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# Beech Bark Disease: Proceedings of the Beech Bark Disease Symposium

Saranac Lake, New York  
June 16 – 18, 2004



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**Beech Bark Disease:**  
**Proceedings of the Beech Bark Disease Symposium**

**Saranac Lake, New York**

**June 16 – 18, 2004**

**Edited by**

**Celia A. Evans and Jennifer A. Lucas**  
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## Foreword

Beech bark disease (BBD) has been in North America for over a century. It is a forest health problem that has received varying amounts of attention through the years, but it has not produced headlines like chestnut blight or gypsy moth, in large part because the species it attacks is not generally valued as highly as some others. In recent years, though, an increasing interest in invasive species in general has rekindled interest in BBD among a larger group of people.

Beech bark disease is one of the most dramatic introduced pest problems of eastern forests, causing significant and lasting changes in the composition of the forest, affecting wildlife, and resulting in significant economic losses with the commercial and recreational uses of the eastern forest. While we know more now about beech bark disease, there is yet much we need to know if we can hope to stop its spread throughout the remaining range of beech and to restore the species to its centerpiece role within the eastern deciduous forest.

The symposium from which these proceedings are drawn began as an idea from Dan Twardus, a forest health specialist with the USDA Forest Service, State and Private Forestry, Northeastern Area, who noted this opportunity. He secured funding to sponsor this, the first comprehensive review of the state of knowledge about BBD since a IUFRO Working Party Conference in 1982. The symposium had multiple purposes – to compile current knowledge, to introduce people working on similar aspects of the system in different geographic areas, and to generate information that could be used to develop a new research agenda.

Dan and I began by assembling a committee of people with interest and knowledge of the variety of aspects of BBD. That committee included Celia Evans, David Houston, Charles Canham, Matthew Ayres, Cynthia Ash, Martin Mackenzie, and Manfred Mielke as well as Dan and myself. We wanted to include in the symposium review papers addressing the breadth of the system – the ecology of the host and the disease organisms, the effects on other parts of the forest, approaches to recover from or control the problem, and management implications – plus extended discussions of each topic. We chose a format for the symposium that included two invited review presentations on each topic and an open poster session for anyone wanting to present individual studies to the group. Following the plenary discussions of all topics, the meeting broke into small groups to focus on knowledge gaps and research needs for each of the topics. The choice of the Hotel Saranac in Saranac Lake, NY, as the venue for the meeting was based on its location within the region affected by BBD and the availability of field sites, the ability of the facility to handle a meeting of the size we wanted, and the attractiveness of the area. A field day following the two days of formal presentations took the group to field research sites, where attendees saw areas with active BBD and other areas where it had affected the forest much less.

The symposium attracted nearly 100 registrants, exceeding the expectations of the planning committee. Discussions were lively, and the informal interactions were many. The papers that follow in these proceedings provide the record we sought of the current state of knowledge of BBD. The proceedings are organized by the six major topics of the symposium, and within each section are one or two summary papers based on the review presentations, short contributions from poster presenters, abstracts from those additional presenters who were not able to provide extended contributions, and a list of recommendations for additional work. It is our hope that these proceedings will be useful to further understanding of BBD, invasive species, and forested ecosystems.

Mark Twery  
February 2005

## Keynote Address

### BEECH BARK DISEASE: 1934 TO 2004: WHAT'S NEW SINCE EHRLICH?<sup>1</sup>

David R. Houston<sup>2</sup>

Some time in the mid-to-late 1800's, a ship from England arrived at the busy Canadian port of Halifax, N.S. On board was a consignment of plant material, including European beech (*Fagus sylvatica* L.) saplings, destined for the city's Public Gardens. These trees prospered in this northern city whose latitude and maritime climate were similar to those of England. Around 1890, some of the trees were found to be infested with the "felted beech coccus", *Cryptococcus fagi* Baerensprung.

Some 30 years later, large numbers of American beech (*F. grandifolia* Ehrl.) trees in forests around Halifax began dying of unknown cause, and in the late 1920's, John Ehrlich, a Canadian graduate student at Harvard, began a PhD study of the cause and consequence of the emerging problem. His work, published in 1934, (Ehrlich 1934) named the disease, described the causal insect/fungus complex, and laid the groundwork for nearly everything that has been learned since. Indeed, his research was so comprehensive that aside from the establishment of plots to monitor the disease, trials to control it using chemicals, and silvicultural attempts to slow its course or lessen its impact in forests, few critical examinations of or additions to his understanding of the disease system occurred in North America until the 1960's.

Ehrlich determined that the disease was caused by a complex of the felted beech coccus, (soon after named the "beech scale"), and a bark killing fungus of the genus *Nectria*. He provided experimental evidence that feeding by the scale predisposed bark to infection by the fungus. He did not name the fungus, but determined that it was closely related to *Nectria coccinea*. Ehrlich's framework for this complex can be stated as:

Beech + Beech scale + *Nectria* sp. = Beech bark disease

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<sup>1</sup>Expansion of a paper presented at the Beech Bark Disease Symposium, June 16-18, 2004, Saranac Lake, NY.

<sup>2</sup>Principal Plant Pathologist, USDA Forest Service, Northeastern Research Station, Retired.

So, at this conference on beech bark disease (BBD), convened approximately 120 years after the scale arrived on this continent, it seems appropriate to review the information that has been added to our understanding of this complex pathosystem in the 70 years since publication of Ehrlich's classic paper.

### The Forest/disease Relationship

Ehrlich's study focused on how disease incidence and severity were affected by such forest stand values as beech abundance, basal area, position on slope, degree of slope, aspect, and length of time affected, and by such tree traits as DBH, crown class, and the presence of stem mosses and lichens. In the Canadian forests he studied, overall 54% of the stems were beech; nearly all trees in diseased stands were infested and 89.6% (of 4,483 trees over 3 inches dbh) were infected by the fungus. He found that degree of infection was a more reliable indicator of disease severity than scale infestation because evidence of infection persisted while the presence of wax was ephemeral. The best index of disease effect was mortality at time of observation, and mortality was strongly correlated with length of time of infestation/infection. Thus, while mortality can begin soon after infection begins, it may extend over a period of years: ca 20% in 4 years, 50% in 10 years (climate and other differences being equal).

Definite positive correlations were found between percent beech with *Nectria* infection and percent beech in the stand, and with position on ridge and steepness of slope. Severity of infection was correlated with tree size; mortality (% of trees killed over 3 inches) with diameter, crown class and position on ridge (bigger trees were more severely infested, infected and killed; trees growing on steep slopes and near tops of ridges were more heavily infected and killed).

Ehrlich's research arena was constrained both spatially and temporally by the geographic extent of the then newly emerging epidemic. In the ensuing 70 years the disease complex has continued to affect the forests he studied, and also has spread to forests differing in climate, species composition and structure, and use history. However, its relatively slow rate of spread (compared to other exotic diseases such as chestnut blight and Dutch elm disease) has provided opportunities to

observe both long and short-term forest effects and responses. Of interest today are what long-term impacts on stand composition and structure have occurred, whether silvicultural treatments designed to minimize impacts have been effective, and if differences exist in either the course of the disease or its effects in forests to the west and south.

Dynamic changes in beech abundance have occurred throughout post-glacial time (Cogbill, these Proceedings). Consequently, it may be important when evaluating current disease impacts, to do so against the backdrop of pre-BBD fluxes in beech abundance and to consider the influence of other stand disturbance factors, past and present. The papers by Cogbill, Canham, and Latty, (these Proceedings) describe early beech populations in different geographic regions, and emphasize the need to understand how other stressors might augment the effects of the BBD causal agents.

Although the consequences of BBD are still developing, marked changes have occurred in forests long-affected. Shigo (1972) characterized three arbitrary temporal stages of the disease. The first two, the “advancing front”: areas recently invaded by beech scale where many large old trees support sparse populations, and the “killing front”: areas where high scale populations and severe *Nectria* infections are resulting in heavy tree mortality, would have been most familiar to Ehrlich. Less familiar to him, however, would have been the “aftermath zone”: areas where tree mortality has occurred in the past and which now possess a few large residual trees, and many stands of small trees—often of both seedling and root sprout origin (Shigo 1972; Houston 1975). As the trees in these stands develop in the presence of the causal complex, they often are rendered highly defective through the interactions of beech scale, *Nectria* fungi and, sometimes, another scale insect, *Xylococcus betulae* (Perg.) Morrison (Shigo 1962). Widespread mortality due to BBD is rare in the aftermath zone (Houston 1975). The aftermath zone is well developed in most of the beech forests of the Maritime Provinces and ME, in some forests of VT, NH, NY, and is developing in a few of the longest-affected forests of PA and WVA.

In terms of forest response and forest management considerations, the advancing and killing front temporal stages, which encompass the initial establishment and buildup of the causal complex and resultant high tree

mortality, comprise the “first phase” of the disease; the aftermath stage, where the now endemic populations of the causal organism complex cause accumulating defect in young, emerging stands, the “second phase” (Houston 1994a). A third temporal phase is now occurring in some longest-affected stands, especially those not subjected to recent harvesting disturbance. Here, severely affected trees, often in patches, lose vigor, slow in growth, and eventually succumb, survived by beech that are either less severely diseased or resistant, and by other species. Harvest operations in such stands can trigger anew the development of highly susceptible thicket stands (Houston 1975, 1994a).

From the foregoing, it is apparent that the options for managing a particular disease-affected beech forest will depend on the temporal phase of the disease. Dealing with current or impending high mortality in Phase I situations is little different now than in Ehrlich’s day, but managing the long-affected, highly defective, beech-dense aftermath stands has, in the interim, become ever more difficult as trees have become increasingly defective and slow-growing. Management approaches and harvesting systems have been proposed (e.g., Crosby and Bjorkbom 1958; Filip 1978; Mielke et al. 1986; Ostrofsky and McCormack 1986; Burns and Houston 1987; Ostrofsky and Houston 1989). Most of these approaches embrace the ultimate objective of increasing the proportion of disease resistant beech. In practice this has proven difficult, because American beech possesses a unique suite of ecological characteristics that renders it difficult to manipulate silviculturally. Together, these features (extreme shade tolerance, longevity, prolific seed production and aggressive root sprouting) insure that once established, beech as a species will survive and even increase with stand disturbance, and that its genes, including those for traits such as susceptibility, will be perpetuated.

The inability to effectively manage beech comprises a major stumbling block to managing the disease. Several papers and working group sessions at this symposium (these Proceedings) address the need for research on this problem. A number of studies have examined the relationship of forest stand composition and structure to BBD. In British beech plantations, trees 25 to 45 years old, growing on midslope, or downwind of old, large infested trees, often were the first affected (Parker 1975; Houston et al. 1979a, b). In North America, probability

of mortality was greatest among big trees of low vigor (Mize and Lea 1979). In Massachusetts and in New Hampshire, Twery (1983, 1984) found that mortality and defect attributable to BBD were significantly greater in stands dominated by hemlock (*Tsuga canadensis* (L.) Carr.). While BBD mortality resulted in a decrease in beech and yellow birch (*Betula alleghaniensis* Britton) and an increase in hemlock, understory composition (and consequently, that of the future forest) was little changed. In New York, harvesting of diseased or healthy beech often led to dense, nearly pure beech stands (Tierson et al. 1966). Studies now underway in the outbreak areas in Michigan (Storer et al. and Witter and Petrillo these Proceedings) and in the Great Smoky Mountains National Park promise to add to our understanding of disease effects in forests that may differ in origin and composition.

In aftermath forests in Maine, thickets largely of root sprout origin developed after death or salvage of mature overstory beech (Houston 1975). Root sprouting in beech results when roots are wounded by disturbances such as frost heaving, browsing, logging, exposure to light and higher temperatures (Maini and Horton 1966; Held 1983; Jones and Raynal 1986, 1988). Sprouts arise from adventitious buds that originate within callus tissues associated with wounds (Jones and Raynal 1986). Jones and Raynal (1987, 1988) found that fewer sprouts occurred around isolated low-vigor trees compared to high-vigor trees, and on roots that were wounded in the fall compared to those wounded in the spring. Houston (2001) monitored the initiation and development of root sprouts and the development of seedlings around (a) resistant and susceptible beech trees that were (b) cut or left standing in stands (c) either clearcut or partially cut in (d) winter or summer of 1991. By 1994, significantly more sprouts occurred around the resistant trees. Interactions occurred between the amount of root disturbance (triggering root sprouts) and the amount of light available for growth. Thus, more sprouts developed after clearcuts than after thinnings, and sprout growth was best around resistant trees left standing and poorest around susceptible trees that were cut. Summer clearcuts sharply reduced the number of existing seedlings and prevented “new recruits”. Seedling growth was related primarily to the amount of light received as a consequence of the harvests or disease-caused crown thinning.

The impact of BBD on the growth and survival of beech has been examined in both Europe and North America. In young (age 20–45 years) or old (age 100+ yrs) European beech plantations, BBD-caused mortality was highest in stands where trees were stressed by competition (Peace 1954; Parker 1980, 1983). In England and in France, the disease was most severe in dense, pure stands and during times of water shortage, especially on sites with excessively drained soils and on thin soils over chalk (Peace 1954; Lonsdale 1980a; Perrin 1983; Parker 1983). In Europe and in North America, thinning of stands only temporarily reduced scale populations and the course of the disease (Parker 1980, 1983; Perrin 1983; Crosby and Bjorkbom 1958).

In North America, several studies have documented the effects of the disease on growth of beech stands and individual trees. Runkle (1990) found a 25% reduction in beech basal area (6.7% annually) over an eight year period in aftermath stands in the Adirondacks. Surviving trees, whose growth rates about equaled that of other species and was greatest in stands with highest tree mortality, seemed to benefit from the disease-caused reduction in competition. Mize and Lea (1979) used remeasurement data (1954 to 1976) to gauge decline and mortality of individual beech trees in an Adirondack forest. Mortality beginning in 1967 was mainly of trees of large diameter and crown class. Measured trees declined in diameter growth by 26% from predisease to aftermath periods. Gavin and Peart (1993) compared the effects of disease on trees in old growth and second-growth stands in New Hampshire. In both stands significant growth declines occurred that were related to severity of infection and, for the second-growth stand, with levels of internal stem defect. Significant differences in growth between undiseased and severely infected trees occurred earlier in the old-growth stand. Gove and Houston (1996) used increment core data to compare the growth of matched pairs of susceptible and resistant trees of different crown classes in two locations in Maine. In the more southerly site (88-year series: 1900 to 1987), susceptible codominant trees grew significantly better than resistant ones until the late 1930's. Decline in growth of susceptible codominant trees became significant in 1941, while it didn't occur in intermediate crown class trees until 1975 (35 years later). In the more northerly site (80-year series: 1909 to 1990) there was only a six year difference in decline onset between the two crown classes. Growth patterns were similar to those

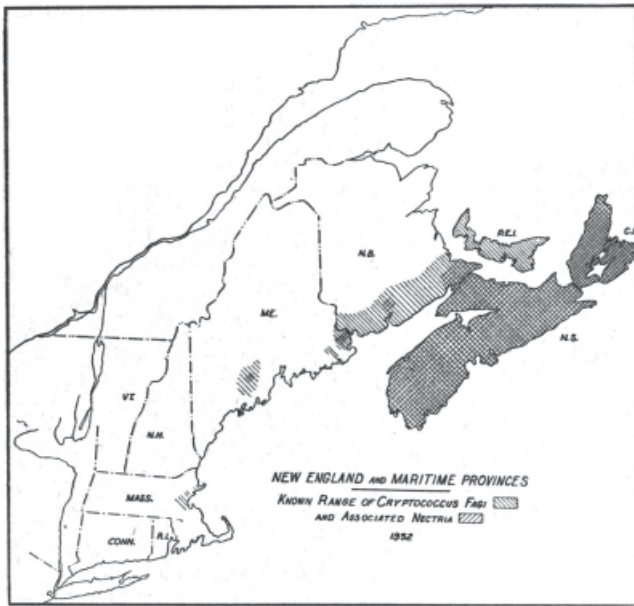


Figure 1.—The distribution of beech scale and *Nectria* as of 1932 (Ehrlich 1934).

in the southern site, with susceptible trees outgrowing their resistant counterparts until they began to decline in 1961 (21 years after onset of decline on the southern site). Differences in timing of decline onset and between the two crown classes probably reflected differences in climate, stand dynamics, and arrival time of the causal agents.

The importance of beech mast for wildlife especially for black bear (*Ursus americanus*) has been well documented (e.g., Beeman and Pelton 1980; Hugie 1982; Costello 1992; Schooley et al. 1994a, 1994b; Jakubas, these Proceedings). However, relatively little research has been done to determine the impacts of BBD on mast production. Costello (1992) monitored seed production on trees in different stages of disease and found that it dropped significantly only after trees became infected by *Nectria* sp. and had lost more than 25% of their crown. Very few beech nuts were produced by infected trees with crowns more than 25% dead. Using stand data from 1948, Costello calculated that by 1989, beech nut production decreased by 37%. The potential impacts of the disease on wildlife are discussed by Storer et al. (these Proceedings).

## The Causal Complex:

### 1) The Beech Scale Predisposer

Ehrlich (1932, 1934) described the insect in North America, and gave the historical account of its discovery

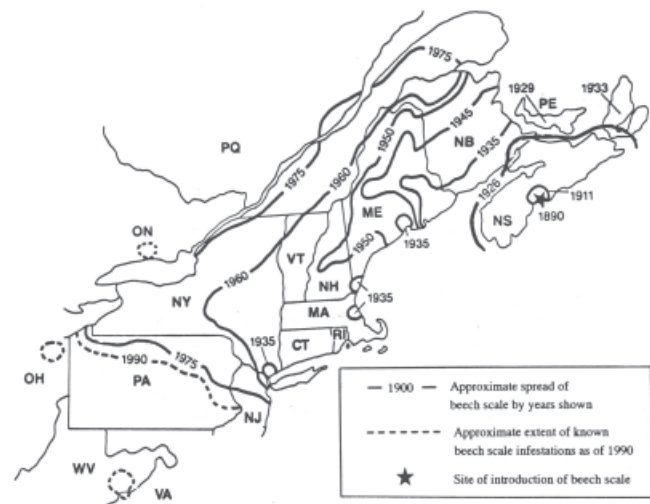


Figure 2.—Isopleths of years of discovery of the beech scale from 1890 to 1990 (Houston 1994a).

and description in Europe. Its distribution in North America as of 1932 was limited to the Maritime Provinces, and a few locations in Maine and Massachusetts (Fig.1). He described the insect's seasonal development patterns, and factors that influence its colonization of individual trees (bark fissures, figures, mosses, lichens, aspect, position within the stand), and he speculated that its buildup could be influenced adversely by cold temperatures and by biocontrol agents, especially the coccinellid beetle, *Chilocorus bivulnerus* Muls.

Ehrlich described the nature and physical effects of the insect's feeding and how the drying and cracking of bark near killed cells allowed penetration and invasion by fungi otherwise unable to successfully infect intact beech bark.

## Distribution

In the past 70 years, *C. fagisuga* Lindinger (as the scale is now named) has inexorably continued to spread west and south. Ehrlich's (1934) account of the insect's probable introduction to the Boston area around 1919, and records of its establishment near New York City by 1934, suggest that perhaps several separate introductions have occurred. Isopleths of discovery dates (Fig. 2) provide an approximation of the temporal—spatial movement. Imbedded in these now seemingly solid fronts are stands that earlier were outliers of infestation. The current

outbreaks in OH, MI, and NC/TN are examples, as once were those at Heart's Content Recreational Area on the Allegheny National Forest in PA and the Gaudineer Scenic Area on the Monongahela National Forest in WV.

Dispersal of the insect has been studied. Eggs, and especially crawlers, are transported passively in the airstream (Wainhouse 1980). The crawler's flattened shape reduces its terminal velocity facilitating its wind dispersal along a short-range steep gradient within stands. A small proportion of the population is wafted upward and is dispersed along a potentially long-range shallow gradient above the canopy (Wainhouse 1980). Infestation patterns within English beech plantations reflected both of these transport modes (Houston et al. 1979a). There is little doubt that the insect is also moved from place to place within stands by insects, mammals, and birds, and probably between stands and regions by birds and people. (See also, papers these Proceedings by Liebhold et al. that used kriging of forest inventory plot data to map the spread of BBD within the United States, and by Gardner, that used forest inventory plot data and range maps to model scale dispersal within a forest preserve in Eastern NY.)

Successful colonization depends on the genetic susceptibility of the trees, the nature and number of favorable spatial niches, and the host/insect/genetic relationship (Wainhouse and Deeble, 1980; Wainhouse and Howell 1983; Houston et al. 1979a). Although parthenogenetic, the scale apparently has some ability to adapt to the host it colonizes (Wainhouse and Howell 1983).

### Resistance

It has long been recognized that some beech trees remain either uninfested and free of signs of BBD or continuously support only low populations (Ehrlich 1934; Thomsen et al. 1949; Shigo 1962, 1964; Wainhouse and Howell 1983; Houston 1983a; Houston and Houston 1987; Houston et al. these Proceedings). European beech that can support only low populations possess bark anatomical features that act as barriers to infestation (layers of difficult-to-penetrate sclerophyll cells that are thicker, more continuous, and nearer to the bark surface than in susceptible trees) (Lonsdale 1983a). Although comparable studies have not been done in North America, similar anatomical barriers to infestation probably occur also in American beech. Resistant

American beech possesses bark that contains significantly less total and amino nitrogen than that of susceptible trees (Wargo 1988). Low amino nitrogen concentration is known to limit establishment and growth of sucking insects (Dadd and Mittler 1965).

The proportion of scale-free trees in American beech stands is very low, usually around 1% or less (e.g., Houston 1983a). In recent years studies have been made of the distribution patterns of such putatively resistant trees and of their genetic relationships. "Clean" trees are especially evident in some aftermath forests where their smooth, uncantered boles stand in sharp contrast to the highly defective stems of their susceptible neighbors. Resistant trees can occur as single individuals, but often they are in groups (Houston 1983). Challenge trials have shown them to be resistant to beech scale attack (Houston, 1982, 1983), a consequence, perhaps, of their significantly lower bark nitrogen content (Wargo 1988).

Higher bark nitrogen content of old-growth forest trees, (presumably the result of nitrogen saturation) compared to that of second-growth forest trees, was correlated with higher disease severity in stands in New York (Latty et al. 2003; Latty these Proceedings).

