933	-86.125383	6/7/2005	Trace
MASON	529	44.145717	-86.221133	6/7/2005	Trace
MASON	1010	44.111760	-86.418540	5/9/2006	Whitewashed
MASON	1011	44.085500	-86.435460	5/9/2006	Dead/Declining
MASON	1012	44.085240	-86.387150	5/9/2006	Whitewashed
MASON	1013	44.092120	-86.366830	5/9/2006	Whitewashed
MASON	1014	44.042450	-86.496280	5/10/2006	Whitewashed
MASON	1015	44.044730	-86.496570	5/10/2006	Dead/Declining
MASON	1016	44.037810	-86.504890	5/10/2006	Dead/Declining
MASON	1035	44.080400	-86.081233	5/24/2006	No Scale
MASON	1211	43.825300	-86.152590	7/10/2006	Dead/Declining
MASON	1229	43.873733	-86.111933	7/13/2006	No Scale
MASON	1230	43.835917	-86.175417	7/13/2006	Trace
MASON	1231	43.838883	-86.201517	7/13/2006	Trace
MECOSTA	1003	43.604767	-85.443333	5/8/2006	No Scale
MECOSTA	1004	43.703533	-85.200650	5/8/2006	No Scale
MECOSTA	1049	43.558017	-85.522833	5/25/2006	No Scale
MECOSTA	1050	43.515617	-85.402700	5/25/2006	No Scale
MENOMINEE	759	45.771767	-87.366917	7/6/2005	No Scale
MENOMINEE	1168	45.433300	-87.375550	6/27/2006	No Scale
MENOMINEE	1169	45.515317	-87.756817	6/27/2006	No Beech
MIDLAND	1193	43.655217	-84.586717	7/6/2006	No Beech
MISSAUKEE	693	44.463367	-84.972467	6/27/2005	No Scale
MISSAUKEE	695	44.305817	-84.994050	6/27/2005	No Scale
MISSAUKEE	707	44.454200	-85.240100	6/28/2005	No Scale
MISSAUKEE	709	44.359867	-85.311217	6/28/2005	No Scale
MISSAUKEE	713	44.294983	-85.135017	6/28/2005	No Scale
MISSAUKEE	715	44.445000	-85.074883	6/28/2005	No Scale
MISSAUKEE	717	44.451800	-85.135450	6/28/2005	No Scale
MISSAUKEE	719	44.367417	-85.203433	6/28/2005	No Scale
MISSAUKEE	721	44.307633	-85.034950	6/28/2005	No Scale
MISSAUKEE	1184	44.291733	-84.890500	6/30/2006	No Beech