Isozyme analyses revealed that within groups of resistant trees, some individuals are genetically identical (i.e., clonal, derived from root sprouts), while others have unique isozyme "genotypes" (derived from seed) (Houston and Houston 1987). Unique trees within groups appear closely related and probably are half- or full-sib families (Houston and Houston 1987). Spatial patterns of the unique individuals within groups (Houston and Houston 1987) appear to reflect the beech nut caching patterns of eastern blue jays, *Cyanocitta cristata* (Johnson and Adkisson 1985; Johnson et al. 1987). Such patterns were often clearly displayed in the easily discerned groups of resistant trees in many aftermath forests (Houston 1983a; Houston and Houston 1987). The use of isozyme analysis was extended to compare population genetic structure in beech stands in P.E.I., N.S., ME, MA, and WVA where groups of resistant trees had been identified. Analyses showed that both susceptible and resistant beech trees in these stands were substructured into mosaics of putative clones and trees of seedling origin (Houston and Houston 1994). Although no unique genotypes for identifying resistant trees occurred among the 17 enzymes (with 9

polymorphic and 14 monomorphic loci) analyzed, resistant tree populations exhibited consistent heterozygote deficiencies (Houston and Houston 2000).

Genetic markers for resistance would greatly enhance efforts to determine modes of inheritance and, perhaps, to identify resistant forest trees in advance of the disease. The search for such markers using molecular level approaches is now underway, as are also trials to clarify modes of inheritance via cross-breeding resistant and susceptible individuals (see papers by Koch and Carey, these Proceedings).

One strategy to raise the proportion of resistant genotypes within a given stand includes augmentation using rooted cuttings or plantlets derived from resistant trees. Vegetative propagation of beech, as with other members of the Fagaceae, has proven difficult. Indeed, even though micropropagation techniques to derive plantlets from beech bud tissues have been developed (Barker et al. 1997), and some rooted cuttings have been obtained from root and stem tissues (Loo et al. these Proceedings), rooted beech plantlets have not been successfully overwintered. This problem remains a major hurdle for programs attempting to restore high quality American beech.

### Biocontrol

No insect parasites of *C. fagisuga* are known in Europe or North America despite repeated searches, including recent ones in Asia (Wainhouse and Gate 1988; R. Reardon, pers. comm.). A number of predators are known. The most common is the twice-stabbed lady beetle, *Chilocorus stigma* Say, (identified by Ehrlich as *C. bivulnerus*). Although both larvae and adults of this native coccinellid beetle prey on the sedentary life forms of *C. fagisuga*, its effectiveness is limited by its propensity to disperse following eclosion, its apparent failure to feed on the scale's crawler stage, pupal mortality, and high rates of host reproduction (Mayer and Allen 1983). Other coccinellids (*Exochomus* spp.) and a cecidomyid fly (*Lestidiplosis* sp.) are also common, and all are usually confined to trees with moderate to heavy scale populations (Wainhouse and Gate 1988). While predators have been shown effective in reducing scale populations on individual trees, their influence on the course of the disease is of little consequence.

The entomophagous fungus, *Verticillium lecanii* Viegas, was found to be associated with colonies of *C. fagisuga* in Great Britain (Lonsdale 1983b). Studies suggest that the spread of the fungus between insects on individual trees may depend on scale colonies increasing to levels where they coalesce. Observations and isolations suggest that the fungus, after reducing heavy scale populations, persists within the resultant isolated colonies and effectively maintains them at low levels (Lonsdale 1983).

Bark epiphytes including mosses and foliose lichens provide favorable habitats for establishment of *C. fagisuga* (Ehrlich 1934; Houston et al. 1979a). Not all lichens are favorable, however. On some steep, south-facing slopes in Nova Scotia, the stems of beech trees remain remarkably free of beech scale and of defect caused by BBD compared to trees on other nearby sites. These 'clean' trees were heavily colonized by dense mosaics of compact crustose lichens—the majority of which have thalli that are thick, elevated above bark surfaces (epigenous), and have smooth surfaces that provide little spatial habitat for *C. fagisuga* (Houston 1983b). Conditions which favor development of these 'preclusive' lichen mosaics may include the relatively low level of lichen-damaging air pollution, and slow tree diameter growth, attributable to reduced moisture availability on the steep slopes, that may allow growth of lichen thalli to maintain complete coverage of the lower stems.

The bark-inhabiting fungal parasite, *Ascodichaena rugosa* Butin, attacks both *F. sylvatica* and *F. grandifolia* (Butin 1977). Studies in Great Britain showed that patches of *A. rugosa* stroma on beech trees supported far fewer colonies of beech scale than did stroma-free bark (Houston et al. 1979). Butin and Parameswaran (1980) studied the ultrastructure of *A. rugosa* and its effects on tree bark. Invasion by the fungus triggered cork cambium to produce thicker layers of cork periderm. Speer and Butin (1980) found that stylets of *C. fagisuga* could penetrate through thickened periderm to the bark parenchyma below, and except for cases where secondary periderms were formed, actually favored the insect. Stromatic patches of *A. rugosa* on *F. grandifolia* are less frequent, less continuous and less compact than on *F. sylvatica*, and the stroma, often thinned and fractured as stems increase in diameter, appears to constitute a favorable spatial niche for the scale.

## The Causal Complex: 2) The *Nectria* Pathogens

Ehrlich recognized that the fungus associated with BBD belonged to the *N. coccinea* group, but was different enough from those known from North America and Europe to be considered a variety. Lohman and Watson (1943) named it *Nectria coccinea* var. *faginata* Lohman, Watson and Ayers, and it was recently renamed *Neonectria coccinea* var. *faginata* (Rossman et al. 1999). (To avoid confusion in this paper, *Nectria* is used to designate the genus.) Studies of its population genetics revealed it to be more closely related to the *N. coccinea* spp. of Europe than of North America, and strongly suggest that it was introduced, probably about the same time as was the scale (Mahoney, et al. 2001). It is likely that isolates of *N. coccinea* var. *faginata* (Ncf) vary in pathogenicity as do those of *N. coccinea* var. *coccinea* (Pers.) Fries (Ncc) in Europe (Perrin 1979; Lonsdale 1980b). In addition, *Nectria galligena* Bres. (Ng), which only rarely infects healthy beech, was shown to readily infect beech scale-infested bark (Spaulding et al. 1936; Cotter and Blanchard 1981). In forests where beech scale is introduced ahead of Ncf, inoculum of Ng from non-beech hosts, if present, can infect scale-infested beech trees and cause “full blown” BBD (Mielke, et al 1982; Houston 1994a). When Ncf arrives on the scene, it eventually replaces Ng and becomes the dominant pathogen (Fig. 3) (Houston 1994b).

Another *Nectria* species, *Nectria ochroleuca* (Schwein.) Berk. (now named *Bionectria ochroleuca* (Schwein.) Schroers and Samuels (Rossman and Samuels 1999), was found associated with dead trees and dying, scale-infested trees in several stands in WV, PA, and in woodlots near Toronto, Ontario (Houston and Mahoney 1987). While sometimes found together with Ng, it was often the only *Nectria* present on dying trees. LaMadeleine (1973) frequently isolated the anamorph of this fungus, *Gliocladium roseum* (now named *Clonostachys rosea*) from the bark of chlorotic trees in the initial stages of the disease. Indeed, *G. roseum* was the most common fungus isolated from the few trees he sampled from stands in PA and NY where the killing front was in its early stages. The role of the fungus is unclear, as it was significantly less pathogenic than either Ncf or Ng when inoculated into dormant, scale-free beech logs. Further study is needed to determine if this *Nectria* species can successfully invade bark predisposed by scale attack (Houston and Mahoney 1987).

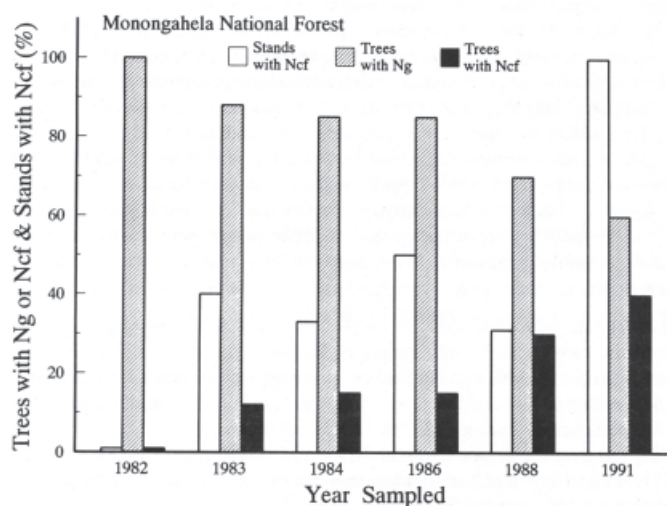


Figure 3.—The shift in percentage of stands and trees on the Monongahela National Forest, West Virginia, that yielded Ng or Ncf from 1982 to 1991 (Houston 1994a, b).

Many *Nectria* species and several other fungi are infected by the biotrophic contact mycoparasite, *Nematogonium ferrugineum* (Pers.) Hughes (*Gonatorrhodiella highlei* A. L. Smith) (Blyth 1949a,b; Gain and Barnett 1970). In North America, Ncf on beech and Ng on beech and other tree species are hosts (Ayers 1941; Ehrlich 1942; Houston 1983c). While parasitized isolates of Ncf and Ng produce fewer spores (Shigo 1964; Houston 1983c) and both species are rendered markedly less pathogenic (Houston 1983c), the effects on BBD development in individual trees or stands appear to be of little consequence.

### The Beech Scale-*Nectria* Relationship

Ehrlich demonstrated through exclusion and removal experiments that infestation immediately prior was required for infection by *Nectria* to occur. In Nova Scotia, infection usually occurred within 1 to 5 years after infestation and, while tree mortality resulting from bark death could occur as soon as 1 year after infection, it sometimes took many years for trees to die.

In Europe, Ehrlich's causal complex hypothesis was supported a decade later in a noteworthy study by Thomsen et al. (1949). In spite of what must have been harrowing times (1939-1943), these authors tracked an apparently unprecedented rise and decline of the beech scale and of BBD in Danish European beech plantations. Of interest here is that the associated *Nectria*, as determined by Wollenweber in Germany on the basis of

ascospore size (as we do today), was Ng. (Today, throughout Europe, the causal fungus is considered to be Ncc.) Slime fluxes, or exudates, “which disclose the disease” were, as today, considered non-specific, i.e., they can result when bark is killed by a variety of abiotic or biotic factors. The role of ambrosia beetles, notably *Xyloterus domesticus* L. and *Hylecoetus demestoides* L, as well as many decay fungi, were well described.

Other, more recent studies have reconfirmed the scale-fungus causal relationship. Perrin (1980) in France, and Lonsdale (1980b) in England, showed that wound inoculation of bark with Ncc caused cankers, the nature and size of which were related to the severity of *C. fagisuga* infestation. However, these studies also showed that infestation by *C. fagisuga* does not simply provide entrance courts for infection as Ehrlich hypothesized, but also lowers resistance to fungal invasion. Heavy scale infestation results in reduced growth and in restricted callus formation that favors rapid and unrestricted canker enlargement. In these inoculation trials, isolates of Ncc varied greatly in their virulence and trees varied in their susceptibility.

Yet, conclusive “proof” of this scale-*Nectria* interaction remains difficult to obtain or demonstrate. The conditions that either allow or limit infection and invasion by weakly pathogenic, facultative organisms may vary widely from place to place and from time to time (e.g., Houston 1992). Because such conditions are often difficult to identify, and impossible to reproduce, verification of the scale-*Nectria* relationship has depended in large part on careful observation of the timing and consequences of the organism association, and on experiments to clarify portions of the relationship. Many ‘variations on the theme’ have resulted—a consequence, perhaps, of studies being made at different times in forests of different ages, origins, disturbance histories, and stages of the disease (e.g., Houston et al. 1979b).

The temporal pattern of canker development (the beech/scale/*Nectria* interaction) was examined in two eastern Maine aftermath forests (Houston and Valentine 1987). Increased rates of cankering occurred over time, and year-to-year fluctuations in canker incidence were synchronous between trees and stands. Cankering was negatively correlated with October rainfall and the number of cold days (< 15 F) in December through March of the previous fall and winter. Low rates of

cankering presumably resulted from the adverse effects of these variables on the establishment and survival of *C. fagisuga* and/or the development of, or infection by, *Nectria* spp. Temperatures of -30 F (-34 C) are known to be lethal to *C. fagisuga* (Barter 1953). In Denmark, declines in scale populations were associated with unusually cold winter temperatures (Thomsen et al. 1949), and in France, low rainfall in October was followed by increases in scale populations the next year (Perrin 1979).

## Conclusion

It is clear that much knowledge has been gained in the 70 years since publication of Ehrlich’s paper about the beech scale-*Nectria* spp causal complex, as well as the beech host and the forests in which it grows. Yet, it is apparent also that much more information is needed if BBD is to be controlled at the forest level. The following list contains a few of the most obvious needs; many more items are identified in the papers and discussions that follow in these Proceedings.

### The host-causal complex relationship: the beech scale

1. Determine the nature of host resistance to beech scale. Confirm that low bark nitrogen content conveys resistance.
2. Explore the genetic mode of inheritance of resistance.
3. Identify genetic markers of resistance.
4. Continue the search for scale predators, especially in Eastern Europe and Asia.
5. Investigate the role, if any, of the entomophagous fungus, *Verticillium lecanii* in North America.

### The host-causal complex relationship: the *Nectria* fungi

6. Clarify the mechanisms by which the beech scale predisposes beech bark to infection by a seemingly congeneric fungal complex.
7. Clarify the role of *Nectria ochroleuca* in BBD, especially in early stages of the disease.

### The forest-disease relationship

8. Develop practical silvicultural approaches, with and without herbicides, to effectively manage

beech populations, and especially, to manipulate the initiation of root sprouts.

9. Develop protocols to vegetatively propagate resistant beech genotypes.
10. Develop protocols to introduce and establish resistant beech genotypes in a variety of forest situations.
11. Develop management systems to exploit existing resistant trees.

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## **Section 1:**

# **Ecology and Biogeography of Beech**

## HISTORICAL BIOGEOGRAPHY OF AMERICAN BEECH

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### Abstract

American beech (*Fagus grandifolia*), now a centerpiece species of the eastern deciduous forest, has had a continually changing historical biogeography. This paper reviews the paleoecology, the presettlement occurrence, the modern range, and the current abundance pattern of beech. It synthesizes these four databases into maps representing the distribution and abundance of beech at specific periods from glacial maximum to the present. The post-glacial history of beech is a consistent broad northward expansion from refugia in the deep South. Beech reached its modern Canadian limits about 7,000 years ago and flourished with remarkable dominance south of the Great Lakes (regional >20% pollen) until 3,000 years ago. The contrast between presettlement (>35% witness trees) and modern beech abundance (<15% basal area) in the Northeast is just part of the regionally declining trend of beech dominance that began 2,000 years ago. The maxima of paleoecological representation, presettlement density, and current abundance are all centered in northern Pennsylvania and align in an broad axis of beech importance reaching northeast into Canada. The beech range has sharply defined boundaries and scattered southern and western populations are usually associated with riparian zones or on sheltered mesic slopes. The new distribution map extends the modern range more than 140 km north and identifies distinct outliers not found in the former mapped range. This detailed historical and geographic baseline of beech forests before it was affected by beech bark disease forms an important quantification of range, composition, and structure of beech that should be used to assess the effects of natural, land use, and new disturbances.

### Introduction

American beech (*Fagus grandifolia* Ehrh.) is currently a central component of the eastern deciduous forest. Beech has great shade tolerance and is moderately long-lived and is thus, together with sugar maple (*Acer saccharum* Marsh), the archetypical dominant in the so-called climax “northern hardwood forest” (Tubbs and Houston,

1990). According to E. Lucy Braun’s (1950) classic treatise, the deciduous forests of eastern North America are the product of differential post-glacial migration and filtering of forest composition from an original southern refugium of the last glacial maximum. Significantly, beech is widespread in all nine of Braun’s (1950) forest regions, a characteristic species for four regions, including the residual mixed mesophytic core. It is also the dominant in two regions lying to the north, including the namesake beech-maple region. Furthermore, this species is a prominent component in most exemplary stands in the Northeast, and well represented in many old growth models, including the larger landscape tracts of the Great Smoky Mountains NC/TN, Five Ponds, NY, and Big Reed, ME (Whittaker, 1956; Roman, 1980; Cogbill 1996). Therefore, beech is unquestionably pivotal to both the theoretical development of the eastern hardwood forests and the empirical composition and dynamics of reference sites from Nova Scotia to Texas (Schafale and Harcombe, 1982; Greenridge, 1987; Peters, 1997). This preeminence extends to the role of beech in many realms of research: post-glacial migration and dispersal of tree species (Davis, 1983; Dexter et al., 1987); gap dynamics and hardwood regeneration processes (Forcier 1975; Woods, 1984; Runkle, 1981); and, how to conserve natural areas and significant animal habitat (Hunter, 1990; Davis, 1996). Interestingly, despite its current abundance, Siccama (1963) has observed that, at least in Vermont, beech was dramatically more abundant 200 years ago than it is today. This decline of beech is apparently not the purposeful result of land use activities (the Siccama enigma) and predates recent beech bark disease (Houston, 1975, 1994).

### Postglacial Distribution and Abundance

The past range and abundance of beech is based on a collection of over 750 dated pollen cores from across eastern North America (Williams et al., 2004). Numerous summaries of beech pollen percentages from 24,000 years ago (radiocarbon dates corrected to calendar years) to the present are published, but various interpretations of the inferred pattern of tree abundance are conflicting (Davis and Webb, 1975; Lenk, 1982; Davis, 1983; Bennett, 1985, 1988; Davis et al., 1986; Delcourt and Delcourt, 1987; Webb, 1987; Dexter et al., 1987; Jackson et al., 2000; Williams et al., 2004) To establish an approximate range limit, a threshold beech pollen percentage that balances the ambiguity of

occasional pollen transported long distances—pollen without local presence—and limited collection efficiency from restricted populations—local presence without pollen,. must be determined. Here a 0.5% threshold is invoked as a useful indicator (Davis et al., 1991). In addition, beech pollen is under-represented relative to tree density, but is only crudely equivalent to half of the regional proportion of trees (Davis et al., 1991). Thus, detailed reconstructions of the timing of migration and associated patterns of abundance of this tree species are still somewhat speculative (McLauchlan and Clark, 2004). This paper synthesizes various studies and reconsiders pollen profiles from specific sites, independently mapping the approximate range limit and relative regional abundance of beech at past intervals.

The post-glacial history of beech is clearly that of a consistent northward expansion (Fig. 1) with two major periods of flourishing and then associated declines. In summary, between 24,000 and 17,000 years ago beech was present at low levels, presumably in very localized populations, in the extreme Southeast (Delcourt and Delcourt, 1987). These southern refugia expanded rapidly, reaching a maximum of over 10% pollen across the southeastern Coastal Plain and Interior Plateaus by 14,000 years ago (Williams et al 2004). Interestingly, there was a single site in north central Pennsylvania which had possibly 15,000 year old beech pollen, indicating either rapid migration or early establishment well beyond the general range (Cotter and Crowl, 1981). The Southeast beech maximum faded from 11,000 to 8,000 years ago, but was accompanied by the continued northward spread of beech. The migration was on a broad front averaging roughly 85 m/yr (sustained 4 km per reproduction). This movement was perhaps accelerated by long-distance establishment of outliers (e.g. the jump across Lake Michigan 7,000 years ago), presumably mediated by dispersers such as passenger pigeons or blue jays (Webb, 1986; Davis et al., 1991). The present northern limits were nearly approached across Quebec as early as 7,000 years ago (Bennett, 1988). A second historic pollen maximum centered around the Great Lakes was well established 7,000 years ago and rose to more than 20% pollen at 3,000 years ago (Williams et al., 2004). At the same time, the range expanded slowly into the Maritimes and across the Upper Peninsula of Michigan, perhaps decelerated by limited ability to invade established forests (Green, 1981;

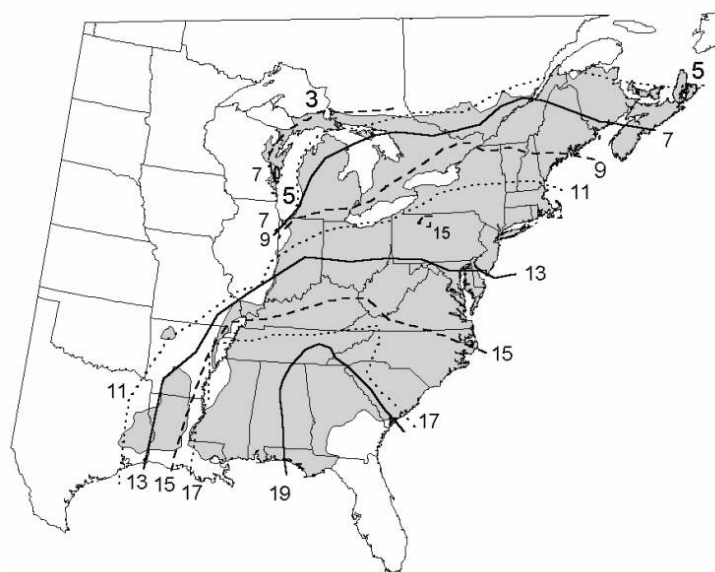


Figure 1.—Isochrones of the postglacial migration of the general northern distributional limit of beech in eastern North America. The numbers at the ends of the lines are the age in thousands of calendar years ago (Ka) inferred from pollen studies. The shaded area mapped is the resultant modern (0 yr) range of beech.

Bennett, 1987; Davis et al., 1991). Starting 2,000 years ago, the widespread maximum over the Northeast dramatically shrank and lessened. By roughly the time of presettlement 500 years ago only a small restricted area of more than 10% pollen remained just south of the Lake Erie. Current pollen show the continued decline of beech to less than 5% throughout its range and only scattered remnant traces in the South (Williams et al., 2004).