MISSAUKEE	1185	44.205033	-84.872183	6/30/2006	No Beech
MONROE	1201	41.878633	-83.695767	7/7/2006	No Beech
MONTCALM	1001	43.290167	-85.013983	5/8/2006	No Scale
MONTCALM	1002	43.427467	-85.084433	5/8/2006	No Scale
MONTCALM	1028	43.408017	-85.013883	5/23/2006	No Beech
MONTCALM	1029	43.460652	-84.886467	5/23/2006	No Scale
MONTCALM	1051	43.432283	-85.343550	5/25/2006	No Scale
MONTCALM	1053	43.329667	-85.535333	5/25/2006	No Scale
MONTCALM	1071	43.127500	-85.283167	5/26/2006	No Beech
MONTCALM	1072	43.285417	-85.255750	5/26/2006	No Scale
MONTMORENCY	559	44.960200	-84.371333	6/13/2005	No Scale
MONTMORENCY	561	44.868183	-84.198717	6/13/2005	No Scale
MONTMORENCY	1077	45.135400	-84.121067	5/29/2006	No Scale
MONTMORENCY	1095	44.957200	-84.006267	5/30/2006	No Beech
MUSKEGON	141	43.131483	-86.266750	5/24/2005	No Scale
MUSKEGON	142	43.263333	-86.358650	5/24/2005	No Scale
MUSKEGON	143	43.344733	-86.396050	5/24/2005	No Beech
MUSKEGON	144	43.454600	-86.266183	5/25/2005	No Scale
MUSKEGON	1056	43.431750	-86.099383	5/25/2006	No Scale
MUSKEGON	1057	43.337150	-86.082250	5/25/2006	No Scale
MUSKEGON	1058	43.364750	-86.189017	5/25/2006	No Scale
MUSKEGON	1059	43.139983	-86.087383	5/25/2006	No Scale
NEWAYGO	1023	43.779267	-85.911217	5/10/2006	No Beech
NEWAYGO	1026	43.815267	-85.643100	5/10/2006	No Scale
NEWAYGO	1027	43.663767	-85.627483	5/10/2006	No Scale
NEWAYGO	1039	43.742100	-86.018817	5/24/2006	No Scale
NEWAYGO	1044	43.588333	-85.900033	5/24/2006	No Scale
NEWAYGO	1046	43.699150	-85.812767	5/25/2006	No Beech
NEWAYGO	1047	43.610650	-85.761117	5/25/2006	No Scale
NEWAYGO	1048	43.558800	-85.662067	5/25/2006	No Scale
NEWAYGO	1052	43.458867	-85.582133	5/25/2006	No Beech
NEWAYGO	1055	43.480200	-85.788150	5/25/2006	No Scale
OAKLAND	1198	42.794333	-83.509850	7/6/2006	No Scale
OAKLAND	1199	42.644650	-83.549717	7/6/2006	No Scale
OCEANA	1	43.617950	-86.499583	7/16/2004	No Beech
OCEANA	2	43.617350	-86.479050	7/16/2004	No Beech
OCEANA	3	43.621150	-86.439100	7/16/2004	No Beech
OCEANA	4	43.667700	-86.488650	7/17/2004	Trace
OCEANA	5	43.631800	-86.488050	7/17/2004	No Beech
OCEANA	6	43.632000	-86.473583	7/17/2004	Patchy
OCEANA	7	43.632117	-86.457383	7/17/2004	No Beech
OCEANA	8	43.624500	-86.517933	7/17/2004	No Beech
OCEANA	9	43.624717	-86.509600	7/17/2004	Trace
OCEANA	10	43.623717	-86.498800	7/17/2004	No Beech
OCEANA	11	43.638967	-86.511833	7/17/2004	No Beech
OCEANA	12	43.639167	-86.497017	7/17/2004	Trace
OCEANA	13	43.638933	-86.467983	7/17/2004	No Beech
OCEANA	14	43.639100	-86.459150	7/17/2004	No Scale

OCEANA	15	43.642550	-86.460000	7/17/2004	No Beech
OCEANA	16	43.633850	-86.534333	7/18/2004	Whitewashed
OCEANA	17	43.667750	-86.458217	7/18/2004	Trace
OCEANA	18	43.660767	-86.451900	7/18/2004	No Scale
OCEANA	19	43.661150	-86.438517	7/18/2004	Trace
OCEANA	20	43.663533	-86.432183	7/18/2004	No Beech
OCEANA	21	43.656633	-86.480500	7/19/2004	No Beech
OCEANA	22	43.674733	-86.442733	7/19/2004	No Beech
OCEANA	23	43.672100	-86.418267	7/19/2004	No Beech
OCEANA	24	43.646267	-86.427267	7/19/2004	No Beech
OCEANA	25	43.616983	-86.408317	7/19/2004	No Scale
OCEANA	26	43.617167	-86.438150	7/19/2004	No Beech
OCEANA	27	43.610050	-86.475133	7/19/2004	No Beech
OCEANA	28	43.607233	-86.518400	7/19/2004	Trace
OCEANA	29	43.681883	-86.444467	7/19/2004	No Beech
OCEANA	30	43.651600	-86.398100	7/19/2004	No Scale
OCEANA	31	43.645283	-86.382617	7/22/2004	No Scale
OCEANA	32	43.633567	-86.405783	7/22/2004	No Beech
OCEANA	33	43.630300	-86.451217	7/22/2004	Patchy
OCEANA	34	43.620283	-86.468450	7/22/2004	No Scale
OCEANA	35	43.588167	-86.513533	7/22/2004	Patchy
OCEANA	36	43.569250	-86.508483	7/22/2004	Patchy
OCEANA	37	43.541350	-86.491967	7/22/2004	No Scale
OCEANA	38	43.551967	-86.478417	7/22/2004	Trace
OCEANA	39	43.556567	-86.416717	7/23/2004	No Scale
OCEANA	40	43.544783	-86.415767	7/23/2004	No Scale
OCEANA	41	43.527950	-86.418033	7/23/2004	No Beech
OCEANA	42	43.517700	-86.440167	7/23/2004	No Scale
OCEANA	43	43.531200	-86.461733	7/23/2004	No Scale
OCEANA	44	43.544950	-86.452333	7/23/2004	Trace
OCEANA	45	43.558883	-86.447400	7/23/2004	No Beech
OCEANA	46	43.566267	-86.422800	7/23/2004	Patchy
OCEANA	47	43.569700	-86.417850	7/23/2004	No Beech
OCEANA	48	43.591400	-86.406750	7/23/2004	Trace
OCEANA	49	43.582950	-86.377717	7/23/2004	No Scale
OCEANA	50	43.563400	-86.387250	7/25/2004	Trace
OCEANA	51	43.561633	-86.365567	7/25/2004	Trace
OCEANA	52	43.576867	-86.300683	7/25/2004	No Beech
OCEANA	53	43.675783	-86.457717	7/26/2004	Trace
OCEANA	54	43.714583	-86.474833	7/26/2004	Trace
OCEANA	55	43.756367	-86.434117	7/26/2004	No Beech
OCEANA	56	43.740683	-86.430283	7/26/2004	Trace
OCEANA	57	43.726500	-86.409233	7/26/2004	No Scale
OCEANA	58	43.775933	-86.417967	7/26/2004	Trace
OCEANA	59	43.761000	-86.346867	7/26/2004	No Beech
OCEANA	60	43.768517	-86.374533	7/26/2004	No Scale
OCEANA	76	43.510150	-86.357050	8/1/2004	No Scale
OCEANA	77	43.556383	-86.325133	8/1/2004	No Scale