## Presettlement Composition

A quantitative assessment of the beech abundance unaltered by land use is based on land surveys done in anticipation of European settlement (Cogbill et al., 2002). An interpolated grid of the proportion of witness trees in 710 towns of New England and New York maps the frequency of beech in the unsettled forests (Fig. 2). In ca. 1800, beech was ubiquitous and common in the forests of the Northeast. It was found in samples from 97% of the towns and averaged 27% of the sampled trees across the northern hardwood region. Beech was only a minor component in the warmer and drier conditions south of the dramatic “tension zone” running across southern New England and northern Pennsylvania (Cogbill et al., 2002). The incredible beech dominance, first noted by Siccama (1963, 1971), is seen in a broad swath with greater than 35% proportion of beech trees from the Allegheny Plateau of Pennsylvania to mountains of northern New Hampshire. Within this zonal belt,

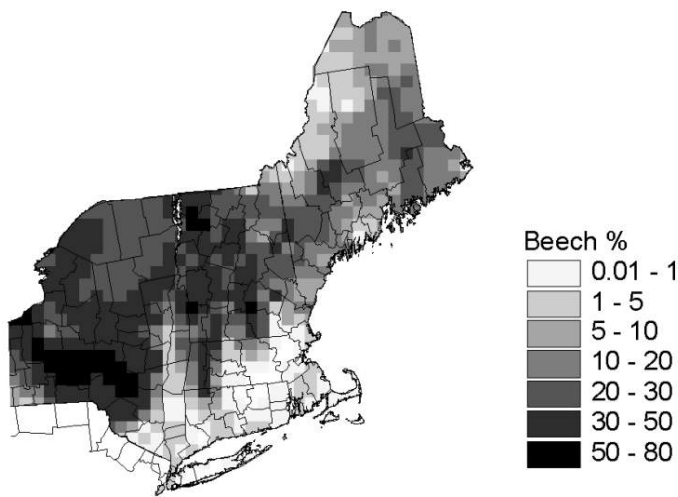


Figure 2.—Presettlement (ca. 1800) relative abundance of beech in the forests of New England and New York. Percentages are the interpolated grid proportions of beech based on witness trees cited in town-wide land surveys (Cogbill, unpublished data).

there were significant maxima in the hill country of the Green Mountains, the Catskills, and reaching a maximum abundance of 73% in west-central New York. This pattern from the presettlement tree records is reflected in the pollen record of 500 years ago with 5 to 10% beech pollen composition occurring in a zone through the mountains of the Northeast. Significantly the presettlement period pollen maximum area just south of the Great Lakes, matches the position of the presettlement tree maximum.

### Modern Range

The map of beech's current geographic distribution is compiled from actual trees clearly documented in numerous land, forest, floristic, and ecological surveys. The modern range of beech is mapped as a contiguous region within which beech commonly occurs, albeit sometimes in low abundance and only on scattered sites. In addition, disjunct outliers are included where a specific beech population is restricted to a particular, often unusual, location. This new map refines the distribution map of Little's (1971) classic atlas and is brought up-to-date by incorporating recently available data. A particular advancement is the clear delimiting of the northern edge of the range, which Little based on secondary sources and was broadly generalized (Little, 1971; Farrar, 1995). The new Canadian distribution is based on observations from over 17,000 forest inventory plots in Québec (Ministère des Ressources naturelles, de

la Faune et des Parcs, Direction des inventaires forestiers, Ste.-Foy, Québec, unpublished data), some 160 insect disease plots from Ontario (Canadian Forest Service, Sault-Ste.-Marie, ON, unpublished data), and floristic and ecological surveys from Ontario to New Brunswick (e.g. Rousseau, 1974; Lenk, 1983; McMahon et al., 1990; Maycock, 1994; Hinds, 2002). Details of the distribution in the Midwest of the United States are derived from presettlement forest surveys, herbarium collections, and natural history narratives (e.g., Davis et al. 1991; Iverson et al., 1999; Greenberg, 2002; Cofrin Center for Biodiversity, 2004; Missouri Botanical Garden, 2004). Changes in Little's map at the southern and western limits reflect the fine scale distribution derived from thousands of FIA inventory plots (Forestry Inventory & Analysis, United States Forest Service), county floristic checklists, and data collected in a series of ecological natural areas (e.g. FIA summarized in Prasad and Iverson, 2003; Davis, 2003; USDA Plants Database, 2004).

Beech's modern distribution covers temperate eastern United States and southeastern Canada (Fig. 3). The only exception to the compact range are Mexican stations which are disjunct by 1000 km and have been recently treated as a distinct variety (*Fagus grandifolia* var. *mexicana* (Martinez) Little) of American beech (Little, 1965). Mexican beech grow in ten restricted and very small populations in the "mesophilous" cloud forest of the mountains eastern Mexico (Williams-Linera et al., 2003). Throughout its range, beech is found on most mesic sites which have escaped fire. Beech occurs from sea level along the Atlantic Ocean to the Gulf Coast and up to 2000 m elevation in the beech gaps of the southern Appalachian Mountains (Russell, 1953). The range of beech has a sharply defined northern boundary suggesting environmental limitation, perhaps cold hardiness. On the new distribution map (Fig. 3), beech extends northward some 140 km beyond the previously mapped range (cf. Little, 1971; Hosie, 1979; Tubbs and Houston, 1990; Flora of North America Editorial Committee, 1997) and there are a few isolated populations established up to 100 km beyond the continuous range. At the northern edge of the range, beech occurs under locally moderated temperature and moisture conditions up to about 800 m on mountain slopes. It is especially abundant on well drained soils in valley sides or on hardwood ridges. The western limit of the range appears to be tied to moisture availability, with a particularly strong fidelity to river bluffs. Intriguingly



Figure 3.—Map of the modern range of *Fagus grandifolia* in eastern North America. The shaded area is the region of relatively continuous distribution of multiple populations. The dots are restricted documented outliers populations. The outlines are states of the United States, provinces of Canada and Mexico. General range is based on Little (1971) with major modifications and refinements based on various field surveys.

rivers seemingly form a hard edge to beech distribution as the range barely crosses west of the Wabash, the Mississippi (including its former channel west of Crowley's Ridge), or the Yazoo Rivers. To the southwest, the limit to the distribution is more extended, with several diffuse patches and scattered outlier populations well beyond the Mississippi River. Populations approaching the western and southern limits are usually associated with riparian zones or on sheltered mesic slopes, such as "coves". For example, beech is found in ravines around Chicago (IL), in hollows on Crowley's Ridge (AR & MO), on loess bluffs along the lower Mississippi Embayment (LA, MS, & TN), on valley floodplains (i.e. along Buffalo and Osage Rivers) within the Ozarks (AR & MO), in creek bottomlands of the Big Thicket (TX), and in hammocks (islands of isolated hardwood in bottoms) on the southern pine flatwoods (FL & GA).

### Current Abundance

Beech's modern compositional importance across its United States range is most easily documented by the Forest Inventory and Analysis (FIA) program of the

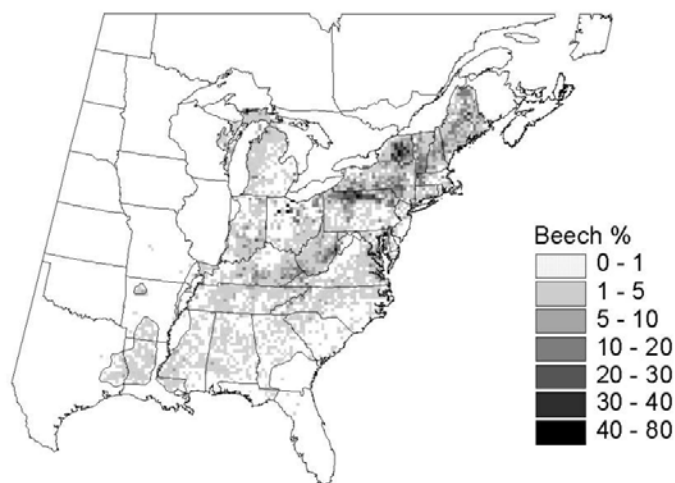


Figure 4.—Modern relative abundance of beech in the forests eastern North America. Grid map is interpolated from Forest Inventory and Analysis (FIA) plot data and adapted from Prasad and Iverson (2003). States are indicated and the additional thin line outlines the general contiguous range of beech from this study.

United States Forest Service. Averaging data from over 100,000 FIA sample plots, Prasad and Iverson (2003) have compiled a grid map of the geographic distribution of the beech's proportion of forest composition (Fig. 4). Beech averages 2.3% of the total forest basal area within its range, but the distribution across the landscape varies from less than 1% over much of the South and Midwest to being the dominant in widespread regions of the Northeast. There is a broad maximum of beech tree abundance scattered along the Appalachian Mountains from Kentucky to Maine (FIA average 11.1%), with local centers of greater than 20% (maximum 51%) beech landscape abundance in the Adirondacks (NY), northern Allegheny Plateau (PA) and central Allegheny Mountains (WV). Although Canadian forest inventory surveys have not yet been mapped, the 17.1% average beech forest proportion for its Quebec range indicates that the Northeast landscape maximum apparently continues through southern Canada almost to its northern range limit (Québec inventaires forestiers, unpublished data). This regional distribution is reiterated by modern pollen representation, in which beech pollen is found consistently, but predominantly at less than 5%, in an axis from the Great Lakes to Nova Scotia (Williams et al., 2004).

### Baseline Character

The modern geographic pattern of beech on the landscape is dependent on three major factors: its

**Table 1.—*Fagus grandifolia* abundance at the landscape and stand scales under different scenarios in reference sites in eastern North America.**

Item	Stands/ Plots (#)	Beech Constancy (%)	Total BA (m <sup>2</sup> /ha)	Beech BA (%)	Max. dbh (cm)	Mean dbh Dquad (cm)
Historic						
N. Hardwood region <sup>1</sup>	16	86	-	20	-	
Waterville, NH <sup>2</sup>	50ac	-	31.6	31	66	30.9
Tionesta, PA <sup>3</sup>	651	70	27.2	35	102	26.0
Modern outside BBD <sup>†</sup>						
Five Ponds, NY <sup>4</sup>	71	79	34.1	23	70	24.4
Joyce Kilmer, NC <sup>5</sup>	30	-	-	5	66	27.2
Walker Cove RNA <sup>§</sup> , NC <sup>6</sup>	18	100	33.3	18	60	26.6
Modern BBD <sup>†</sup> aftermath—no cutting						
Big Reed, ME <sup>7</sup>	88	89	32.4	12	60	20.9
Bowl RNA <sup>§</sup> , NH <sup>8</sup>	126	67	31.1	13	51	23.3
The Cape RNA <sup>§</sup> , VT <sup>7</sup>	28	93	28.5	2	45	19.9
Modern BBD <sup>†</sup> aftermath—managed						
Gifford Woods, VT <sup>7</sup>	21	76	38.2	4	61	23.0
Lords Hill, VT <sup>7</sup>	51	41	32.3	5	80	51.3
Hubbard Brook valley, NH <sup>9</sup>	431	67	29.2	11	72	24.4
Hubbard Brook W6, NH <sup>10</sup>	118	98	25.7	27	87	23.0

Sources: <sup>1</sup>Braun, 1950; <sup>2</sup>Chittenden, 1905; <sup>3</sup>Hough, 1936; <sup>4</sup>Roman, 1980; <sup>5</sup>Lorimer, 1980; <sup>6</sup>Dickison, 1980; <sup>7</sup>Cogbill, unpublished data; <sup>8</sup>Martin and Bailey, 1999; <sup>9</sup>Schwartz et al., 2003; <sup>10</sup>Hubbard Brook Long-term Ecological Research site, derived from data on <http://www.hubbardbrook.org>

<sup>†</sup>Beech Bark Disease

<sup>§</sup>Research Natural Area in National Forest

background, albeit naturally changing, regional abundance; the alterations due to centuries of land use (e.g. land clearance, agricultural regeneration, and forest management); and the recent effects of beech bark disease (BBD). The influence of these regimes on the structure of beech forests is potentially factored by historical and geographic grouping of ecological samples. In the region of current maximum beech importance, four groups of quantitative reference studies have been investigated: 1) sampled historically before local occurrence of BBD; 2) sites outside the influence of BBD; 3), unmanaged reference sites, but well after the effects of BBD or so-called aftermath forests; and 4) managed, but still primary aftermath forests (Table 1).

## Discussion

The history of beech is not a simple northern migration and attenuation of the deciduous zone after glacial retreat

(Braun, 1950). At glacial maximum beech was a minor species in the deep South and apparently associated with species (e.g. magnolia, oaks and pine) which are neither typical mixed mesophytic nor northern hardwoods (Delcourt and Delcourt, 1987). Later, beech migrated independently of other components of the eastern forest and was indeed a rather late northern arrival (Davis, 1983). In addition, beech has flourished twice in the past within its range, but both times its strong dominance has faded. Apparently, its abundance was not especially responsive to specific climate changes, and the movement of the range boundary appears independent of overall abundance within the range. Both the northern and western range distribution have distinct outliers which seem to be restricted to special environments, but are presumably relatively stable populations established long ago. Paleoecological and presettlement abundance records indicate that an ongoing long-term decline (but not

contraction) of beech in the Northeast began some 3,000 years ago. Interestingly, the current abundance maxima in northern Pennsylvania and in upstate New York seem to be the remainders of an even greater abundance of a late-Holocene center of beech around the Great Lakes. This regional decline has certainly been accelerated by land use after settlement, but many activities such as beech being a poor timber species and its tendency to sprout after disturbance may have slowed beech decline. Recent introduction of BBD, is only adding to the strong established trends already affecting beech populations.

The dramatic contrast between beech tree abundance in the presettlement landscape (widespread >35%) and modern abundance (only locally >20%) indicates that the Siccama enigma applies to much of the Northeast. An analysis of the geographic-specific ratio of the presettlement (Fig. 2) to the FIA modern composition (Fig. 4) indicates a typical fraction of only 30% remaining from the original presettlement beech density. Similarly, parallel data from Wisconsin indicate a beech decline from 27% in presettlement (Davis et al. 1991) to less than 5% today (FIA: Prasad and Iverson, 2003). The magnitude of the historic decline varies across the region ranging from severe in northern Vermont and central New York (beech less than 10% of presettlement values and a species switch in 40% of the composition) to little change in the Adirondacks or northern Pennsylvania. For example, at Five Ponds in the western Adirondacks a presettlement witness tree survey in 1815 indicate that the 29% beech trees had changed little to the present (35% in 1975, Roman, 1980; or 32% 1993 FIA. The only areas with any consistent increase in beech abundance over the last 200 years are south of the tension zone or at the northern extremes in Maine where initial beech abundance was relatively low.

A broad perspective on the baseline compositional, size, and age structure of the deciduous forest unconfounded by BBD is derived from old databases and remnant forest stands beyond BBD. Braun (1950) found beech in 63% of 300 plots sampled across the range before 1950, with beech comprising 21% and a maximum of 63% of the stems. Similarly, a sample of 54 modern northeastern “old-growth” deciduous forest stands average 15%, with a maximum of 53% beech basal area (Cogbill, unpublished

data). Regardless of its past history, northern hardwood landscapes tend to have beech found in 70 to 100% of the stands across sites and beech forms 5 and 25 % of the remarkably consistent 28 to 34 m<sup>2</sup>/ha basal area over all forested sites (Table 1). A typical beech tree is only about 25-30 cm in diameter and forest trees over 50 to 80 cm diameter seldom survive under any conditions. Although there are speculation of up to 700 year old trees, the greatest documented ring count in any American beech is only 412 years (northwest PA, Hough 1936). Significantly, even in “old-growth” stands trees over 250 years old are only occasionally recorded (Cogbill, unpublished data). The typical 0.66% to 1.25% annual natural mortality found in old deciduous forests infers an average longevity of 80 to 150 years for beech unaffected by BBD (Runkle, 2000). Thus canopy trees are seldom expected to survive more than 150 years, presumably due to individual tree death by wind, ice, or snowload. BBD causes direct mortality as well as a predisposition to environmental disturbances shortening beech’s lifespan. For example, at Lords Hill, VT some 59 beech trees followed from 1977 to 2004 display a 2.5% annual mortality indicating a 40 year turnover for beech (Cogbill, unpublished data). Despite the large size (80 cm) of remnant stems, this stand is rapidly transitioning to an aftermath forest, with reduced beech influence (Table 1). Although BBD may have accelerated beech decline the aftermath forest still maintains a sustainable forest structure albeit with an increase in smaller sprout (e.g. Siccama’s so-called “beech hell” at Hubbard Brook) compensating for fewer large canopy trees (Table 1).

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# THE COMPARATIVE ECOLOGY AND POPULATION DYNAMICS OF BEECH (*FAGUS GRANDIFOLIA* EHRH.) IN NORTHERN HARDWOOD FORESTS

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The American beech (*Fagus grandifolia* Ehrh.) is a late-successional canopy dominant in forests from Nova Scotia to east Texas. I will focus on the comparative ecology and population dynamics of beech in glaciated regions of the northeastern U.S., drawing heavily on 15 years of research on the dynamics of beech-dominated forests at Great Mountain Forest in southern New England. Our research has identified 3 major axes of niche differentiation in the distribution and abundance of beech relative to other common tree species in the region: light (as it relates to successional status and response to canopy disturbance), soil nutrient availability (particularly nitrogen and calcium availability relative to its close competitor sugar maple), and soil moisture availability (with beech as the most sensitive to drought stress of the 9 dominant species at our sites). On moist, acidic soils with low base saturation, beech is the overwhelming competitive dominant in late-successional stands. Canopy beech trees promote soil and forest floor conditions that favor regeneration by beech seedlings at the expense of competitors such as sugar maple and hemlock. Limited dispersal ability (of both sprouts and seeds) plays an important role in limiting competitive exclusion by beech of other tree species. Beech trees uninfected by beech bark disease (BBD) are highly resistant to wind damage, and all but the most severe wind disturbances generally accelerate succession and dominance by beech because of the high rates of survival of small beech trees and the response of often abundant advance regeneration.

**Section 2:**  
**Tree and Stand Level Factors and Ecosystem  
Consequences**

# EFFECTS OF BEECH BARK DISEASE ON TREES AND ECOSYSTEMS

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## Abstract

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

## Introduction

Beech bark disease is a complex composed of a scale insect and a fungal pathogen. This disease complex attacks both American beech (*Fagus grandifolia*) and

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

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

## Beech Scale Distribution and Abundance on Individual Trees

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

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

important to beech scale populations because they have a greater amount of bark surface area available for scales to colonize.

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

Many organisms in addition to beech scales may colonize a tree's bark. These other colonizers commonly include flora such as lichens, algae, and fungi, and fauna such as a variety of insects. The way in which beech scales are impacted by the presence of these other organisms is very variable. For instance, presence of the common crustose lichen *Lecanora conizaeoides* on trees in southern England increases survival of scale crawlers and leads to higher scale population build-up (Houston et al. 1979a). Algae colonizing beech bark also can protect scale crawlers, inducing increased scale population levels (Wainhouse and Gate 1988). On the other hand, in Nova Scotian forests the presence of the crustose lichen *Graphis scripta* has a negative effect on beech scale populations, greatly depressing scale colonization of trees and decreasing subsequent population growth on those trees (Houston 1983). In England, the presence of the fungus *Ascodichaena rugosa* on beech trees has been found to prevent scale establishment and population growth; further negative effects for scales may occur due to reduced presence of the scale-benefiting *L. conizaeoides* lichen when the *A. rugosa* fungus is densely present (Butin 1977, Houston et al. 1979a). Unlike some of the microflora colonizing bark, insects on the bark of beech trees have relatively little effect on beech scale populations. There are no insects that are known to parasitize beech scales. The most common predators on

beech scales are generalist beetles in the family *Coccinellidae* and a specialized fly genus in the family *Cecidomyiidae*. None of these predators are usually seen when scale populations are light. On trees with moderate to heavy scale populations, the various predators may build up higher levels. While heavy predation has occasionally been observed on individual trees, the insects often have relatively little effect on scale population levels overall in beech stands (Wainhouse and Gate 1988, Mayer and Allen 1983).

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

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

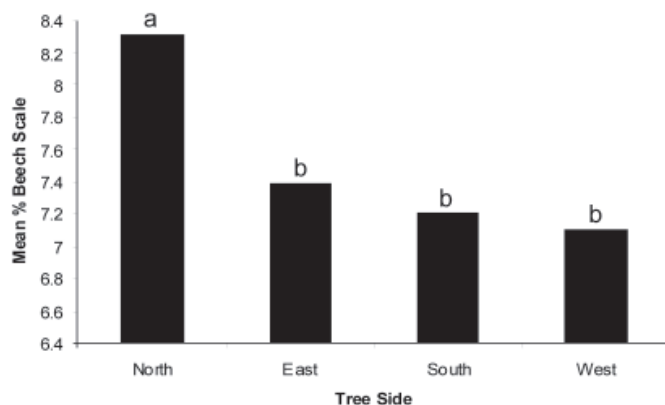


Figure 1.—Mean percent beech scale on different aspects of beech trees in low beech scale intensity stands. Different letters indicate mean values that are significantly different among tree sides.

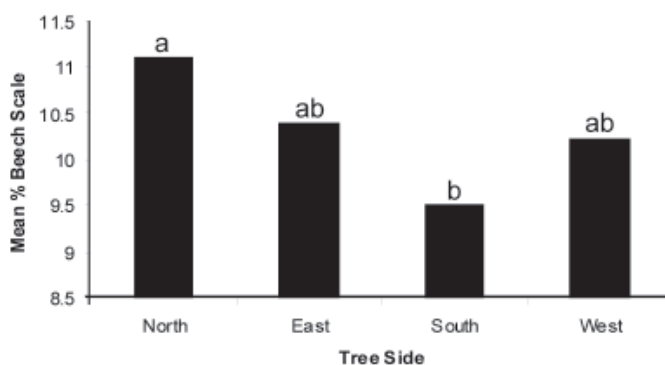


Figure 2.—Mean percent beech scale on different aspects of beech trees in low beech density stands. Different letters indicate mean values that are significantly different among tree sides.