OCEANA	78	43.582533	-86.338017	8/1/2004	No Beech
OCEANA	79	43.609783	-86.338317	8/1/2004	No Scale
OCEANA	80	43.659217	-86.326200	8/1/2004	No Scale
OCEANA	81	43.702417	-86.337350	8/1/2004	No Beech
OCEANA	82	43.698367	-86.416683	8/1/2004	No Beech
OCEANA	83	43.797900	-86.338183	8/1/2004	No Scale
OCEANA	87	43.802183	-86.393483	8/2/2004	No Beech
OCEANA	126	43.737517	-86.186550	8/5/2004	No Scale
OCEANA	128	43.679733	-86.412667	5/17/2005	No Scale
OCEANA	129	43.659083	-86.369417	5/17/2005	No Scale
OCEANA	145	43.485400	-86.359483	5/25/2005	No Beech
OCEANA	146	43.530633	-86.439467	5/25/2005	No Beech
OCEANA	147	43.534833	-86.437717	5/25/2005	No Scale
OCEANA	148	43.543750	-86.358867	5/25/2005	No Scale
OCEANA	149	43.614967	-86.431067	5/25/2005	No Scale
OCEANA	150	43.614433	-86.468333	5/25/2005	No Scale
OCEANA	151	43.660750	-86.497083	5/25/2005	Trace
OCEANA	152	43.648967	-86.498067	5/25/2005	No Scale
OCEANA	153	43.664067	-86.482983	5/25/2005	Patchy
OCEANA	154	43.667633	-86.468100	5/25/2005	Whitewashed
OCEANA	155	43.696300	-86.454400	5/25/2005	No Scale
OCEANA	156	43.691500	-86.487450	5/25/2005	No Scale
OCEANA	157	43.733500	-86.471333	5/25/2005	No Beech
OCEANA	166	43.697233	-86.392767	5/26/2005	Patchy
OCEANA	167	43.495750	-86.371500	5/26/2005	No Scale
OCEANA	168	43.758817	-86.214267	5/31/2005	No Scale
OCEANA	169	43.772133	-86.128567	5/31/2005	No Scale
OCEANA	170	43.802700	-86.087133	5/31/2005	No Scale
OCEANA	507	43.816483	-86.358533	6/6/2005	Trace
OCEANA	508	43.798433	-86.298167	6/6/2005	No Beech
OCEANA	509	43.787700	-86.292217	6/6/2005	Trace
OCEANA	510	43.817533	-86.268883	6/6/2005	No Scale
OCEANA	515	43.790667	-86.174950	6/6/2005	No Scale
OCEANA	516	43.793433	-86.244883	6/6/2005	Trace
OCEANA	1017	43.648180	-86.519170	5/10/2006	Patchy
OCEANA	1018	43.630133	-86.331450	5/10/2006	Trace
OCEANA	1019	43.614733	-86.278200	5/10/2006	Patchy
OCEANA	1020	43.599817	-86.266383	5/10/2006	No Scale
OCEANA	1021	43.620633	-86.178800	5/10/2006	Whitewashed
OCEANA	1022	43.672817	-86.139283	5/10/2006	No Scale
OCEANA	1040	43.731767	-86.167150	5/24/2006	No Scale
OCEANA	1041	43.625450	-86.126317	5/24/2006	No Scale
OCEANA	1042	43.587717	-86.153000	5/24/2006	No Scale
OCEANA	1043	43.532200	-86.113550	5/24/2006	No Scale
OCEANA	1202	43.545440	-86.452320	7/10/2006	Whitewashed
OCEANA	1203	43.543840	-86.358630	7/10/2006	Trace
OCEANA	1204	43.509870	-86.357320	7/10/2006	No Scale
OCEANA	1205	43.614470	-86.468380	7/10/2006	No Scale