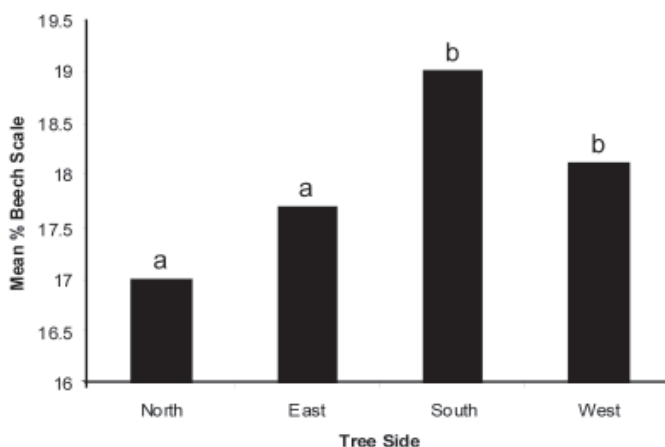


Figure 3.—Mean percent beech scale on different aspects of beech trees in high beech density stands. Different letters indicate mean values that are significantly different among tree sides.

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

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

## Disease Development and Subsequent Spread through the Ecosystem

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

tree infection and the beginning of tree death in the stand (Shigo 1964, Houston 1994).

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

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

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

Whether a given stand is likely to become infected and experience this three-stage mortality process is due to a number of factors. A key factor in determining infestation

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

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

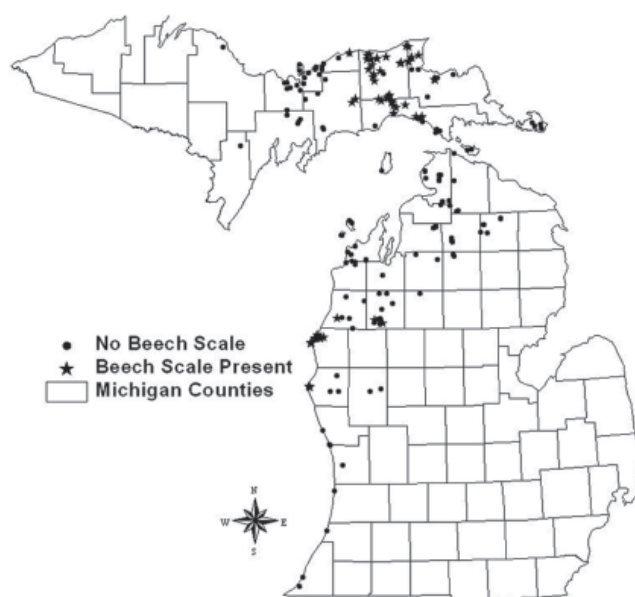


Figure 4.—Map location of plots in the Michigan Beech Bark Disease Monitoring and Impact Analysis System.

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

## Effects of Beech Bark Disease on Tree Health

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

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

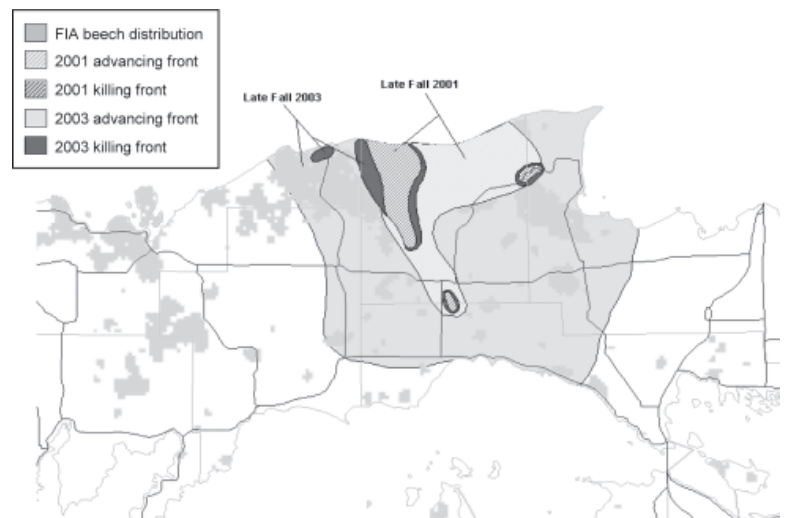


Figure 5.—Map showing beech distribution and the spread of beech bark disease in the Upper Peninsula of Michigan between 2001 and 2003.

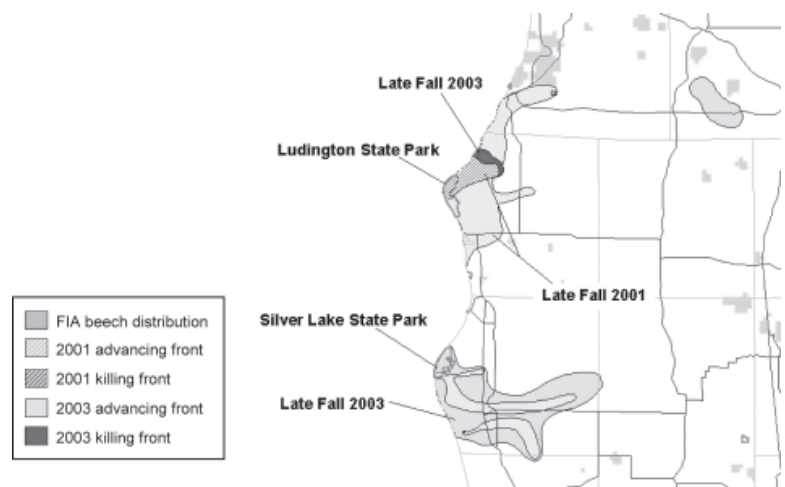


Figure 6.—Map showing beech distribution and the spread of beech bark disease in the Lower Peninsula of Michigan between 2001 and 2003.

trees and trees located in old-growth areas—both conditions that are typically associated with higher scale populations.

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

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

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

## Knowledge Gaps

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

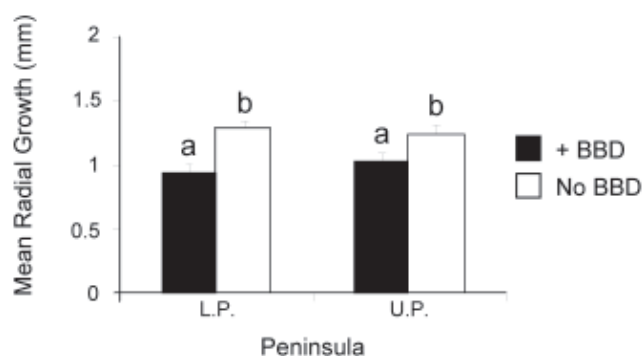


Figure 7.—Mean radial growth (mm) of beech trees in northern hardwood stands in the Lower Peninsula (L.P.) and Upper Peninsula (U.P.) of Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different among tree sides.

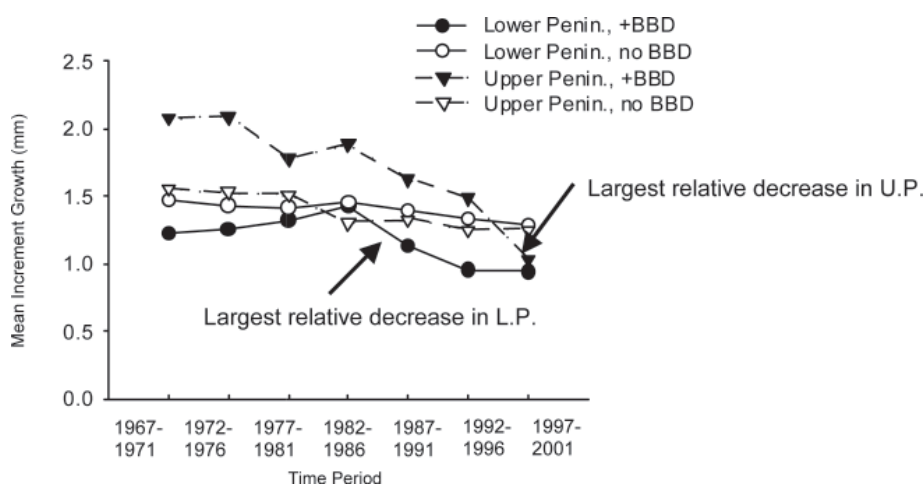


Figure 8.—Mean increment growth (mm) of beech trees in the Lower Peninsula (L.P.) and Upper Peninsula (U.P.) of Michigan with and without beech bark disease (BBD) present. Arrows point to the largest relative decrease within each Peninsula. Circles indicate northern hardwood stands in the L.P. and squares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

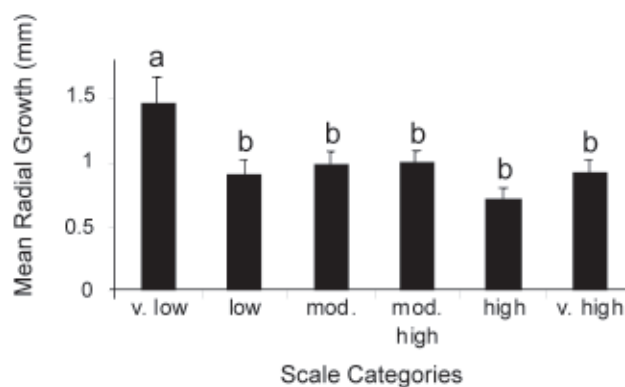


Figure 9.—Mean radial growth (mm) of beech trees in northern hardwood stands with different beech scale ratings. Bars indicate standard errors. Different letters indicate mean values that are significantly different among tree sides.

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

## Acknowledgments

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# STAND-LEVEL PATTERNS AND ECOSYSTEM CONSEQUENCES OF BEACH BARK DISEASE

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## Abstract

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

## Introduction

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

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

## Literature Review

### Disease Progression and Severity

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

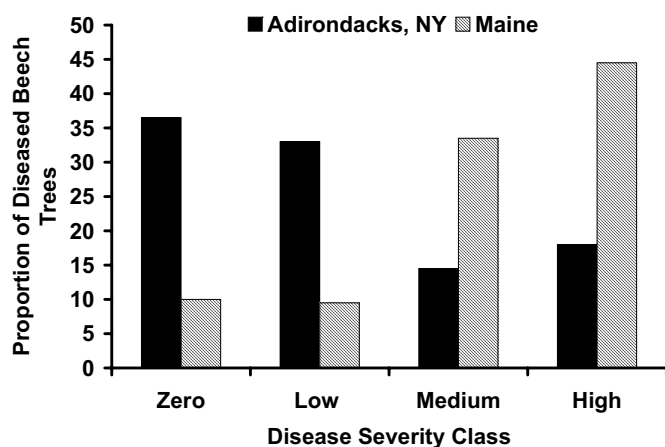


Figure 1.—Proportion of beech trees in four disease severity classes in New York and Maine. Source: Modified from Latty et al. 2003.

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

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

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

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

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

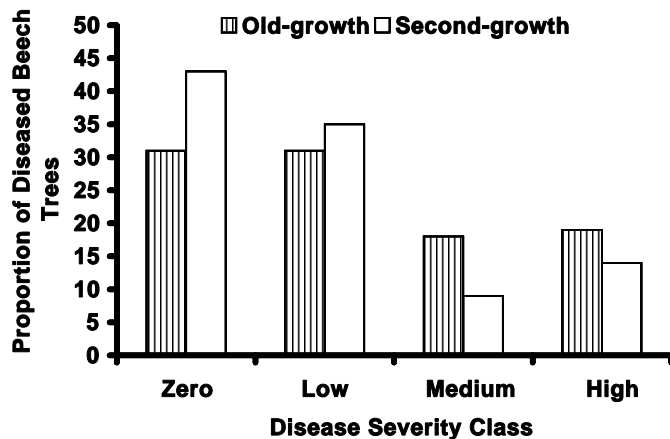


Figure 2.—Proportion of beech trees in four disease severity classes in old-growth and second-growth forests of Adirondack Park. Source: Modified from Latty et al. 2003.

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

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

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

## Structure and Function of Aftermath Stands

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

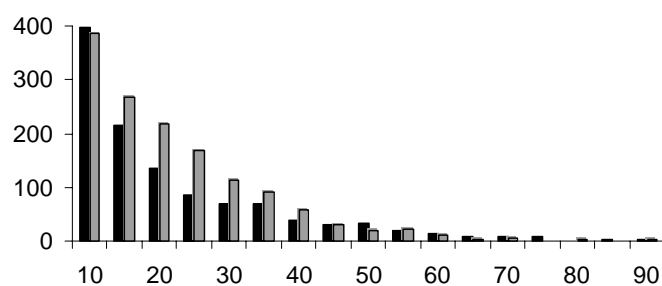
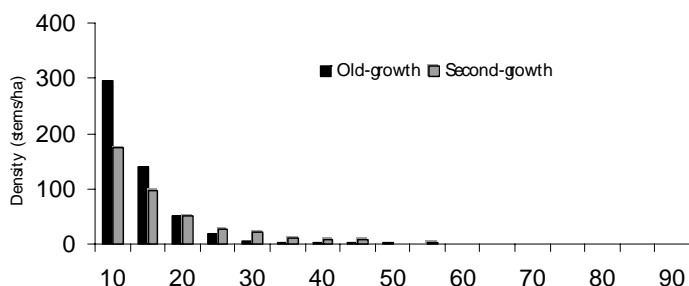


Figure 3.—Canopy stem density per size class for (A) beech trees only and (B) all canopy trees. Source: Modified from Latty 2001.

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

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

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

## Interactions with other Forest Disturbances

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

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

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

## Conclusion

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

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

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# SPATIAL AND TEMPORAL DEVELOPMENT OF BEECH BARK DISEASE IN THE NORTHEASTERN UNITED STATES

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## Abstract

For most of a century, beech bark disease has been spreading south and west from its point of introduction in Nova Scotia. The objective of this paper is to illustrate the impact of disease progression on beech trees across the northeastern United States. Beech trees were observed at each of 22 plots during summer months between 1979 and 1992. The plots were located throughout 7 States in the northeastern U.S. They are drawn from regions where BBD has been present for varying lengths of time, including some that have been affected for 50 years or more, and some that were first affected during the study. In general, plots were visited annually. Some areas were characterized by sharp increases in mortality shortly after the initial invasion of the disease and a subsequent lower constant mortality (consistent with a typical killing front and aftermath zone). In other cases, the killing front mortality was delayed or extended for decades. A small number of trees never became infested with scale, indicating probable strong resistance. Moreover, as many as 20% showed only slight scale activity, indicating probable partial resistance. Immediately following initial *Nectria* infection, trees that died quickly showed higher levels of fruiting than those that survived at least 5 years.

## Introduction

Beech bark disease (BBD), caused by the combined effects of the beech scale insect *Cryptococcus fagisuga* Lind. and bark-killing fungi in the genus *Nectria* (native *N. galligena* Bres., and introduced *N. coccinea* var. *faginata* Lohman and Watson), has continued to spread west and south from its point of introduction at Halifax, Nova Scotia, sometime before 1890. The spatial-temporal stages of the disease have been characterized as 1) the advancing front (where the scale insect occurs and whose populations are building), 2) the killing front (where high populations of both the scale and fungi

occur and large numbers of big beech are being killed), and 3) the aftermath zone (where the killing front occurred sometime in the past, and where beech stands, previously dominated by large old trees, now support many young or small beech trees that with time become increasingly cankered and defective)(Shigo 1972).

As the disease agents spread west and south, they have encountered a mosaic of forests differing in composition and structure, use history, and climate regimes, all of which have the potential to either limit or enhance their populations and/or their disease-causing interactions (Houston et al. 1979). This paper describes the temporal patterns of development of beech scale and *Nectria* spp populations and the consequent mortality patterns on beech trees in forests of Northeastern United States affected for varying lengths of time.

## Materials and Methods

### Trees and Plots

Fifty to 266 beech trees were observed at each of 22 plots during summer months between 1979 and 1992 although not every plot was measured in every year. Plots, located in seven Northeastern States (Fig. 1), were selected to represent examples of beech-rich forests in different temporal stages of disease development—some had been affected for over 50 years, some were first affected during the study. Some plots were in locations where BBD monitoring plots (NY), or Continuous Forest Monitoring plots (MA) had been established earlier by State personnel. An attempt was made to include at least 200 trees > 4.0 dbh in each plot but this was not always possible. Plots, determined by distribution of trees, varied in size and shape.

### Measurements

Annual measurements were taken of tree diameter at 4.5 ft (DBH), crown class (Avery and Burkhart 2002), and of the population levels of the disease agents.

Population levels of *C. fagisuga* and *Nectria* spp on the lower 2 meters were estimated annually. *C. fagisuga* populations were estimated on the basis of the amount of bole covered by wax and scored as: 0 (no colonies visible); 1 (trace = from one colony to very light scattered colonies, one or two larger colonies sometimes present); 2 (light = light to moderate scattered colonies, possible as few larger colonies); 3 (moderate = many colonies

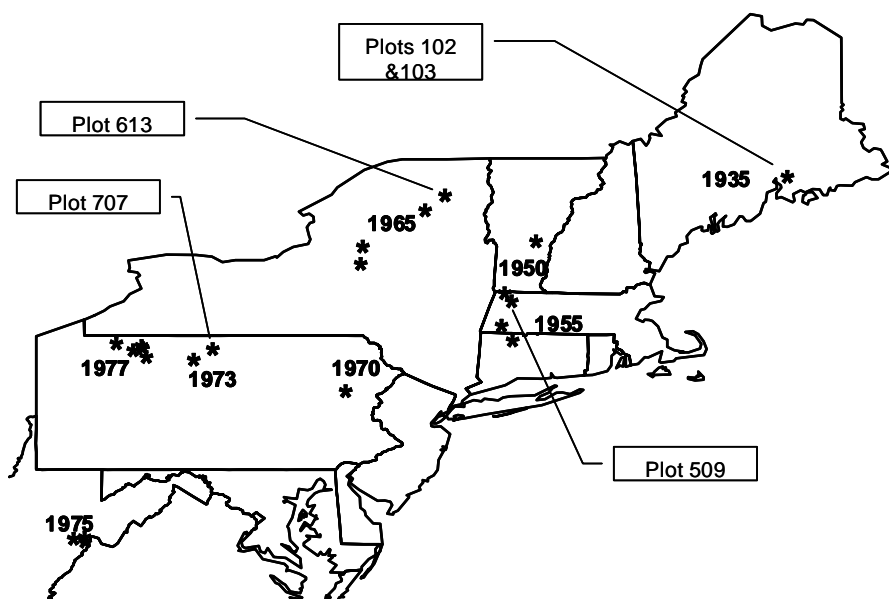


Figure 1.—Plot locations and approximate years of arrival of BBD. Plots referred to in Fig. 2 (below) are labeled.

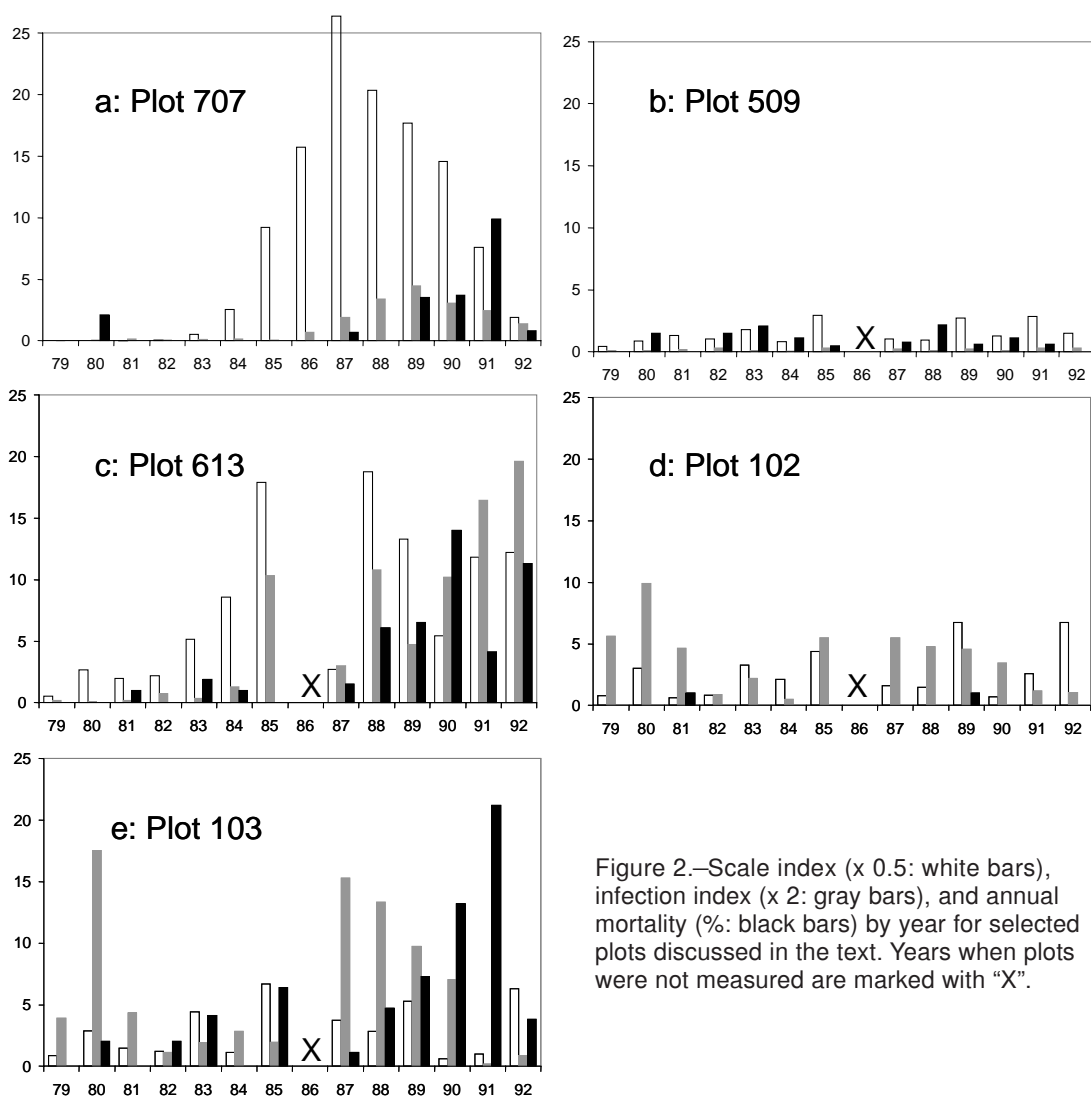


Figure 2.—Scale index (x 0.5: white bars), infection index (x 2: gray bars), and annual mortality (%: black bars) by year for selected plots discussed in the text. Years when plots were not measured are marked with "X".

present, substantial number of larger colonies sometimes present); 4 (heavy = many large colonies present, some coalescing), or 5 (very heavy = much of the bark conspicuously white with wax).