OCEANA	1206	43.648730	-86.497970	7/10/2006	Trace
OCEANA	1207	43.768710	-86.374470	7/10/2006	Trace
OCEANA	1208	43.797430	-86.338240	7/10/2006	No Scale
OCEANA	1209	43.790370	-86.175200	7/10/2006	No Scale
OCEANA	1210	43.790920	-86.178850	7/10/2006	Trace
OCEANA	839	43.617150	-86.408417	8/8/2005	No Scale
OCEANA	840	43.645667	-86.382683	8/8/2005	No Scale
OCEANA	845	43.541583	-86.491550	8/8/2005	No Scale
OCEANA	844	43.548033	-86.427650	8/8/2005	No Scale
OCEANA	846	43.527300	-86.462733	8/8/2005	No Scale
OCEANA	843	43.584617	-86.377933	8/8/2005	No Scale
OCEANA	842	43.507517	-86.353517	8/9/2005	No Scale
OCEANA	841	43.797483	-86.338200	8/9/2005	No Scale
OGEMAW	704	44.445650	-84.146967	6/30/2005	No Scale
OGEMAW	706	44.272183	-84.307200	6/30/2005	No Scale
OGEMAW	1089	44.470100	-83.944933	5/30/2006	No Scale
OSCEOLA	676	44.148733	-85.324500	6/28/2005	No Scale
OSCEOLA	678	44.073417	-85.382483	6/28/2005	No Scale
OSCEOLA	680	44.110100	-85.187083	6/28/2005	No Scale
OSCEOLA	692	44.055817	-85.503083	6/29/2005	No Scale
OSCEOLA	1005	43.970617	-85.266183	5/8/2006	No Scale
OSCEOLA	1033	43.894750	-85.433833	5/23/2006	No Scale
OSCODA	555	44.536217	-84.356017	6/13/2005	No Beech
OSCODA	1090	44.706967	-84.217017	5/30/2006	No Scale
OSCODA	1091	44.616033	-84.129600	5/30/2006	No Scale
OSCODA	1092	44.632317	-83.941100	5/30/2006	No Beech
OSCODA	1094	44.754033	-84.060633	5/30/2006	No Scale
OTSEGO	556	44.939133	-84.599283	6/13/2005	No Scale
OTSEGO	557	44.971200	-84.447033	6/13/2005	No Scale
OTSEGO	558	45.015750	-84.590200	6/13/2005	No Scale
OTSEGO	560	44.880183	-84.677950	6/13/2005	No Scale
OTSEGO	606	44.958217	-84.706717	6/16/2005	No Scale
OTSEGO	608	44.921117	-84.776683	6/16/2005	No Scale
OTSEGO	610	44.888017	-84.787417	6/16/2005	No Scale
OTSEGO	620	45.113000	-84.816450	6/20/2005	No Scale
OTSEGO	622	45.027600	-84.755550	6/20/2005	No Scale
OTSEGO	624	45.099617	-84.699017	6/20/2005	No Scale
OTSEGO	626	45.061767	-84.623483	6/20/2005	No Scale
OTSEGO	670	45.159083	-84.512067	6/22/2005	No Scale
OTSEGO	672	45.156167	-84.417450	6/23/2005	No Scale
OTTAWA	1045	43.169117	-85.890017	5/25/2006	No Beech
OTTAWA	1060	43.001900	-86.184883	5/25/2006	No Scale
OTTAWA	1061	42.935450	-86.126383	5/25/2006	No Scale
OTTAWA	1062	42.875150	-86.178867	5/25/2006	No Scale
PRESQUE ISLE	687	45.435767	-84.224883	6/23/2005	No Scale
PRESQUE ISLE	689	45.356683	-84.152450	6/23/2005	No Scale
PRESQUE ISLE	1073	45.396183	-84.055283	5/29/2006	No Beech
PRESQUE ISLE	1074	45.413117	-83.886333	5/29/2006	No Scale

PRESQUE ISLE	1075	45.222533	-83.621933	5/29/2006	No Beech
PRESQUE ISLE	1076	45.260683	-83.483500	5/29/2006	No Scale
SCHOOLCRAFT	216	46.289850	-86.570883	8/12/2004	No Beech
SCHOOLCRAFT	217	46.279617	-86.542617	8/13/2004	No Scale
SCHOOLCRAFT	218	46.264900	-86.490883	8/13/2004	No Scale
SCHOOLCRAFT	220	46.346650	-86.353550	8/13/2004	No Beech
SCHOOLCRAFT	221	46.348167	-86.278450	8/15/2004	No Beech
SCHOOLCRAFT	222	46.502517	-86.271767	8/15/2004	Trace
SCHOOLCRAFT	223	46.428200	-86.361800	8/15/2004	No Scale
SCHOOLCRAFT	224	46.371683	-86.291417	8/15/2004	No Scale
SCHOOLCRAFT	225	46.345400	-86.104800	8/15/2004	No Beech
SCHOOLCRAFT	226	46.269600	-85.928233	8/15/2004	No Beech
SCHOOLCRAFT	228	46.277667	-86.259500	8/16/2004	No Scale
SCHOOLCRAFT	229	46.220583	-86.229933	8/16/2004	No Scale
SCHOOLCRAFT	230	46.154450	-86.198950	8/16/2004	No Beech
SCHOOLCRAFT	231	46.125150	-86.227983	8/16/2004	No Scale
SCHOOLCRAFT	232	46.070900	-86.262150	8/16/2004	No Beech
SCHOOLCRAFT	233	46.000583	-86.272083	8/16/2004	No Beech
SCHOOLCRAFT	234	45.979050	-86.188950	8/16/2004	No Scale
SCHOOLCRAFT	235	46.021483	-86.116183	8/16/2004	No Beech
SCHOOLCRAFT	236	46.043067	-86.082600	8/16/2004	No Scale
SCHOOLCRAFT	237	46.099800	-86.026350	8/16/2004	No Beech
SCHOOLCRAFT	238	46.160500	-86.001083	8/16/2004	No Beech
SCHOOLCRAFT	239	46.216017	-85.970667	8/17/2004	No Beech
SCHOOLCRAFT	240	46.241750	-85.944117	8/17/2004	Trace
SCHOOLCRAFT	245	46.185783	-85.928283	8/17/2004	No Scale
SCHOOLCRAFT	246	46.159350	-85.928250	8/17/2004	Trace
SCHOOLCRAFT	708	46.291750	-86.447750	7/5/2005	No Scale
SCHOOLCRAFT	710	46.068083	-86.468200	7/6/2005	No Scale
SCHOOLCRAFT	712	45.967133	-86.364000	7/6/2005	No Scale
SCHOOLCRAFT	720	45.840167	-86.368867	7/6/2005	No Scale
SCHOOLCRAFT	722	45.981267	-86.136433	7/6/2005	No Scale
SCHOOLCRAFT	724	46.071750	-86.058467	7/6/2005	No Scale
SCHOOLCRAFT	734	46.164983	-85.927850	7/12/2005	Patchy
SCHOOLCRAFT	771	46.459117	-86.170917	7/7/2005	Trace
SCHOOLCRAFT	773	46.419367	-86.157517	7/7/2005	No Scale
SCHOOLCRAFT	1175	46.428200	-86.361800	6/28/2006	No Scale
SCHOOLCRAFT	1176	46.502583	-86.271917	6/28/2006	Patchy
SCHOOLCRAFT	1177	46.502150	-86.272000	6/28/2006	Whitewashed
SCHOOLCRAFT	1178	46.461100	-86.261550	6/28/2006	Whitewashed
SCHOOLCRAFT	1179	46.426650	-86.083033	6/28/2006	No Beech
SCHOOLCRAFT	1260	46.413700	-86.146800	7/25/2006	Whitewashed
SCHOOLCRAFT	1261	46.419483	-86.157633	7/25/2006	Dead/Declining
SCHOOLCRAFT	1262	46.371600	-86.291317	7/26/2006	No Scale
SCHOOLCRAFT	1263	46.371817	-86.291400	7/26/2006	Trace
SCHOOLCRAFT	1264	46.277500	-86.260050	7/26/2006	No Scale
SCHOOLCRAFT	1265	46.220633	-86.229783	7/26/2006	No Scale
SCHOOLCRAFT	1266	46.125200	-86.227967	7/26/2006	No Scale