*Nectria* populations were scored based on the presence of clearly visible red or brownish perithecia as: 0 (absent); 1 (sparse = a few localized perithecia or perithecia in a few scattered circular infections); 2 (light = scattered moderate fruiting); 3 (moderate = many isolated circular infections with abundant perithecia); and 4 (heavy = large areas of bark with heavy fruiting—parts of the tree's bark conspicuously red or brownish). The recent infection by *Nectria* was also assessed indirectly by the presence of tarry spots, i.e., recently-formed dark, weeping bark exudates reflecting localized invasion and killing of bark. The number of tarry spots was scored as: 0; 1 (1-5); 2 (6-10); or 3 (> 10).

### Data Summarization and Analysis

Data for each plot were summarized to provide yearly estimates of tree condition and mortality. Weighted mean scale infestation and *Nectria* infection indices were calculated where wax scores of 1 to 5 were cubed and equated to 1, 6, 27, 48, and 125 respectively, and where *Nectria* scores were similarly cubed and added to the tarry spot scores (score numbers cubed).

To demonstrate the possible patterns of scale infestation, *Nectria* infection, and beech mortality, indices were developed to describe the annual average wax and infection levels and the annual percent mortality for all locations.

To evaluate the frequency of different levels of wax occurring on surviving trees, a maximum wax index was calculated for each tree. The maximum index is equal to the largest wax index value assigned to the tree during any year in which it was measured. Maximum wax indices for all trees which survived the study were plotted by diameter class.

Lastly, in order to predict the eventual fate of trees which become infected by *Nectria*, trees were selected from the dataset which showed no signs of *Nectria* during the first year measured and developed *Nectria* during the study. This subset of trees was divided into two groups: trees which survived the study and those that did not. For

survivors, only observations at least 5 years before the last observation were used in order to eliminate trees “in the process of dying”. The cumulative *Nectria* infection indices of selected trees were calculated starting from year of first infection (i.e., cumulative infection index for the second year since infection = infection index from the first year + infection index from the second year, etc.).

### Results and Discussion

The temporal records at each location illustrate potential patterns of the spread and development of BBD (Fig. 2). At many locations, spread patterns follow the generally accepted concepts of an advancing front, killing front and aftermath zone. Plot 707 in Pennsylvania (Fig. 2a) is an example of the typical disease progression as the advancing and killing front move quickly through an area. Beech scale arrived in the general area during the 1970's but was not common at the sampling location until the 1980's. Scale populations built up quickly from the early 1980's and peaked in 1987. By 1989, high levels of *Nectria* fruiting were observed and, by 1991 beech mortality was high. Plot 509 in Connecticut (Fig. 2b) is more representative of an aftermath forest. Beech bark disease had been present in this area for approximately 25 years before the present study began. Low levels of beech scale, *Nectria* fruiting, and beech mortality occurred throughout the study.

In other locations, disease progression is less typical. For example, BBD had been present for almost 20 years at Plot 613 in New York (Fig. 2c), before our study began. Nevertheless, there had never been a severe outbreak of the disease typical of the killing front. Approximately 5 years into our study, scale populations finally began to increase. This scale outbreak was soon followed by increases in *Nectria* fruiting and beech mortality.

Our results also indicate that site conditions can influence the impact of BBD dramatically. Figs. 2d and 2e show the patterns of scale accumulation, *Nectria* fruiting, and beech mortality for Plots 102 and 103 in Maine. These two locations are approximately 2 miles apart, yet Plot 103 experienced greater levels of scale and *Nectria* accumulation and dramatically more mortality than Plot 102.

Resistance to beech scale is an important element in the BBD dynamics; trees completely free of infestation occur

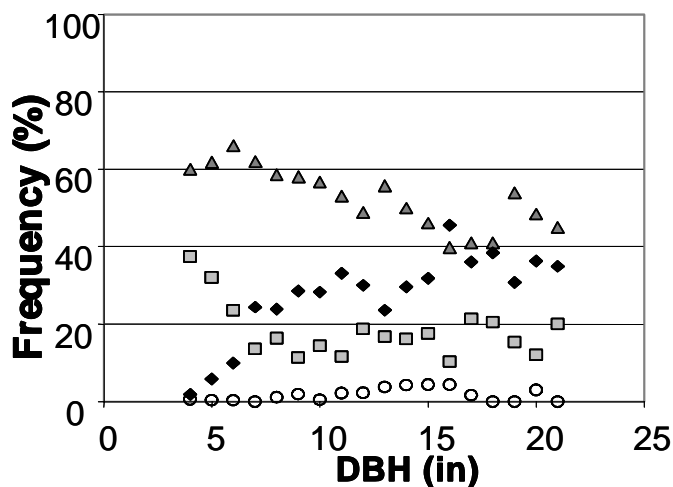


Figure 3.—Frequency of different levels of maximum wax index on trees that survived: 1 = circles; 2 = squares; 3 = triangles; 4 or 5 = diamonds.

in low numbers (Houston 1983, Houston and Houston 1987). In our study, a small percentage of trees (< 5%) never became infested despite the fact that scale was present at all locations. Similarly, approximately 20% of trees > 5 in dbh, from all locations combined, experienced trace levels of scale infestation at some time during the study, but the infestation never progressed to moderate or high levels (Fig. 3). Severe levels of infestation (scale indices of 4 or 5) were more common on large trees than small trees (Fig. 3).

For trees that were infected with *Nectria* during the study (i.e., trees that had an infection index of 0 during their first measurement year but subsequently showed signs of active fruiting) the average cumulative infection index increased at a relatively constant rate every year post infection. The rate of increase was significantly higher for trees that eventually died during the study than for those that survived (Fig. 4). These results suggest that it may be possible to develop a method of predicting the eventual fate of infected trees using an index similar to the cumulative infection index used in this study.

## Summary and Conclusions

At many locations, the spread pattern described as an advancing front, killing front, and aftermath zone was clearly observable. However at some locations the pattern was altered or delayed, possibly due to site or climate conditions. The apparent complete resistance to beech scale of a low percentage of trees is consistent with the

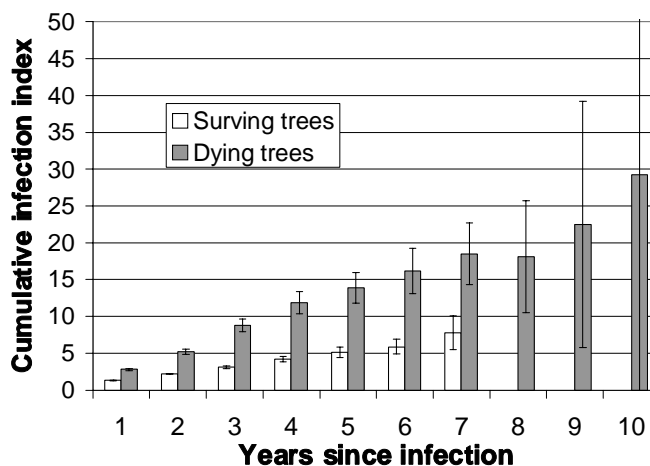


Figure 4.—Cumulative infection index (*Nectria* fruiting + tarry spots) on trees that survived (white bars) or died (gray bars) during the study. Error bars show  $\pm 1$  standard error.

results of earlier studies with American beech elsewhere. However, of special interest is the finding that for a significant proportion of the trees (ca. 20%) in all size classes, scale infestation levels remained very low throughout the study. Such trees may possess a partial resistance to the insect, perhaps similar to that noted for European beech. During the first 7 years after infection the spread of *Nectria* on trees which die was significantly faster than on trees which survive.

## Acknowledgments

We wish to acknowledge the many people who, over the course of this study, established plots and took data. Special thanks for this go to Mike Ferrucci, Manfred Mielke, and Bill Jackson (USFS); Barbara Burns (VT Dept. Forests, Parks and Recreation); and Barry Towers, Gary Laudermilch, Edwin Blumenthal, and Norman Kauffman DCNR, PA Bureau of Forestry). David Schneider and Gino Luzader (USFS) contributed significantly early on to the massive job of data management

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# MICHIGAN BEECH BARK DISEASE MONITORING AND IMPACT ANALYSIS SYSTEM

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## Abstract

A beech bark disease monitoring and impact analysis system was established in Michigan in 2001 to measure the condition and change of overstory vegetation due to beech bark disease and other disturbances. Beech bark disease (BBD) is a disease complex involving the exotic beech scale (*Cryptococcus fagisuga* Lind.) and at least 3 species of *Nectria* fungi affecting the American beech tree (*Fagus grandifolia* Ehrh.). BBD was first discovered in Michigan in 2000, although experts now believe it has been present in the state for about 20 years. The plot system was established during the summers of 2001-2003. It currently consists of 202 extensive plots (less detailed) and 62 intensive plots (more detailed subset of extensive plots) distributed through the eastern Upper Peninsula and western and northern Lower Peninsula of Michigan. Beech scale is now present in 36% of the plots. Significantly higher transparency and dieback ratings and reduced vigor ratings occur in plots with beech scale as compared to plots without scale in both peninsulas. Dead beech basal area is also significantly greater in plots with beech scale present. In 2004, extensive plots established in 2001 were remeasured and data is being compared from 2001 and 2004 to determine the impact BBD is having in these areas.

## Introduction

The University of Michigan and the Michigan Department of Natural Resources established the Michigan Beech Bark Disease Monitoring and Impact Analysis System (BBDMIAS) in 2001 in response to the presence of beech bark disease (BBD) in Michigan's northern hardwood forests. The objectives of BBDMIAS are to: 1) identify the extent of Michigan's beech resource that is affected by BBD, 2) collect baseline data on current conditions of the beech resource and northern hardwood stands containing beech before this resource is affected by BBD and 3) monitor changes in the

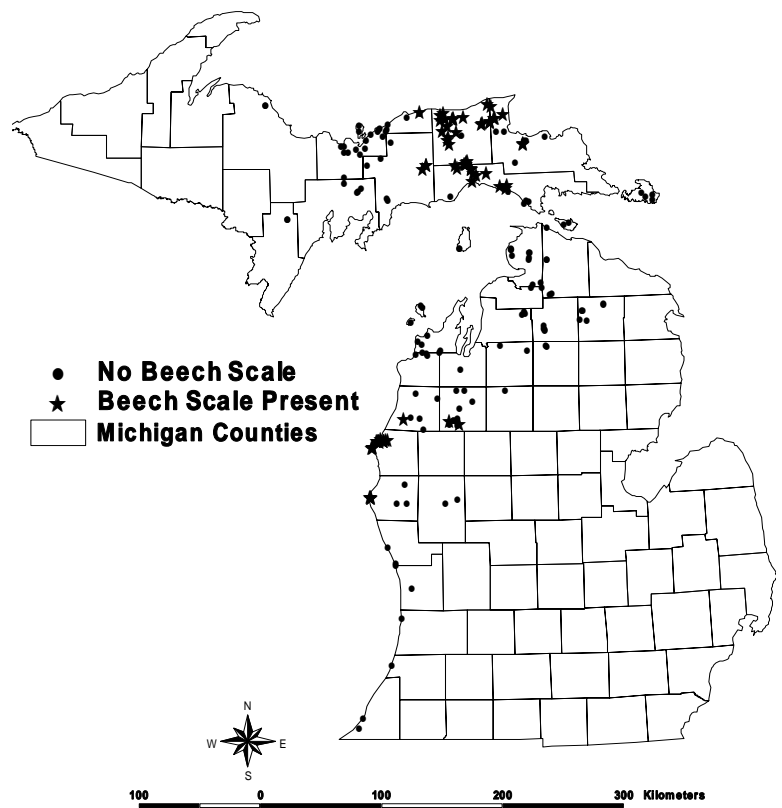


Figure 1.—Location of plots in the Michigan Beech Bark Disease Monitoring and Impact Analysis System.

condition of beech resource and northern hardwood forests due to BBD and other disturbances.

This monitoring system consists of two plot types: extensive and intensive (Thompson and Witter 2002). The extensive plot is composed of a matrix of 30 sampling points where basal area is determined. Tree crown and damage data, along with presence and abundance of BBD indicators, are also collected on the American beech (*Fagus grandifolia* Ehrh.) tree nearest each sampling point. Currently, 202 extensive plots are established throughout the northern and western Lower Peninsula (LP) and eastern Upper Peninsula (UP) (Figure 1).

The intensive plot consists of five circular subplots established within the sampling point matrix of the extensive plot. Intensive plots are established within a subset of the 202 extensive plots. Currently 62 intensive plots are established with 30 in the Lower Peninsula and 32 in the Upper Peninsula. In this plot type, data are collected on all tree species and on both live and dead trees.

## Methods

The Michigan Beech Bark Disease Monitoring and Impact Analysis System is comprised of two types of plots: Type 1 (extensive) and Type 2 (intensive). The Type 1 plot system provides baseline data on northern hardwood forests and American beech trees before major disturbances due to beech bark disease occur. Type 1 plots primarily consist of one of sampling grids: 5 X 6 or 3 X 10. The particular sampling grid depends on the stand dimensions. If possible, the grid should be positioned so that one edge is parallel to the nearest road. Observations within the plot are made at 30 prism points that are spaced 40 m apart, with the first sample point being at least 40 m into the plot.

The azimuth and distance from the first sampling point to the reference point on the road is recorded. The location of the first sampling point in the plot is determined using a Trimble Geoexplorer® GPS unit. If the location of the first prism point cannot be determined due to GPS interference, a GPS location for the witness tree is taken. The azimuth and distance from each prism point to the beech tree sampled at that point is recorded. In most cases, the beech trees sampled are tagged with a numbered metal tag placed on the buttress root. For each beech tree sampled, the following variables are measured: tree status, DBH, tree number, live crown ratio, crown density, crown dieback, foliage transparency, crown light exposure, tree vigor/condition, crown class/position, tree damage, and % beech scale coverage.

After examination of the 202 stands, 30% of the stands are studied using a Type 2 plot system. Each subplot center is marked with a metal stake and a ribbon wrapped around the stake. A GPS location of each subplot center is recorded so that the stands can be relocated for additional sampling. The Type 2 plot design consists of a series of fixed-area, circular subplots tied to a cluster of five points with a subplot at the center and four others 36.6 m (120 ft) apart radiating in the four cardinal directions. The individual circular subplots are 1/59<sup>th</sup> ha (1/24<sup>th</sup> ac) in size with a 7.32 m radius (24 ft). In each plot, every living and dead tree 12.5 cm (5 in) or greater in diameter at DBH is marked with a numbered metal tag attached to the base of the tree (buttress root). The azimuth and distance from subplot center to the midpoint of these trees is recorded. For each tree within the subplots the following variables are measured: tree

status, DBH, tree number, live crown ratio, crown density, crown dieback, foliage transparency, crown light exposure, tree vigor/condition, crown class/position, tree damage, and % beech scale coverage.

## Results and Discussion

Beech scale infestation is currently present in 6 counties in the Lower Peninsula (Emmet, Grand Traverse, Manistee, Mason, Oceana, and Wexford) and 5 counties in the eastern Upper Peninsula (Alger, Chippewa, Luce, Mackinac, and Schoolcraft). Overall, both beech scale and BBD affect the vigor and condition of beech trees and northern hardwood stands in Michigan. Trees with scale have less photosynthetic material available based on average foliage and crown dieback levels. Slightly more trees with damage also are associated with trees with scale. Average mortality for beech is higher in infested stands. These findings agree with previous studies in the eastern U.S., which showed that levels of dieback, defects, and mortality increased, and radial growth decreased as BBD progressed through a stand (Yocum, 2002; Gavin and Peart, 1993; Burns and Houston, 1987; Houston and O'Brien, 1983; Mize and Lea, 1979; Shigo, 1972; Ehrlich, 1934).

Along with site conditions that intensify the effects of BBD, higher populations of scale and fungi that are present as the disease progresses place increasing demands on the physiological functioning of the tree (Shigo, 1964; Ehrlich, 1934). Although the etiology of BBD and the specific effects of the scale and disease on the tree's transport system are not completely understood, there is evidence in BBDMIAS plots that higher levels of scale and the presence of BBD do affect the transport system. Significantly greater amounts of dieback are found in high scale plots in the Lower Peninsula compared to no and low scale plots (Figure 2). In the Upper Peninsula, dieback increases significantly as scale intensity increases (Figure 2). In the Lower Peninsula, significantly greater crown transparency ratings are found in the high scale plots compared to no and low scale plots (Figure 3). In the Upper Peninsula, crown transparency ratings increase significantly as scale intensity increases (Figure 3).

High scale plots also show significantly reduced tree vigor compared to the no and low scale plots in both the Lower and Upper Peninsulas (Figure 4). Levels of mortality for beech also are greatest in stands in the

highest scale infestation category; in both peninsulas, significantly greater amounts of dead beech BA are found in high scale plots compared to plots with no or low scale (Figure 5). The cumulative effects of beech scale and BBD infestation along with more frequent moisture stress may lead to poorer tree crown condition and higher tree mortality. Other studies have found similar increased crown dieback and tree mortality in northern hardwood stands experiencing drought-defoliation interactions (MacDonald et al., 1998; Brooks, 1994; Bauce and Allen, 1991).

BBD appears to be more advanced and/or having greater effects in the Lower Peninsula compared to the Upper Peninsula. Both the average level of scale infestation and mean amount of dead beech basal area were significantly higher for stands with BBD in Lower Peninsula. Another sign that BBD may be more advanced in the Lower Peninsula is the higher number of tarry spots recorded here compared to the Upper Peninsula. Tarry spots are commonly associated with *Nectria* infection, which is more abundant in the later stages of BBD (Shigo, 1972).

During the 2004 field season, we remeasured the intensive plots that were established during 2001, 2002, and 2003 and resampled the extensive plots established in 2001.

## Acknowledgments

We thank the USDA McIntire-Stennis Program, the USDA Forest Service, Michigan Department of Natural Resources Forest, Mineral and Fire Management Division, and the University of Michigan School of Natural Resources and Environment for financial support for this research.

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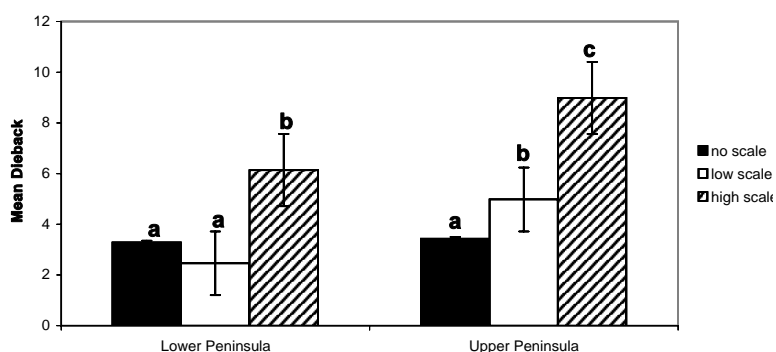


Figure 2.—Mean dieback ratings for plots with no, low and high beech scale in the Lower and Upper Peninsulas of Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different within each scale rating.

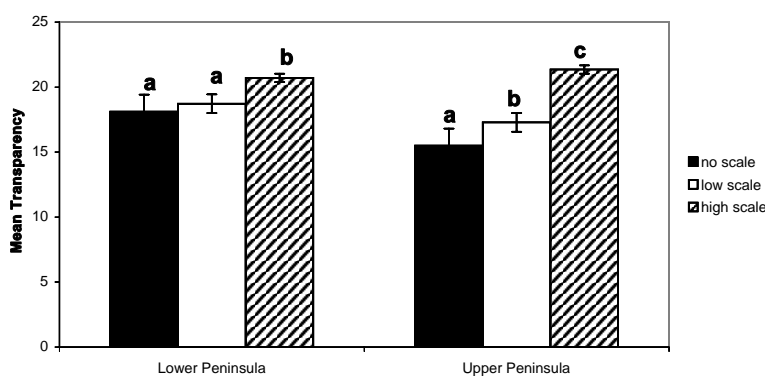


Figure 3.—Mean transparency ratings for plots with no, low and high beech scale in the Lower and Upper Peninsulas of Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different within each scale rating.

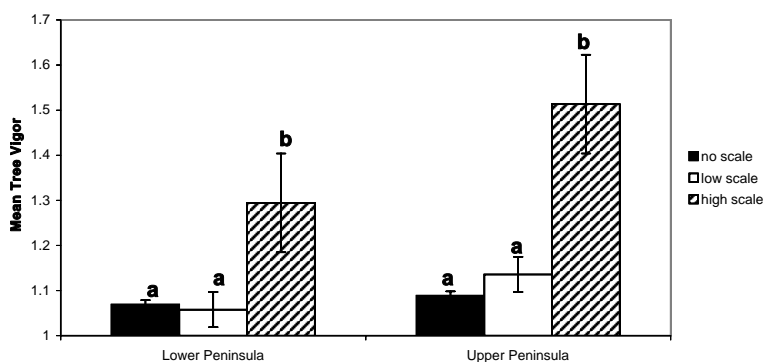


Figure 4.—Mean vigor ratings for plots with no, low and high beech scale in the Lower and Upper Peninsulas of Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different within each scale rating.

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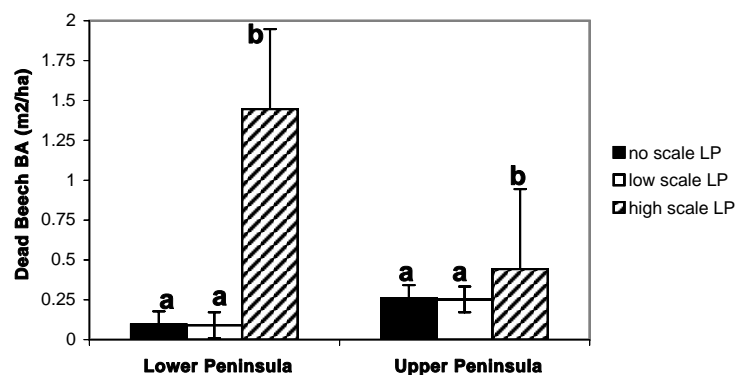


Figure 5.—Mean amounts of dead beech basal area (BA) (m<sup>2</sup>/ha) for plots with no, low and high beech scale in the Lower and Upper Peninsulas of Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different within each scale rating.