SCHOOLCRAFT	1267	45.966150	-86.363650	7/26/2006	No Scale
SCHOOLCRAFT	1268	45.981917	-86.136200	7/26/2006	Dead/Declining
SCHOOLCRAFT	1269	46.071700	-86.058217	7/26/2006	No Scale
TUSCOLA	1195	43.459900	-83.365883	7/6/2006	No Beech
VAN BUREN	836	42.330550	-86.304533	8/8/2005	No Scale
VAN BUREN	837	42.337033	-86.306933	8/8/2005	No Scale
VAN BUREN	1189	42.298383	-85.790067	7/5/2006	No Scale
WAYNE	1200	42.431667	-83.519750	7/7/2006	No Scale
WEXFORD	115	44.201217	-85.799050	8/4/2004	No Scale
WEXFORD	117	44.325033	-85.820250	8/4/2004	No Beech
WEXFORD	565	44.497133	-85.608100	6/14/2005	No Scale
WEXFORD	674	44.251800	-85.359633	6/28/2005	No Scale
WEXFORD	682	44.217867	-85.500717	6/29/2005	No Scale
WEXFORD	684	44.222467	-85.603867	6/29/2005	No Scale
WEXFORD	686	44.246383	-85.703717	6/29/2005	No Scale
WEXFORD	688	44.185600	-85.708067	6/29/2005	No Scale
WEXFORD	694	44.265800	-85.608917	6/29/2005	No Scale
WEXFORD	696	44.275883	-85.619667	6/29/2005	No Scale
WEXFORD	698	44.280733	-85.640267	6/29/2005	Trace
WEXFORD	700	44.284083	-85.641467	6/29/2005	Trace
WEXFORD	701	44.330483	-85.407133	6/28/2005	No Scale
WEXFORD	702	44.329100	-85.609867	6/29/2005	Trace
WEXFORD	703	44.453983	-85.412083	6/28/2005	No Scale
WEXFORD	705	44.425150	-85.373317	6/28/2005	No Scale
WEXFORD	711	44.260150	-85.336167	6/28/2005	No Scale
WEXFORD	723	44.303517	-85.489400	6/29/2005	No Scale
WEXFORD	725	44.378150	-85.536033	6/29/2005	No Scale
WEXFORD	727	44.406550	-85.619117	6/29/2005	No Scale
WEXFORD	729	44.443583	-85.697483	6/29/2005	No Scale
WEXFORD	731	44.469067	-85.771000	6/29/2005	No Scale
WEXFORD	733	44.352517	-85.738767	6/29/2005	No Scale
WEXFORD	735	44.251467	-85.660950	6/29/2005	Patchy
WEXFORD	737	44.251150	-85.699667	6/29/2005	No Scale
WEXFORD	739	44.251667	-85.644567	6/29/2005	No Scale
WEXFORD	813	44.208817	-85.604567	7/25/2005	No Scale
WEXFORD	815	44.202800	-85.657533	7/25/2005	No Scale
WEXFORD	817	44.206000	-85.640500	7/25/2005	No Scale
WEXFORD	819	44.237000	-85.623267	7/25/2005	No Scale
WEXFORD	821	44.240417	-85.647800	7/25/2005	Whitewashed
WEXFORD	823	44.277217	-85.707467	7/25/2005	No Scale
WEXFORD	825	44.343967	-85.675917	7/25/2005	No Scale
WEXFORD	827	44.344133	-85.675583	7/25/2005	Trace
WEXFORD	829	44.381333	-85.616433	7/25/2005	No Scale
WEXFORD	831	44.353367	-85.567017	7/25/2005	No Scale
WEXFORD	833	44.303500	-85.559600	7/25/2005	No Scale
WEXFORD	835	44.222667	-85.609667	8/25/2005	Trace
WEXFORD	1006	44.246820	-85.703310	5/9/2006	No Scale
WEXFORD	1007	44.248100	-85.674600	5/9/2006	Trace