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# CHANGES TO THE ADIRONDACK FOREST: IMPLICATIONS OF BEECH BARK DISEASE ON FOREST STRUCTURE AND SEED PRODUCTION

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## Abstract

We assessed forest structure and tree seed production over 14 years in an unmanaged, 250-year-old northern hardwood stand in the central Adirondack Mountains. American beech (*Fagus grandifolia* Ehrh.) trees in the stand have been affected by Beech Bark Disease (BBD), caused by a combination of an invasive scale insect and a fungus that weakens and kills the tree. Following the initial spread of BBD in the 1960s, a cascade of changes was predicted to occur, including loss of large beech and lowered production of beechnuts, the primary hard mast species in the central Adirondacks and an important wildlife food. Large beech were indeed lost from the forest. However, contrary to predictions, more beechnuts were produced in the stand from 1994-2003 than 1988-1993. Since 1994, beechnut production was cyclical: an estimated 391,198-638,690 nuts/ha were produced every even year in the hardwood site. Other changes due to BBD have manifested in the stand. Although the very largest beech trees died when BBD originally invaded the stand, larger (>38cm diameter) trees continued to be lost. The number of medium-sized (15-38cm diameter) beech was stable over the 14-year period. While beech sapling abundance increased, these smaller trees showed advanced progression of BBD since 1989. Dominant sugar maples (*Acer saccharum* Marsh.) >38 cm diameter were lost from the stand and were among several northern hardwood species not regenerating. However, species richness and abundance in the shrub layer increased, perhaps as a result of gaps created by fallen canopy trees. Down woody material abundance increased but was of smaller size. BBD has continued to affect stand structure and production of hard mast in both predictable and unexpected ways.

## Introduction

The American beech (*Fagus grandifolia* Ehrh.) is an integral component of the northern hardwood forest that covers parts of eastern Canada, the Adirondack Mountains of New York State, and New England.

Beechnuts are the primary hard mast and the best source of energy in the region: beechnuts are used by at least 20 species (Martin et al. 1951) and perhaps as many as 40 species of wildlife (McCullough et al. 2000). Beech trees in northeastern North America have been affected by Beech Bark Disease (BBD), caused by a combination of an invasive scale insect, *Cryptococcus fagisuga*, and a native fungus, primarily *Nectria coccinea*, that weakens and kills the tree (Houston et al. 1979). Based on forest research in plots initially measured in 1954, the Advance Front of BBD arrived in the central Adirondack area in 1967, the Killing Front began in 1971 and the Aftermath Forest established in approximately 1974 (Mize and Lea 1978). After BBD initially moved through the region, a cascade of changes was predicted to occur. Costello (1992) estimated that BBD-affected trees >15 cm diameter would have lowered production of beechnuts. We assessed vegetative structure and composition and seed production over 14 years in an unmanaged, 250-year-old stand subjected to BBD to evaluate changes in the central Adirondack forest.

## Methods

Fifty circular plots were established in 1988 on Huntington Wildlife Forest (HWF), a 6,000 ha research facility in Newcomb, NY in the central Adirondack Mountains operated by the State University of New York, College of Environmental Science and Forestry (74° 15' N, 44° 00' W). Twenty-five plots were established in an upland deciduous stand that contained primarily northern hardwoods such as sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis* Britton), SAF Type 25 (Society of American Foresters 1980). The other 25 plots were located downslope in a mixed deciduous/coniferous stand (hereafter, the mixed stand) that contained yellow birch, red maple (*A. rubrum* L.), red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* [L.] Mill.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.), associated with sugar maple, beech, white pine (*Pinus strobus* L.) or Northern white cedar (*Thuja occidentalis* L.) (SAF Type 30). Soils in the study area were primarily glacial till (Somers 1986).

Vegetation structure and composition were measured in 1989 and remeasured in 2002. We measured live trees  $\geq 11.4$  cm ( $\geq 4.5$  in) diameter at breast height (dbh, taken at 1.3m above the ground) on 0.04 ha circular plots (0.1 ac). We calculated Importance Value (IV) of tree species as:

$$((BA*n) / \text{Total } BA*N)*100,$$

**Table 1.—Number of trees >11.4cm dbh, Basal Area/ha (m<sup>2</sup>/ha), importance value, and percent of total Basal Area, Huntington Wildlife Forest, 1989 and 2002**

Species	Number of Trees				Basal Area				Importance Value				Percent Total Basal Area			
	Hardwood		Mixed		Hardwood		Mixed		Hardwood		Mixed		Hardwood		Mixed	
	1989	2002	1989	2002	1989	2002	1989	2002	1989	2002	1989	2002	1989	2002	1989	2002
American beech	313	269	50	72	11	9.9	1.1	1.8	21.08	26.83	0.45	1.08	30	35	3	5
Balsam fir	7	5	0	0	0.3	0.3	0.02	0.01	0	0	1	1				
Eastern hemlock	12	6	96	87	2	1.8	10.1	10.8	0.15	0.11	8.28	8.03	6	6	32	34
Paper birch	2	1	0	0	0.2	0.1	0	0	0	0	1	0				
Red maple	1	70	69	0.1	0	4.9	5.3	0	2.92	3.12	0	0	16	16		
Red spruce	13	6	65	62	0.8	0.6	4.4	4.8	0.07	0.04	2.46	2.56	2	2	14	15
Sugar maple	77	48	11	10	18.2	12.4	1.6	1.2	8.53	6.02	0.15	0.1	50	44	5	4
White ash	1	0	0	0	0	0	0	0	0	0						
Yellow birch	35	24	74	59	4.1	3.4	8.8	7.8	0.87	0.82	5.53	3.97	11	12	28	25
Total	452	353	375	365	36.3	28.1	31.4	32	100	100	100	100				

where n = number of individuals of one species and N = number of individuals of all species.

In 1989, only trees >24 cm dbh were measured, while in 2002 we recorded all variables for all live trees ≥11.4 cm dbh. We counted small trees <11.4 cm dbh and measured abundance (sparse, common, or abundant) of saplings and shrubs <1 cm dbh (hereafter called the shrub layer) on a 0.004 ha plot. In the 0.04 ha plot, we counted stumps, and counted snags and logs ≥11.4 cm dbh and ≥1.5 m long, and classified them after Maser *et al.* (1979) as having been dead <1 year (still had fine branches), 1-5 years (no fine branches, decay class 2), or >5 years (decay classes 3-5).

We recorded BBD progression (0 = no disease; 1 = light scale; 2 = moderate to heavy scale; 3 = light *Nectria* fungus, scale may be disappearing at this time; 4 = heavy fungus, bark cracked/pock-marked; 5 = heavy fungus, bark falling off, tree still alive), crown position, and crown condition (percent of dead crown). For the purposes of this study, only the 25 hardwood plots were used to evaluate BBD due to the low proportion of beech in the mixed site.

We established seed traps (13.9 L [5 gal] capacity buckets) in the center of each plot and collected seeds annually from July to November. If a bucket was tipped over due to disturbance by a bear or some other factor, we censored it from the survey for that year. We calculated mean beech and sugar maple seeds per trap

and estimated seed production for the hardwood and mixed areas, but could include ranges and standard errors (SE) only for 1996-2003 due to a lack of per-trap data for earlier years.

## Results

Basal Area/ha decreased in the hardwood site from 36 to 28 m<sup>2</sup>/ha (158 to 122 ft<sup>2</sup>/ac) from 1989 to 2002. BA/ha did not change in the mixed plots (31 to 32 m<sup>2</sup>/ha or 137 to 139 ft<sup>2</sup>/ac) from 1989 to 2002 (Table 1). The decrease in BA/ha in the hardwood site was due primarily to loss of sugar maples. Although there was also a decrease in beech and yellow birch BA/ha, the IV of beech increased over the study while the IV of sugar maple and yellow birch decreased. In the mixed site, beech IV increased and yellow birch IV decreased.

The total number of trees >10 cm dbh decreased markedly on hardwood plots from 452 in 1989 to 353 in 2002, but not on mixed plots (375 to 365 trees; Table 1). Number of beech trees declined in all size classes on hardwood plots except the 20-29.99 cm class which increased, but beech on mixed plots increased in the 10-19.99, 20-29.99, and 30-39.99 cm size classes (Table 2). The number of beech saplings (1-10 cm dbh) on hardwood plots increased from 71 to 115 over the study, yet the proportion of hardwood plots with beech in this size class was roughly the same in 1989 and 2002. Shrub layer richness increased from 3 to 9 species in the hardwood site. However, the proportion of plots with beech in the shrub layer increased from 68 to 80%.

Beech snags tended to be older in 2002: 71% died within the last 5 years in 1989, whereas only 41% died within the past 5 years in 2002 (Table 2). The number of beech snags and stumps did not change, but the number of logs increased six-fold. However, the mean size of logs ( $\pm$  SD) declined from  $43 \pm 10$ cm to  $26 \pm 10$ cm.

No trees were found without some trace of scale. In the hardwood site in 1989, 56% of beech trees had light scale infestation, 21% were heavily infested with scale, 22% had both scale and *Nectria* fungus, and 2% had severe *Nectria* infestation and damage ( $n = 63$ ). By 2002, 12% of trees had light scale infestation, 66% had heavy scale and 22% had heavy *Nectria* infestation ( $n = 269$ ).

Beechnut masting occurred on a 2-year cycle (high in even years, low or none in odd years). Mean annual total number of beechnuts in the hardwood site was  $26 \pm 7$  (range 0-76), and in the mixed site was  $6 \pm 2$  (range 0-28). Mean number of beechnuts per trap ranged from 0 in several years to 4 in the hardwood site and 0-1.4 in the mixed site (Figure 1a). Estimated beechnut production ranged from complete failure to 638,690 nuts/ha in the hardwood site and was 0-223,542 nuts/ha in the mixed site. If we assume that odd years contribute little to the trend over time, in even years beechnut production tended to increase over time in the hardwood ( $R^2 = 0.55$ ) and mixed ( $R^2 = 0.73$ ) areas.

Over that same period, mean annual total number of sugar maple seeds in the hardwood site was  $199 \pm 60$  (range 0-772) and was  $39 \pm 11$  in the mixed site (range 0-131). Sugar maple seed production was highest in 1988 with a mean 31 seeds per trap (Figure 1b) and an estimated 4,930,689 seeds/ha in the hardwood site. Sugar maple also tended to mast in even years, though sugar maple produced some seed in most years and was not as strongly cyclical as beech. In even years, sugar maple seed production declined weakly over time in the hardwood site ( $R^2 = 0.20$ ), but did not trend in the mixed site ( $R^2 = 0.02$ ).

## Discussion

Although by the 1980s the largest beech in this 250-year-old hardwood site were dead, from 1989-2002, the site continued to lose larger ( $>38$ cm dbh) trees to BBD. Basal area declined in the hardwood site, and beech increased

**Table 2.—Comparison of characteristics of 25 hardwood plots, Huntington Wildlife Forest, 1989 and 2002**

Characteristic	1989	2002
Number of Beech Trees $>10$ cm dbh		
by Size Class (cm)		
10-19.99	199	143
20-29.99	80	103
30-39.99	24	17
40-49.99	7	3
$>50$	3	3
Total stems $>10$ cm	313	269
Small Beech Trees 1-10 cm dbh		
Number stems	71	115
Percent stems (%)	97	94
Shrub Layer $< 1$ cm dbh		
Number species	3	9
Percent plots with beech (%)	68	80
Beech Coarse Woody Debris		
Number snags/stumps	62	63
Percent snags dead in last 5 yrs (%)	71	41
Number logs	13	85
Average size logs $\pm$ SD (cm)	$43 \pm 10$	$26 \pm 10$

in importance while other hardwoods decreased. Despite four decades of BBD presence on HWF, smaller trees appear to be increasingly affected by BBD. By 2002, even trees as small as 11.4 cm dbh all had signs of the disease. The number of large beech stabilized between 1989 and 2002, while the number of  $<25$  cm trees declined in our study area. Didier (2003), using US Forest Service Forest Inventory and Analysis data, showed that after 1968, larger beech declined tremendously and smaller beech increased in number throughout the Adirondack region. If the trend continues, BBD is likely to weaken or kill increasingly smaller trees in the future.

Other characteristics of the area in our study also changed. While there were many more logs on the ground in 2002 than in 1989, mean log diameter was roughly half as large. This difference in coarse woody debris may affect small mammal and salamander populations that rely on dead woody material for feeding sites and cover (Bowman et al. 2000, Dupuis et al. 1995). Alternatively, the increase in species richness and abundance of shrub layer species may indicate that gaps left by dead canopy trees are enabling some shrubs and

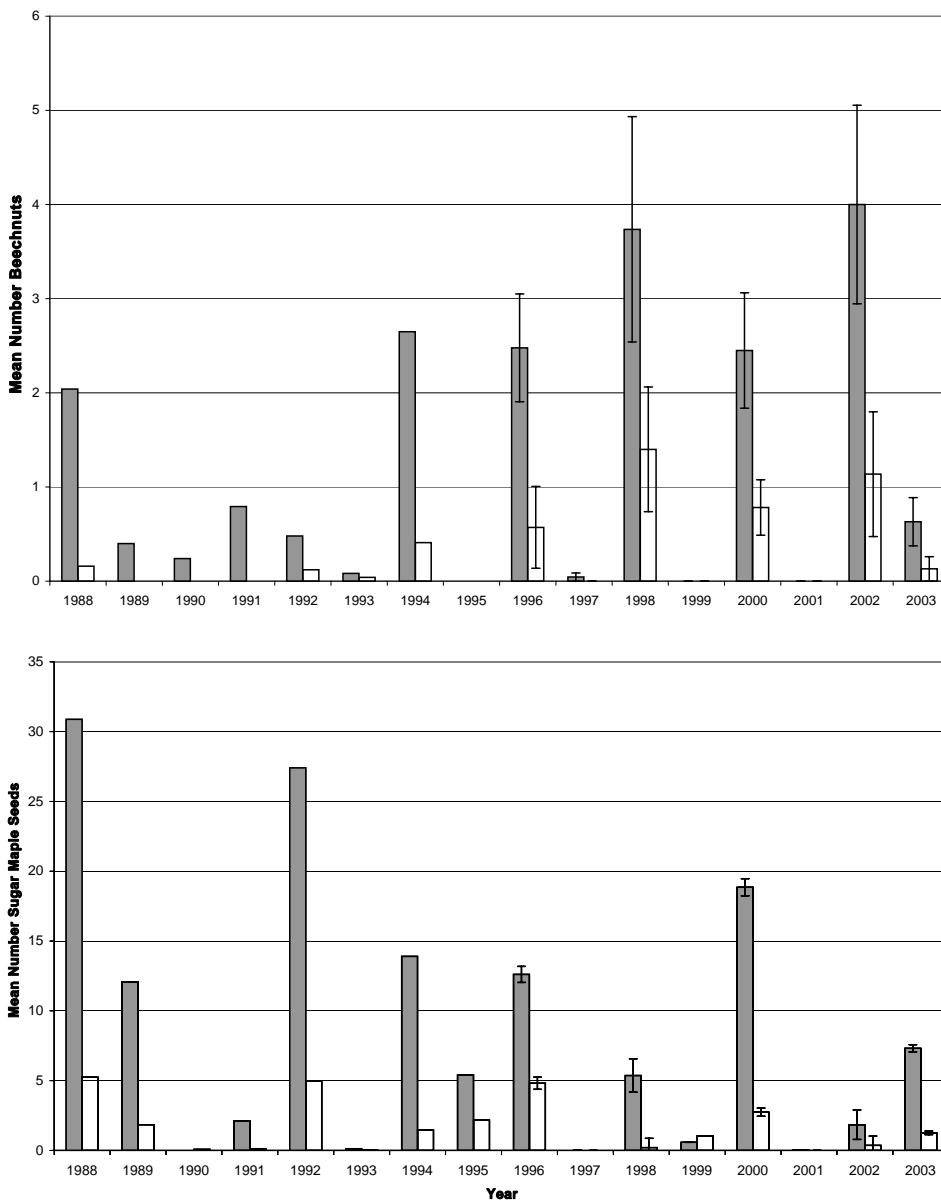


Figure 1.—Mean number of a) American beech and b) sugar maple seeds, in hardwood (gray bars) and mixed hardwood/conifer (white bars) stands, Huntington Wildlife Forest, NY, 1988-2003, with 1 SE in 1996-2003.

saplings to establish. However, sugar maple, yellow birch and white ash are not regenerating, and beech and witch hobble (*Viburnum alnifolium*) are increasing in abundance in the shrub layer. White-tailed deer (*Odocoileus virginianus*) undoubtedly had some impact on regeneration through browsing vegetation at this height (Kelty and Nyland 1981), but deer densities during the 1990s on HWF were approximately 2-4/km<sup>2</sup> (Adirondack Ecological Center, unpublished data) and deer at such low densities should have affected regeneration far less than the higher densities found elsewhere in the northeastern US (Horsley et al. 2003).

Beechnuts in the hardwood site were produced on a two-year cycle beginning in 1994, with an estimated >391,198 seeds/ha in even years and near or total failure in odd years. Qualitative phenological data from HWF indicate that the even-year beechnut cycle also occurred from 1984-1989 (R. Masters, unpublished data). However, without quantitative data it is difficult to compare nut production before and after BBD infestation (i.e., what is termed “good” today may have been “poor” in the 1950’s). It is possible that between-trap variation in seed production (based on individual trees above each trap) may obscure trends over time.

However, our data indicate higher beechnut production since 1994. This is true on both the mixed and hardwood plots, although the trends are more pronounced on the hardwood site where there are more beech. With loss of sugar maple from the canopy and lack of replacement, sugar maple seeds as a food source will continue to decline, which may affect small mammals and other seed predators. In contrast, production of more beechnuts could be beneficial to black bears (*Ursus americanus*), deer, blue jays (*Cyanocitta cristata*), and the myriad other wildlife species dependent on this major source of energy in the northern hardwood forest.

Predictions of declining nut production have not yet proved correct; on the contrary, nut production over the duration of the study appeared to increase over time. One possible explanation for this that is the cohort of beech trees that grew up in the presence of BBD are now large enough for nut production. These younger beech may be viable despite the stress of BBD and may continue to produce nuts, if not further stressed by pathogens or other disturbances. Alternately, perhaps there are so many small to medium size beech trees that the cumulative result of their fruiting results in more nuts/ha than the forest of fifty years ago that contained only a few large beech.

On both managed and unmanaged stands on HWF, beech have been decimated by BBD. In a summary of forest measurements on Continuous Forest Inventory plots located at 400 m intervals throughout HWF, Sage (1996) reported that between 1965 and 1980, nearly 80% of the beech >41 cm dbh died from BBD. After 1980, most large beech were dead or in decline, and mortality of 25-38 cm dbh trees increased. There was limited mortality of trees <25 cm dbh, but crown dieback or yellowing and stem defect occurred on 40% of trees. Our study indicates that the smaller beech have begun to die. Similar results were reported in a separate study on HWF (Forrester et al. 2003). Adirondack beech increased in volume but decreased in density (Didier 2003) since 1968. Indeed, BBD was the primary cause of mortality for beech trees >30 cm dbh in the Adirondacks (Manion and Griffin 2001).

Nearly 40 years after the arrival of BBD, the northern hardwood forest in the central Adirondacks continues to

undergo major changes in structure and composition. Our study site may be analogous to other unmanaged, mature forests, including portions of the state-owned Adirondack Forest Preserve. Comparison of this study area to similar sites not yet affected by BBD would explain the contribution of BBD to changing forest conditions. It is important to understand beechnut production both at local and rangewide scales; therefore, we recommend adoption of a simple, regionwide nut production survey. As the Killing Front of BBD continues to move westward, such a survey would illuminate the impact of BBD on wildlife populations.

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# IMPACTS OF BEECH BARK DISEASE ON UNDERSTORY COMPOSITION IN MICHIGAN

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## Abstract

Beech bark disease was discovered in Michigan in 2000 and will likely kill at least 50% of mature American beech trees. Our study was designed to determine how understory composition will be affected as beech bark disease spreads and intensifies throughout Michigan. We assessed the potential impact in forest stands with varying beech densities (low, moderate, and high) and abundance of *Cryptococcus fagisuga* (absent, light, and heavy). Variables were measured in 62 stands throughout the Upper and Lower Peninsulas of Michigan in 2002 and 2003. We found no significant difference in density of beech stems among stands. Significantly fewer sugar maple stems occurred in stands with heavy *C. fagisuga* than in stands with absent or light *C. fagisuga*. No current evidence suggests dense beech thickets will regenerate in stands impacted by beech bark disease in Michigan.

## Introduction

Beech bark disease (BBD) was discovered in Michigan in 2000, although evidence suggests it had been established for at least 10 years prior to identification (McCullough et al. 2001). Spreading from its origins in Luce and Mason Counties, BBD is now confirmed in at least eight counties in both the Upper and Lower Peninsulas. The impacts of BBD specific to Michigan's forests are largely unknown but will likely include changes in understory species composition. Michigan State University (MSU) is working in conjunction with the University of Michigan on a long-term research project to investigate the impacts of BBD as it spreads in range and intensifies throughout the state. The objectives of our research at MSU are to *i*) assess differences in understory vegetation in stands with varying levels of beech bark disease and beech densities and *ii*) compare baseline vegetation with long-term data of stands affected by beech bark disease.

## Study Area

Research was conducted in 62 permanent plots in the Lower and Upper Peninsulas of Michigan. Stands were selected in a two-factorial design and grouped by beech density and *C. fagisuga* abundance. Beech density was classified by absolute basal area of beech as low ( $< 9 \text{ m}^2/\text{ha}$ ), moderate ( $9\text{-}18 \text{ m}^2/\text{ha}$ ), or high ( $>18 \text{ m}^2/\text{ha}$ ). Abundance of *C. fagisuga* in a  $100 \text{ cm}^2$  sample area was estimated on 12 beech trees on the north and south sides of the main bole at 1.3 m on upslope side. Trees were considered "heavily infested" if *C. fagisuga* covered greater than 30% of the area on at least one azimuth. Stands were classified according to the number of trees heavily infested with *C. fagisuga* within the plot boundary as absent (zero), light ( $< 2$ ), or heavy ( $> 2$ ).