WEXFORD	1212	44.435813	-85.738550	7/11/2006	Trace
WEXFORD	1213	44.343350	-85.675340	7/11/2006	Whitewashed
WEXFORD	1214	44.309110	-85.559510	7/12/2006	No Scale
WEXFORD	1215	44.276000	-85.619530	7/12/2006	Trace
WEXFORD	1216	44.237180	-85.617080	7/12/2006	Trace
WEXFORD	1217	44.251660	-85.644580	7/12/2006	Patchy
WEXFORD	1218	44.254340	-85.622660	7/12/2006	Patchy
WEXFORD	1219	44.222590	-85.603540	7/12/2006	No Scale
WEXFORD	1220	44.208710	-85.604630	7/12/2006	No Scale
WEXFORD	1221	44.206550	-85.640520	7/12/2006	No Scale
WEXFORD	1222	44.202800	-85.657532	7/12/2006	No Scale
WEXFORD	1223	44.246270	-85.704010	7/12/2006	Trace
WEXFORD	1224	44.276990	-85.707470	7/12/2006	No Scale
WEXFORD	1225	44.248550	-85.687820	7/12/2006	Trace
WEXFORD	1227	44.351883	-85.706467	7/13/2006	No Scale
WEXFORD	1228	44.380867	-85.617183	7/13/2006	No Scale

Appendix B.

Parameter values and start points to obtain the lowest SSE for the four main models

LP SIMPLE satellite name “model coordinate” (year)

Cadillac FT4775 (2004)

Benzie CP4768 (2004)

Silver BC3159 (1997)

Ludington AO1103 (1989)

Spread Rate = 3 (1.5 km/year)

LP COMPLEX satellite name “model coordinate” (year)

Cadillac FT4775 (2004)

Benzie CP4769 (2004)

Silver BC3151 (1997)

Ludington AO1103 (1989)

Complex model parameter values for LP

Max move = 3 (1.5 km/year)

B = 1 (1.5 km/year)

D = 1.5 (1 km/year)

C = 2 (.75 km/year)

O = 1 (1.5 km/year)

Number of observations LP = 156

SSE LP simple diffusion model = 37

SSE LP land cover based model = 24

UP SIMPLE satellite name “model coordinate” (year)

Bass Lake GP1359 (1990)

Spread Rate = 8 (4 km/year)

UP COMPLEX satellite name “model coordinate” (year)

Bass Lake FW1338 (1990)

Complex model parameter values for UP

Spread rate = 10 (5 km/year)

B = 1 (5 km/year)

D = 2 (2.5 km/year)

C = 2 (2.5 km/year)

O = 6 (1 km/year)

Number of observations UP = 74

SSE UP simple diffusion model = 16

SSE LP land cover based model = 8

Appendix C. Description of Classes Used in the Michigan Statewide Map

This is an explanation of the values present in the Michigan statewide raster map, with the associated rules used to arrive at the class labels. Arabic numbers in bold type are those included in the map. Classification scheme should be viewed as a series of sequential if-then statements. Order counts. For example, consider a forest stand where 50% of the canopy is Aspen, 20% Maple, and 30% Pine. Because Aspen precedes Upland Mix in the decision rules, the forest types out as Aspen (413) rather than Mixed Deciduous (419).

Class numbers were chosen in part to be similar to existing MIRIS Land Cover labels and their decision rule sequence does not necessarily match the numeric order (for example class 110 follows class 122 in the decision rules).

Number in parentheses following classification name is the grid value in the raster map.