## Methods

In each stand, four permanent, fixed radius plots were established at 18 m from the center of the research plot, one in each cardinal direction. We identified number and species of seedlings ( $< 30.5 \text{ cm}$  tall) within a 2.4 m radius, saplings ( $> 30.5 \text{ cm}$  tall and  $< 2.5 \text{ cm}$  dbh) within a 3.5 m radius, and recruits ( $> 2.5 \text{ cm}$  dbh and  $< 12.5 \text{ cm}$  dbh) within a 7.3 m radius.

## Results and Discussion

There was no significant difference in mean stems per ha of beech seedlings, saplings, and recruits among stands with absent, light, or heavy *C. fagisuga*, nor among stands with low, moderate, or high beech density. Results suggest that beech bark disease had not yet altered the abundance of seedlings, saplings, or recruits in Michigan forests. Mature beech trees under stressed conditions, such as disease, are known to generate aggressive root-suckers and create dense thickets (Houston 1975). Beech decline was evident in our intensive research stands with heavy *C. fagisuga* abundance, yet no corresponding increase of vegetative regeneration occurred.

Sugar maple seedlings, saplings, and recruits were significantly less in stands with heavy *C. fagisuga* than in stands with absent *C. fagisuga* ( $p=0.001$ ,  $p=0.004$ , and  $p=0.002$  respectively). Interactive effects of *C. fagisuga* abundance and beech density were significant for seedlings, saplings, and recruits ( $p=0.008$ ,  $p=0.023$ , and  $p=0.001$ ). Sugar maple seedlings and saplings did not differ among stands with low, moderate, or high beech

density. Sugar maple recruits were significantly more abundant in stands with low beech density than in stands with moderate beech density ( $p=0.024$ ). Interactive effects for recruit regeneration of *C. fagisuga* abundance and beech density were significant ( $p=0.001$ ).

Other hardwood species included striped maple (*Acer pensylvanicum*), black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), red oak (*Quercus rubra*), American basswood (*Tilia americana*), ironwood (*Carpinus caroliniana*), serviceberry (*Amelanchier arborea*), common witch-hazel (*Hamamelis virginiana*), sassafras (*Sassafras albidum*) birch sp. (*Betula* sp.), and aspen sp. (*Populus* sp.). Regenerating conifers included eastern hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), and white pine (*Pinus strobus*) but collectively comprised less than 3.9% of total seedling, sapling, and recruit regeneration.

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# A PRELIMINARY EXAMINATION OF BEECH BARK DISEASE AND THE INFLUENCE OF SOIL MOISTURE ON BARK THICKNESS AND DISEASE STATUS IN THE NORTHERN ADIRONDACK UPLANDS

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## Abstract

In a preliminary study of beech bark disease in the 'aftermath' forests of northern Adirondack watersheds, we collected data on disease status in relation to tree diameter and the relationship between soil moisture and bark thickness in 11 plots across 6 northern Adirondack watersheds. Sixty-two percent of trees sampled were  $\leq 13$  cm in diameter and no trees over 29.4 cm were recorded, even though at least two watersheds sampled are considered old growth. As predicted, larger trees were more diseased than smaller trees and the percent dead also increased dramatically with size class. We noted that some number of trees  $\leq 10$  cm had unexpectedly high disease ratings suggesting the need in future studies to collect data on smaller diameter trees so as to be able to predict how the disease will impact the large number of trees coming up in these size classes. Trees grown in plots that had medium soil moisture (as opposed to low) had significantly thicker bark, regardless of diameter, but this had no effect on disease status of trees.

## Introduction

Beech Bark Disease (BBD) has been, and is currently, a major cause of *Fagus grandifolia* (American beech) mortality throughout the northeastern United States and Canada (Houston, 1979a). The disease is caused by the beech scale insect (*Cryptococcus fagisuga*) in combination with one or more fungi in the genus *Nectria* (Ehrlich, 1934). The scale insect possesses a 2 mm long stylet which it inserts into the bark of beech trees in order to feed intracellularly within the bark parenchyma. The damage to the bark from the feeding of the insect allows for the invasion of the bark killing fungus (Houston and O'Brien, 1998; Wainhouse and Gate, 1988). Although some resistant trees exist, the disease cycle typically culminates with the disfigurement and eventual death of the tree. In order to predict the future structure of northeastern forests we need a better understanding of how the infection proceeds in aftermath forests, and how

abiotic conditions (such as soil moisture) influence the status of the disease.

The growth/differentiation balance hypothesis (GDBH) states that when water is not readily available the fixation of carbon through photosynthesis and secondary metabolite production are both reduced. However, when water is not limiting, most of the fixed carbon is allocated to growth (Herms and Mattson, 1992). Yet, when water is available in moderation, photosynthesis is in excess of growth, and excess of carbon can be used in changes which lead to cell specialization or differentiation (Herms and Mattson, 1992) and secondary metabolite production (Ayers 1993; Lombardero, Ayers, Lorio, and Ruel 2000; Lorio 1985). One such secondary process may be the thickness of bark (Figure 1). The goal of this study was to gain a preliminary understanding of BBD and its current status in northern Adirondack uplands in a variety of watersheds, all long into the aftermath stage of the disease (Mize and Lea, 1979). The specific objectives of this study were to find out: 1) what size trees were infected with BBD and the extent to which they were infected, 2) if bark thickness was directly related to moisture availability (GDBH), and 3) if increased bark thickness increased trees defense toward BBD, therefore resulting in less evidence of the disease.

We hypothesized, based on GDBH that where water was not limiting growth (medium soil moisture availability), trees would have thicker bark which may increase their defense against BBD.

Bark Thickness vs. Water Availability

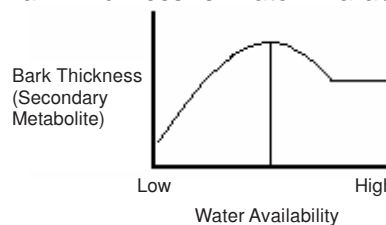


Figure 1.—Graph showing data that would support prediction of the growth/differentiation hypothesis. At periods of moderate water availability, there is an increase in bark thickness (a function of secondary metabolism).

**Table 1.—Summary data for preliminary examination of *Fagus grandifolia* size structure and disease status in 6 northern Adirondack watersheds in 2003. Data are average values and standard deviations.**

All trees				Live trees			
DBH range (cm)	n	% trees	% dead	Avg. scale index	Avg. fungal index	Avg. historical index	Avg. overall disease index
5 - 6.9	42	31	7	1.14±.64	0.29±1.08	0.10±0.37	1.52±1.73
7.0 - 13.0	42	31	9	1.88±1.31	1.14±2.07	0.52±0.92	3.55±3.33
13.1 - 19.8	28	20	20	2.39±1.50	2.61±2.47	1.43±1.55	6.43±4.10
20 - 39.1	24	17	33	2.54±1.28	3.95± 2.07	2.33±1.50	8.83±3.85

## Methods

In the summer of 2003, data were collected in six northern Adirondack watersheds. Three of the watersheds were designated forest preserve (West North Ampersand, Dutton Brook, and Roaring Brook) and three were designated managed forest (Loon Lake North, East Branch of Cold Brook, and North Stephenson Brook) by the Adirondack Park Agency.

In each watershed, two 10 m radius plots were established. Data for a total of 11 plots were analyzed due to the loss of data from one plot in North Stephenson Brook. All of the plots had a minimum of six *Fagus grandifolia* trees. Percent slope, aspect (degree), and elevation (m) were recorded for each plot. The DBH of all living and dead trees  $\leq 5.0$  cm were measured and recorded. The condition of each living tree was recorded. Indices were used to assess the condition of the lower 2 m of the bole of each tree: Scale Index, Fungal Index (D. R. Houston, personal communication), and Historical Evidence of BBD Index. The indices developed by Houston provided a standardized estimate of the presence of scale and fungal fruiting bodies. The Historical Evidence of BBD Index was a composite of two new indices developed for this study: Fissure Index and Canker Index. Since fissures on beech bark can be induced by heavy scale infestation, and cankers are an indication of previous *Nectria* presence, these indices were used to estimate past evidence of BBD even if scale or *Nectria* fruiting bodies were absent at the time of sampling. The sum of the scale, fungal and historical indices was considered an overall rating of the influence of disease (Overall Disease Index).

Bark samples were taken from the least infected area of the bottom 2 meters of each tree, typically close to DBH

if possible, by pounding a circular leather punch into the bark with a rubber mallet until it hit the vascular cambium. The thickness of the plugs was measured to the nearest mm and as a comparison, plugs were oven dried and weighed. As expected, there was a strong positive relationship between the two variables ( $r^2 = 0.80$ ).

We measured soil moisture in each tree plot gravimetrically. A volume of soil (approximately 1000 cm<sup>3</sup>) was collected on August 16<sup>th</sup> and 17<sup>th</sup> from three locations within each tree plot (5m out from the center of the plot at 100, 200 and 300 degrees). There was no precipitation on either of the two sampling dates. In the lab, 15 g of the well-mixed soil was used to determine % water weight. The three replicates were averaged. Regression analyses were used to examine relationships between disease indices, between DBH and disease indices, and between bark thickness and disease indices. Regression lines for the relationship between DBH and bark thickness for trees growing in low, medium, and high soil moisture regimes (as determined by our one time sampling) per plot were compared to determine if slopes were significantly different. A total of 136 live beech trees were sampled.

## Results

### Disease Status

More than half (62%) of trees we sampled were  $\leq 13.0$  cm DBH. Only 17% of trees were 20 cm or larger. The largest living tree has a diameter of 29.4 cm. The percent of dead trees sampled was substantially greater in trees with a diameter  $>13$  cm than in smaller trees. Thirty-three percent of beech trees with a diameter between 20 and 39.1 cm were dead (Table 1). This represents a  $> 4$  fold increase in dead trees in the largest size class over the

smallest. All indices used to estimate disease status of the trees showed an increase from the smallest diameter class to the largest (Table 1), however, the strongest positive correlation was between tree diameter and the overall disease index ( $r = 0.6558$ ,  $P = < 0.001$ ) rather than any single measure (Figure 2).

## Bark Thickness, Soil Moisture, and Disease Index

Bark thickness ranged from 1 mm to 4.4 mm with a mean of 2.11 mm. Larger trees had thicker bark ( $r = 0.8482$ ,  $P = < 0.001$ ). Figure 3 shows the relationship between DBH and bark thickness for trees grown in low, medium and high soil moisture plots. Because of its strong correlation to DBH, bark thickness was also positively correlated to the total index ( $r = 0.5980$ ,  $P = < 0.001$ ).

The minimum average percent soil moisture in plots we sampled was 23.22, the maximum was 89.9. Plots were divided into those that had low, medium, and high average percent gravimetric soil moisture, in order to determine if soil moisture influenced bark thickness as predicted by the GDBH. Four plots had average soil moisture ranging from 23.2 to 33.7% (low), 6 plots had average soil moistures ranging from 51.1 to 58.6% (medium), and only one plot had an average soil moisture of 89.9% (high). Due to the small number of trees represented in the high moisture plot those data were not included in the analyses. A statistical comparison of slopes (Zar, 1984) showed that beech trees grown in medium moisture had significantly thicker bark at a given DBH than those grown in low moisture ( $P = 0.011$ , Figure 3). There was, however, no difference in the relationship between bark thickness and disease severity at any moisture regime (Figure 4).

## Discussion

Griffin et al (2003) reported that 53% of beech stems they sampled in the Catskill Mountains of NY were between 10 and 20 cm in diameter. Similarly, we found that 51% of beech stems were in the 7 to 20 cm diameter class in our Adirondack watersheds. In contrast to Griffin et al. (2003) who reported 19% of their trees had diameters  $> 30$  cm, we sampled no live trees larger than 29.4 cm, even though two of the watersheds are known to be old growth (Ampersand and

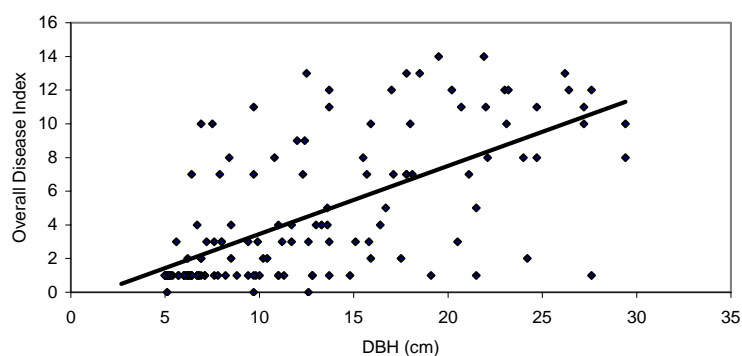


Figure 2.—Correlation between the Overall Disease Index (a composite index) and diameter for *Fagus grandifolia* in 11, 10 m radius plots in 6 northern Adirondack watersheds during the 2003 growing season ( $n = 136$  trees)

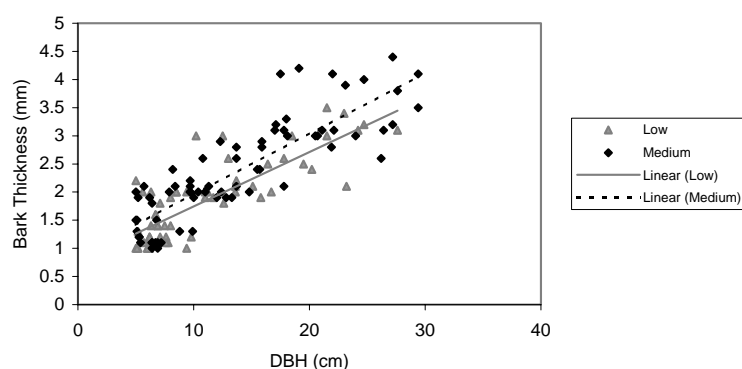


Figure 3.—Diameter vs Bark thickness for beech trees grown in low and medium soil moisture. Trees growing in medium soil moisture plots had thicker bark than those growing in plots in low soil moisture plots.

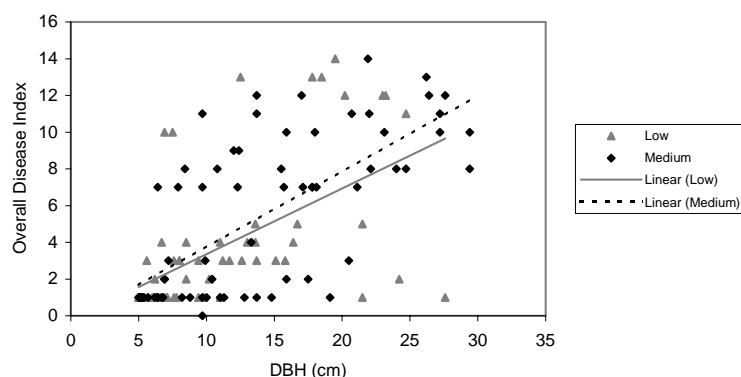


Figure 4.—Diameter vs. Total Disease Index at low and medium average percent soil moisture per plot. Regression lines were not significantly different for trees growing in low versus medium soil moisture.

Dutton Brook). Forrester and Runkle (2000) sampled beech in an old growth beech/maple forest in 1985 (minimally impacted by the disease) and reported that

stems were equally distributed between 10 - 24 cm, 25 - 49 cm, and 50+ cm. It is likely that our small sample size (n=136 trees) precluded us from sampling some larger trees, however, it is reasonable to conclude that the complete absence of large beech, even in plots in old growth forests, is in large part due to mortality of those trees. Based on visual observations of evidence of disease, mortality of all standing dead beech we did measure was apparently due to BBD. An evaluation of coarse woody debris in these forests would provide valuable information, at least with respect to recent history of beech mortality.

Disease severity increased as diameter increased. This trend is corroborated by many other studies that suggest that larger trees are more susceptible to BBD than smaller ones (Gavin and Peart, 1993; Griffin et al., 2003; Forrester et al. 2003). We sampled trees as small as 5 cm in diameter because we were interested in whether smaller trees, in the absence of large trees, may be becoming proportionately more infected by the scale and associated fungi. While there are few published data to compare the disease status of trees smaller than 10 cm diameter, it is worth noting that trees within the 7 - 13 cm diameter class had an overall disease rating of  $3.55 \pm 3.33$  (SD) and seven trees within that size class had much higher overall disease ratings of between 7 and 11. As we develop models to predict the future structure and composition of beech in aftermath forests, it is critical to make reasonable assumptions about the way the disease will affect the growth and reproduction of the 'new' beech understory that often results from the death of large beech.

The fact that large trees had thicker bark as well as higher disease incidence and mortality makes clear that thick bark affords no major protection from disease agents. This is not necessarily surprising since characteristics of bark on older trees such as cracks, fissures, and general roughness are thought by field experts to be at least partially responsible for the increased susceptibility of larger trees to scales and fungi (D. R. Houston, Pers. comm.). We had hypothesized, based on the GDBH, that medium soil moisture would increase bark thickness (at any diameter) and that this difference may afford some protection from BBD. Soil moisture did significantly increase bark thickness, supporting the GDBH. This increase, however, had no influence on the relationship between diameter and disease status.

## Acknowledgments

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**SURVIVAL OF THE FITTEST:  
BEECH BARK DISEASE-RESISTANT  
BEECH WILL LEAVE MORE OFFSPRING**

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**Abstract**

In fully stocked (unthinned) stands on the Monongahela National Forest (MNF), beech bark disease (BBD)-resistant (canker-free) beech trees have the potential to leave more offspring than BBD-susceptible (heavily cankered) trees. Trees susceptible to BBD were replaced by red spruce seedlings and saplings (plot 1) or had their place in the tree canopy filled in by the expanding crowns of cucumber magnolia (plot 1), black cherry (plot 2), or sugar maple (plot 3). It is possible that some of these stands were cutover long before BBD arrived and thus represent stands of stump sprout origin and not seed origin. If this were the case, there would be clonal groups and thus potential pockets of BBD resistance. There were more suckers within 1.5 m of resistant trees than within the same distance of cankered trees and few or no suckers within 1.5 m of dead beech. These dead trees (genes) had already lost out in the struggle for survival.

**Introduction**

Soon after the discovery of beech bark disease in West Virginia by Mielke *et al.* (1982), three populations of beech trees were selected for survival monitoring. Each population contained approximately 200 trees. Within 15 years, mortality attributed to BBD was approaching 50 percent. A small cluster of apparently resistant trees was also detected in one plot. Apparent resistance is being defined as an absence of both beech scale and any cankering. After almost 20 years of exposure to BBD, nine completely smooth-barked trees were found in the original cohorts. All “resistant” trees were found in one cohort. Thus, at least 1.5 percent of the MNF beech population would seem to be resistant based on this sample. However, the resistant trees are highly clustered. Additional resistant trees were found growing adjacent to the plot containing the nine resistant trees.

**Methodology**

Preliminary observations indicated that the root plate for most of the standing beech stems in theses plots was about 3 m in diameter. Observations and some

excavations supported the hypothesis that root sprouts within 1.5 m of the root flare were attached to lateral roots of that tree. It was observed that where standing dead and resistant trees were adjacent to each other, the root plate halo of the dead tree was not invaded by sprouts from the adjacent tree. These observations supported the concept of a 3 m diameter root plate.

**Measurements Taken**

- Trees were classified as **resistant, standing dead, or heavily cankered**. (After 20 years of exposure to BBD there were almost no lightly cankered trees.)
- Root flare diameters were measured so that a 1.5-m radius from the pith could be computed.
- Number of sprouts per tree.
- Height of sprouts.
- Basal caliper (diameter) of sprouts.
- Presence or absence of beech scale.
- Presence or absence of the secondary scale *Xylococcus betulae*.
- Presence or absence of *Neonectria*.

**Results**

**Summary of Results**

	Resistant*	Cankered**	Dead***
Number of Trees	10	15	15
Number of Sprouts	240	51	28
Average Number of Sprouts	24.0	3.4	1.9
Average Diameter (cm)	2.2	1.6	2.6
Average Height (cm)	189	130	196

- \* Resistant = Scale & canker free = smooth bark
- \*\* Cankered = Heavily cankered
- \*\*\* Dead = Standing dead

**Discussion**

In the struggle for life, there are winners and losers; some individuals pass their *superior genes* onto the next generation and the losers simply die out. In the case of BBD in West Virginia, the winners could be viewed as the (superior) resistant trees and losers as the dead and heavily cankered trees. However, as in all games of chance, not all losers are equal. In the case of BBD, dead trees are bigger losers than heavily cankered trees. **Or are they?** The data indicate that although dead trees may have slightly fewer sprouts associated with them, the sprouts will be taller



This dead beech tree with one heavily cankered root sprout growing within the root plate area is a loser in the struggle for survival. The adjacent sapling is one of the beech-replacing sugar maples. The blue tape marks the 3.0 m-diameter root plate.



Heavily cankered (living) beech tree with one root sucker attached within 1.5m of the pith. The large adjacent tree is one of the canopy replacing sugar maple trees. The blue tape is at 1.5 m from the pith. A previously BBD-killed, decaying beech is lying in the background.



A winner in the struggle for survival, this BBD-resistant beech tree shows some of the 41 sprouts growing within 1.5 m of the pith.

and have a larger basal diameter. In the case of dying trees, they give up their growing space to their root sucker, which takes advantage of this growing space and puts on both radial and height growth until it, in turn, becomes attacked by scale insects. Ultimately, it will suffer the same fate as its parent tree. It is these sprouts associated with dead trees that would have produced the aftermath forest were it not for replacement of beech by sugar maple and black cherry. ***One way to easily cause a shift in the beech gene pool would be to cut all suckers within 1.5 m of a BBD-killed beech.*** In the long run (provided there is no global warming), these sites will revert to red spruce. Prior to turn-of-the-century logging, these were red spruce sites.

In Charles Darwin’s “Origin of Species,” we find the following quote: ***“Everyone has heard that when an American forest is cut down a very different vegetation springs up; but it has been observed that ancient Indian ruins in the Southern United States, which must have formerly been cleared of trees, now display the same beautiful diversity and proportion of kinds as in the surrounding virgin forest.”*** Darwin predicted the return of spruce (*sans* man’s intervention).

Occasionally, a heavily cankered pole was observed adjacent to a dead beech tree in our survey. In this case, we are observing the kind of aftermath forest observed in New England, *sensu* Houston (1975), where the aftermath stand was as susceptible to attack as the first rotation. In New England, many of the more valued timber species had been logged and the defective beech was allowed to continue growing into the highly defective aftermath forest. On the MNE, the defective

beech is being outcompeted by healthy sugar maple, aggressive black cherry, healthy cucumber magnolia, and encroaching red spruce saplings.