I Urban

Land areas greater than 10% man-made structures including paved and gravel roads and parking lots.

121 Airports (3)

Impervious land within airport grounds, including runways.

122 Road/Parking Lot (4)

Roads or parking lots.

123 High Intensity Urban (2)

Land area greater than 25% solid impervious cover made from man-made materials, other than airports, roads, or parking lots.

11 Low Intensity Urban (1)

Land area is greater than 10% and less than 25% man-made structures including paved and gravel roads and parking lots.

II Agricultural

Land intensely managed for vegetation production excluding forestry.

2111 Non-vegetated Farmland (5)

Land area tilled for crop production with less than 25% currently vegetated.

2112 Row crops (6)

Vegetation consists of annual crops planted in rows (e.g. corn, soybeans).

2113/212 Forage Crops/ Non-tilled herbaceous agriculture (7)

Vegetation used for fodder production (e.g. alfalfa, hay). Also includes land used for pasture, or non-tilled herbaceous agriculture.

- 222** Orchards/Vineyards/Nursery (9)
Woody trees not grown for Christmas trees.

UPLAND

Land not periodically flooded nor on hydric soils.

- III Upland Openland
Less than 25% of land area is covered by tree canopy, and greater than 25% of land area is vegetated.

- 350** Parks/Golf Courses (13)
Maintained for recreational purposes.

- 320/330** Upland Shrub/Low Density Trees (12)
The combination of woody shrubs and tree canopy (woody cover) covers more than 25% of the land area.

- 310** Herbaceous Openland (10)
Less than 25% of land area consists of woody cover.

- IV Upland Forest
Proportion of trees exceeds 25% of land area.

- A. Upland Deciduous Forest
Proportion of deciduous trees exceeds 60% of the canopy.

- 411** Northern Hardwood Association (14)
Combination of Maples, Beech, Basswood, White Ash, Cherry, Yellow Birch exceeds 60% of the canopy.

- 412** Oak Association (15)
Proportion of Oaks exceeds 60% of the canopy.

- 413** Aspen Association (16)
Proportion of Aspen exceeds 40% of the canopy.

- 414** Other Upland Deciduous (17)
Proportion of any other single species exceeds 60% of the canopy.

- 419** Mixed Upland Deciduous (18)
Proportion of deciduous trees exceeds 60% of the canopy.

B. Upland Coniferous Forest

421/422 Pines (19)

Proportion of pines exceeds 60% of the canopy.

423 Other Upland Conifers (20)

Proportion of non-pine upland conifers exceeds 60% of the canopy.

429 Mixed Upland Conifers (21)

Proportion of coniferous trees exceeds 60% of the canopy.

43 Upland Mixed Forest (22)

Mixed forest not falling into any other category. Proportion of conifers to deciduous ranges from 40%:60% to 60%:40%.

V. Water

50 Water (23)

Proportion of open water exceeds 75% of land area.

LOWLAND

Land is periodically flooded and/or on hydric soils.

VI. Lowland Forest

Proportion of trees exceeds 25% of land area.

611 Lowland Deciduous Forest (24)

Proportion of deciduous trees exceeds 60% of the canopy.

612 Lowland Coniferous Forest (25)

Proportion of coniferous trees exceeds 60% of the canopy.

613 Lowland Mixed Forest (26)

Mixed forest not falling into any other category. Proportion of conifers to deciduous ranges from 40%:60% to 60%:40%.

VII. Non-forested Wetlands

Proportion of trees is less than or equal to 25% of land area.

621 Floating Aquatic (27)

Proportion of floating aquatic vegetation exceeds 60% of non-water cover.

622 Lowland Shrub (28)

Proportion of lowland shrub exceeds 60% of non-water cover.

623 Emergent Wetland (29)

Proportion of emergent vegetation exceeds 60% of non-water cover.

629 Mixed Non-forest Wetland (30)

Non-forested wetlands not falling into any other category.

VIII **Bare/Sparsely Vegetated**
Land is less than 25% vegetated.

710 Sand/Soil (31)

Land cover is formed primarily of sand or bare soil.

720 Exposed Rock (32)

Land cover is formed of solid rock.

730 Mud Flats (33)

If periodically flooded.

790 Other Bare/Sparsely Vegetated (35)

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