In total contrast, in a similar beech plot on the Allegheny National Forest (ANF) that had been thinned to almost pure beech at or before it fell behind the killing front, significantly fewer beech trees have died and residual trees, which have now reached sawlog size, are cankered-frequently heavily cankered. This plot is the closest example of the classical aftermath forest to be found on the ANF. However, other stands on the killing front already heavy to beech might well become classical aftermath forest.

Although only a few of the cankered trees had beech scale, none of the resistant trees had any beech scale. The native, secondary scale (*Xylococcus betulae*) was found on 11 of 15 cankered trees, whereas two resistant trees had one *Xylococcus* scale each.

By combining the dead and cankered classes of beech, the trees can be grouped as winners and losers.

	Winners (Resistant)	Losers (Cankered or Dead)
Average Number of Sprouts	24.0	2.6
Average Diameter	2.2 cm	2.1
Average Height	189 cm	163

Thus, the case could be made that individual winners leave nine times as many sprouts as losers. In addition, winners (resistant trees), on average, had taller and larger-

diameter sprouts. However, as with games of chance, there are many times more losers than winners, and although beech is dropping out of the canopy, it will have a presence in the understory for a long time, if not in perpetuity.

Avoidance of a classical aftermath forest would seem to be dependent upon the presence of other species that can outcompete American beech, which loses its ecological advantage when impacted by the additional stressor, BBD.

## Summary

When beech is a component of a biologically diverse, healthy forest, BBD is a beech-specific stressor that causes the replacement of most beech by more fit species.

The small percentage of resistant trees has the potential to produce nine times as many sprouts as susceptible trees. However, there are more susceptible trees than resistant trees, which produce a larger number of smaller and susceptible sprouts. Beech will not disappear from the forest; its role will change and the wildlife impacts of reduced mast will be important!

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## **SUGAR MAPLE AND BEECH DYNAMICS IN BEECH BARK DISEASE AFTERMATH FORESTS OF THE CATSKILL MOUNTAINS, NY**

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Beech bark disease (BBD) has been present in forests of the Catskill Mountains since the mid 1940's, and currently these forests are in the aftermath stage of disease progression. Previous work has shown that BBD in these aftermath forests is most severe in both elevation bands and watersheds that have the highest basal area of beech. In this study we examined 30 years of stand-level change (1970-2000) in BBD-affected Catskill forests to determine if effects of the disease during this period match the elevational distribution of disease severity. Beech basal area and density declined in mid-elevation aftermath stands, but increased in high and low-elevation aftermath stands. Changes in sugar maple basal area and density mirrored changes in beech; sugar maple basal area and density increased in mid elevation aftermath stands and decreased or remained constant in high and low-elevation aftermath stands. The effects of BBD on community structure in aftermath forests paralleled the distribution of disease severity across elevation found in previous studies. In BBD aftermath forests of the Catskills, the overall abundance of beech and sugar maple has not changed dramatically during the aftermath period. However, BBD has altered the elevational distribution of these two major co-dominant forest species.

## **EFFECTS OF BEECH BARK DISEASE ON CARBON AND NITROGEN CYCLING IN CATSKILL FORESTS**

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Our research in the Catskill Mountains of southeastern NY indicates that one of the effects of beech bark disease in this region is increased dominance of the forest by sugar maple. Because the chemical quality of sugar maple litter is different from that of beech litter, the shift from mixed beech-maple forests to maple-dominated forests may entail significant changes in nutrient cycling. We identified 22 stands along a gradient from relatively healthy mixed beech-maple stands to stands which formerly had a significant beech component but are now dominated by sugar maple. Across this gradient, we found that increasing dominance of sugar maple was correlated with increases in: (1) litter decomposition rates, (2) nitrification fraction (the percentage of mineralized nitrogen that is nitrified), (3) <sup>15</sup>N in soils, and (4) nitrate leaching in soil solution. These results indicate that shifts in species composition resulting from beech bark disease are increasing rates of carbon turnover and N cycling in soils, especially the production of nitrate. This change alters the ability of these forests to retain atmospherically deposited nitrogen.

# EFFECTS OF AN INTRODUCED PATHOGEN ON RESISTANCE TO NATURAL DISTURBANCE: BEECH BARK DISEASE AND WINDTHROW

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Introduced pathogens have caused widespread declines in a number of important tree species in forests of eastern North America, including dominant species such as beech (*Fagus grandifolia* Ehrh.). Most studies have focused on changes in forest composition and structure as a direct result of mortality caused by the pathogen. Our studies of windthrow resistance in forests of northern New York and northern Michigan demonstrate that resistance of beech trees to windthrow is severely reduced by beech bark disease (BBD). Beech and sugar maple (*Acer saccharum* Marsh.) have identical resistance to windthrow in forests of northern Michigan, where BBD is absent, whereas beech has much lower resistance in northern New York, where BBD is present. Within New York, the severity of BBD infection on individual trees has a significant negative effect on resistance to windthrow. We tested potential consequences of this to long-term composition and structure in these forests using a simulation model, SORTIE. We found that species such as yellow birch (*Betula alleghaniensis*) and hemlock (*Tsuga canadensis*) increased dramatically in basal area, and that species evenness early in succession increased due to the effect BBD has on the creation of new seedbed substrates. Our results highlight the indirect effects that host-specific pathogens can have on community dynamics and species coexistence in forests.

## Knowledge Gaps and Research Priorities

### *Knowledge Gaps*

- *What factors affect susceptibility to the disease?*
  - Nitrogen concentrations in bark (the relationship to concentration or C/N ratios in soil?)
  - Drought stress
  - Bark anatomy (fissures cankers overall roughness)
  - Ecology of the scale insect
  - Ecology of the fungus
- Examine these factors in pure stands or plantations versus naturally regenerated NHF
- Need to understand the evolution and mechanisms of resistance (see genetics)
- How does the disease influences regeneration strategies/or how it compares to strategies in Europe?
- What are the mechanisms that influence the point of origin for new infestations?
- What drives population dynamics of the scale insects?
- How does lichen cover relate to disease status?
- Collect empirical data that can feed models — what is the time frame of temporal and spatial changes?
- Beech Regeneration (specifically for regeneration (seedling/sapling) strategies of beech and co-occurring species).
  - Does diseased or newly regenerating beech produce same amount of mast – or will it over time?
  - Does the regeneration of beech preclude the success of other species, i.e. sugar maple?
  - Sprouts versus seeds - how physiology of these different forms of regeneration compare.

### *Research Priorities*

- Develop long-term monitoring of broad geographic distribution of stands
  - Extensive plots
  - FIA plots
  - Research plots
  - Evaluation plots
  - Region specific
  - Impacts on carbon cycling = funding? Ecosystem level
  - Formation of a BBD working group
- Develop intensive monitoring of smaller plots within those stands (extensive plots)
  - Hydrologic effects/responses
  - Soil characteristics
  - Ecosystem processes (cycling rates)
  - Stand characteristics
  - Demographic characteristics

## **Section 3:**

### **Interactions between BBD and Wildlife**

# POTENTIAL EFFECTS OF BEECH BARK DISEASE AND DECLINE IN BEECH ABUNDANCE ON BIRDS AND SMALL MAMMALS

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## Abstract

Non-native forest pests and diseases present an important threat to North American forests. Some impacts of these diseases on wildlife have been documented. We use these documented examples as well as information about the biology of beech (*Fagus* spp.) to discuss some of the potential ecological impacts of beech bark disease on North American forests. Beech bark disease continues to have significant impacts on beech resources within the range of American beech (*Fagus grandifolia*). This paper reviews some of these potential impacts as they relate to wildlife, especially birds and small mammals. The resources provided to wildlife by American beech include vegetation structure, mast, and cavities. As beech bark disease changes the structure of beech populations, these resources will be altered, and subsequent impacts on animal communities are likely. These impacts may result both in population increases and decreases in taxa that rely on beech for various resources, but these effects should be considered to be negative because they are the result of a non-natural disturbance agent.

## Introduction

Along with the threats posed by habitat loss and a changing global climate, the introduction of exotic species is one of the most serious threats to ecosystem processes and biodiversity worldwide (Mooney and Hobbs 2000). Much attention has been drawn to exotic organisms and some of their direct impacts on native ecosystems. Although the autecology of exotic species is of interest, there is a potential to greatly expand our knowledge of general ecological relationships by simultaneously studying exotic species and the environments they invade (Crooks 2002). Few studies

have sought to examine the potential broader influences of exotics in terms of both direct and indirect effects on population and community ecology in newly invaded areas. In recent years, the study of multi-trophic level community interactions has become common in the field of ecology (e.g., Jones et al. 1998). These types of studies are needed to examine the complex relationships between exotics and the systems they invade. Studies of this kind go beyond the historically preferred examination of pair-wise interactions which, while their relative simplicity makes them favorable for short-term investigation, may oversimplify the system.

The invasion of forests by beech bark disease (BBD) presents an opportunity to examine the potential cascading effects of a disease-induced environmental disturbance. This widespread invasion of a highly virulent exotic disease complex allows us to examine a level of environmental manipulation that would not normally be feasible. Any understanding of how exotics behave as they invade a novel habitat and how native organisms respond to invasion is useful in predicting, managing, and potentially preventing similar invasions in the future (Lewin 1987).

Invaders with the largest impacts are those that directly modify ecosystems and have cascading effects through many trophic levels (Crooks 2002). Significant effects on natural communities may also occur if ecosystem engineers are removed from a system (Jones et al. 1994). This may be particularly relevant when considering exotic species that have strong negative effects on dominant tree species that can be considered autogenic engineers, i.e. ecosystem engineers that change the environment via their own physical structures of living and dead tissues.

In this paper we present several documented impacts of forest pests and diseases as well as information about the importance of the beech resource to animal populations. We use this information to discuss the potential impacts of beech bark disease on wildlife populations in North American forests.

## Impacts of Exotic Pests and Pathogens on Forest Systems

A frequent direct impact of exotic species on forests is the loss of overstory trees, and these canopy losses can

directly affect animal populations. For example, in northern Minnesota mixed deciduous forests, Dutch elm disease, drought, and windstorms altered species composition of trees and converted closed canopy forests to a more open habitat. Increased density of ground vegetation and increased light levels resulted in increased breeding by bird species that preferred this type of habitat (Canterbury and Blockstein 1997). Additional evidence documenting wildlife impacts exists from Dutch elm disease in Britain. Some bird species declined from 1971-79 on plots affected by Dutch elm disease compared with unaffected plots, while some bird species experienced short term declines and subsequent recovery. In addition, one species (willow warbler, *Phylloscopus trochilus*) appeared to benefit from the loss (Osborne 1983).

The gypsy moth (*Lymantria dispar*) provides similar examples of wildlife impacts related to changes in canopy structure. In Pennsylvania oak stands with gypsy moth, black capped chickadees (*Parus atricapillus*) and wood thrushes (*Hylocichla mustelina*) were less abundant in defoliated stands, while house wrens (*Troglodytes aedon*) were more abundant in defoliated stands. However, although a defoliated forest may look devastated, the overall breeding bird community may not be greatly affected (DeGraaf 1987). In West Virginia oak stands, gypsy moth defoliation is not likely to be a devastating ecological event for shrub and sub-canopy nesting birds. In fact, more nesting habitat for these birds may be created as a result of defoliation (Bell and Whitmore 2000).

Multi-trophic level studies have demonstrated the wide range of impacts an exotic pest may have on forest communities. For example, in oak dominated forests in Massachusetts, increased density of gypsy moth was associated with declines in density of white-footed mice (Elkinton et al. 1996). Changes in density of white-footed mice were positively correlated with density of acorn crops. Therefore, reduced mast production reduced the population of this gypsy moth pupal predator (Elkinton et al. 1996). Additional evidence suggests that gypsy moth outbreaks result from reduced populations of white-footed mice, while addition of acorns increases mouse density, deer density and black-legged tick density (Jones et al. 1998).

These examples all suggest that the introduction of a non-native forest pest or pathogen can result in changes

to native wildlife populations. In the examples outlined above, changes in vegetation structure and mast availability appear to be the drivers of subsequent changes in animal populations. It is likely that beech bark disease will impact animal populations in a similar manner.

## The Importance of Beech Resources

American beech is an important component of many northern hardwood forests in the eastern United States. Detailed studies of the closely related European beech, *Fagus sylvatica*, have demonstrated the importance of beech to herbivorous and wood-infesting insects (e.g., Nilsson and Baranowski 1997), and insectivorous and granivorous birds and mammals (Nielsen 1977; Nilsson 1985).

As a co-dominant tree within the beech-maple forest type, beech influences many physical and biotic properties of the forest, including maintaining canopy closure and understory light and moisture regimes. American beech also provides other important resources used by arthropods, birds, and mammals. These include food (foliage, mast/beechnuts), foraging locations (bark and foliage; Holmes & Schultz 1988), nest site locations (cavities and open nests; Robb & Bookhout 1995), and travel pathways facilitated by coarse woody debris (Greenberg 2002; Graves et al. 1988). The masting aspect of beech biology is particularly important to some species of birds (Perrins 1966; Linnard 1987) and mammals (Wolff 1996; Jenson 1982) that rely heavily on this periodic food source.

Masting of American beech was monitored in Michigan from 1959-68. During that period, there was one high mast year, 2 years where mast failed, 4 low years and 3 intermediate years. Of beech nuts caught in traps, less than 10% of them were sound (Gysel 1971). In studies of masting of European beech in Denmark from 1967 to 1974, 8-61% of the endosperm in the beech nuts was lost to insects and barren seeds. After dispersal, seed predation was found to be low, and between one and 34 g of seed were available per square meter per year. Of the seed production, 90-95% entered the detritus pathway (Nielsen 1977). The importance of mast has been studied in other systems. For example, in Virginia oak forests, deer consumed 70% of acorns placed out during mast fall, and chipmunks and squirrels consumed 61% of

acorns placed out later in the fall. It was concluded that high deer densities may limit populations of more mast dependent animal species, particularly at low acorn densities (McShea and Schwede 1993). In mast years in European beech forests in Denmark, rodent consumption was estimated at 1.0-10.3% of endosperm production, while in non-mast years, rodent consumption of mast was 30-100%. Bank vole (*Clethrionomys glareolus*) populations varied more than other small mammals, and outbreaks of bank voles occurred in years following high seed production (Jensen 1982).

Beech mast can also have important effects on birds. In European beech forests in Sweden, densities of nuthatches (*Sitta europaea*) in the fall were positively correlated with beech mast crop. Territory size decreased with increased beech mast, and birds assessed winter food supply in the fall and adjusted their territory sizes accordingly (Matthysen 1989). Studies of nuthatches in Belgium indicated that fall survival of juvenile nuthatches was higher in mast years, though the same effect was not evident for adults, and winter survival of nuthatches was not related to beech mast (Enoksson and Nilsson, 1983). In the case of great tits (*Parus major*) in Europe, there are more birds in a given summer than the previous summer if there is a good mast crop during intervening winter. Evidence suggests that eruptive movements of great tits are a result of food shortage rather than high population density (Perrins 1966).

## Description of the Disease and its Effects

Like all tree species, American beech is subject to damage by a broad array of insects and pathogens. Beech bark disease, an exotic disease complex consisting of an exotic scale insect, *Cryptococcus fagisuga*, and several species of Ascomycete fungi in the genus *Nectria*, has the potential to cause dramatic declines in populations of American beech (Houston 1994). Beech mortality ranges from 50-85% in the killing front (Houston et al. 1979; Houston 1994) and may occur in 3-6 years after the scale insect is detected in an area (McCullough et al. 2001).

The beech scale insect, *Cryptococcus fagisuga* (Homoptera: Cryptococcidae) was unintentionally introduced to Nova Scotia in 1890 (Houston and O'Brien 1983). Since that time, it has spread throughout the eastern United States, as far south as North Carolina and Tennessee, and as far north and west as the upper and lower peninsulas of

Michigan (McCullough et al. 2001). *C. fagisuga* has a one year asexual life cycle (Wainhouse and Gate 1988). The crawler or nymph stage is responsible for dispersal, which is facilitated by wind. Second stage nymphs secrete a white, woolly substance that protects them from desiccation, predation, and parasitism and is the most obvious sign of infestation by *C. fagisuga*. There are few natural enemies, although some species of ladybird beetle (Coleoptera: Coccinellidae, *Chilocorus* spp. and *Exochomus* spp.) and gall gnats (Diptera: Cecidomyiidae, *Lestodiplosis* spp.) may be effective in reducing populations of *C. fagisuga*, especially at high scale densities.

The relatively thin bark of *F. grandifolia* makes it both vulnerable to injury and a prime target for sap-feeding insects like the beech scale (Burns and Houston 1987). Colonization is common in bark fissures, callous tissue near old wounds, areas under branches, and patches of bark covered by protective coatings of mosses and lichens (Houston et al. 1979). Older (>15 years in European beech), larger (>8" diameter) trees appear to be more susceptible to attack by the beech scale, although younger trees may also be colonized (Wainhouse and Gate 1988). Colonization and feeding activity of the beech scale leaves host trees vulnerable to infection by various species of *Nectria* fungi (Houston 1994).

In North America, beech trees infested with the beech scale insect are susceptible to infection by three species of *Nectria* fungi; *Nectria coccinea* var. *faginata*, *N. galligena*, and *N. ochroleuca* (McCullough et al. 2001). *N. galligena* typically infects trees in stands recently colonized by beech scale, while the more dominant BBD pathogen *N. coccinea* var. *faginata* often replaces *N. galligena* over time (Houston 1993). *N. galligena* is a native fungus that causes perennial cankers on hardwoods, but *N. coccinea* var. *faginata* is an exotic species that has followed the spread of the beech scale (Houston 1994). *N. ochroleuca* has been found in association with BBD in Pennsylvania, West Virginia, and Ontario (McCullough et al. 2001).

Fungal infection by *Nectria* often results in tarry spots that ooze a brownish fluid (Houston and O'Brien 1983). The outer and inner bark is killed by the fungi; an orange color is present on the inner bark where *Nectria* is invading. If large areas are infected, the tree may be girdled and die; smaller areas of infection cause formation of callus tissue.

The pattern of spread of BBD is usually classified into three stages or fronts (Shigo 1972; Twery and Patterson 1984): the advancing front, the killing front, and the aftermath forest. The advancing front is where the disease appears for the first time with infestation by the beech scale (Houston and O'Brien 1983). Although *C. fagisuga* is present at the advancing front, infection by *Nectria* is just beginning in these areas (Shigo 1972). Stands may be heavily infested with scale without *Nectria* infection for several years, particularly if a forest is isolated from areas where BBD is more prevalent (McCullough et al. 2001). The killing front refers to stands where both beech scale populations and infection by *Nectria* are high with associated high tree mortality (Shigo 1972).

The final stage, the aftermath forest, is characterized by residual beech trees that are declining or trees that escaped the disease through chance or resistance (Shigo 1972); when mortality of beech is high and all agents of the disease complex are endemic, a forest is considered to be in the aftermath zone. Populations of beech scale tend to be lower in these areas (Shigo 1972), and remaining trees are often small and deformed (Houston 1994). The loss of large trees leads to the release of beech sprouts from the roots of the dying trees. These can form dense thickets that inhibit the growth of sugar maple seedlings and saplings and profoundly alter the ground and subcanopy vegetation layers (Holmes and Sherry 2001; Houston 1975). Resistance of American beech to BBD is rare and is the subject of ongoing studies in Michigan (McCullough, pers. comm.).

## Ecological Impacts of Beech Bark Disease

The progression of ecological events associated with BBD can be represented along a continuum of change from a forest with beech as a prominent overstory tree species to a forest with beech as a rare or uncommon overstory species (Figure 1). Numerous ecosystem, population, and community level changes are likely to be associated with this progression. Arthropod and vertebrate communities will likely respond to the initial arrival and spread of BBD as a result of changes in vegetation structure, mast production, and availability of cavities (Figure 2).

We envision a sequence of changes unique to different taxa and functional guilds. These changes will result from the loss of American beech as a dominant canopy tree species and general changes in forest structure as the

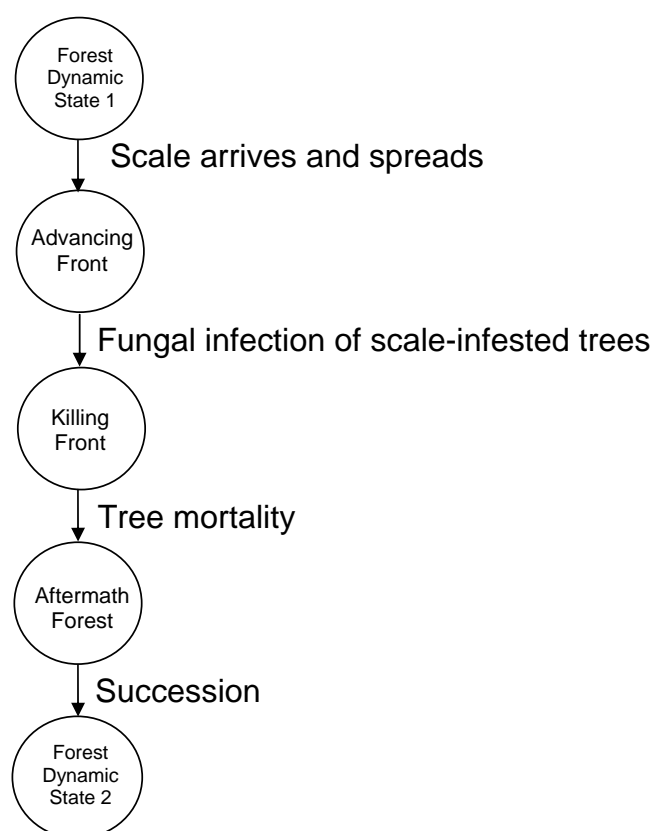


Figure 1.—Ecological progression of events associated with beech bark disease. American beech declines in importance and becomes an uncommon overstory species in forest dynamic state 2.

BBD disturbance progresses. A massive die-off of a large proportion of overstory trees, regardless of species, will result in large-scale changes in habitat structure. Additionally, beech has some unique functional roles (e.g., masting) in the forest community not easily replaced by other tree species. Thus, after recovery of the forest from the BBD disturbance, the forest community will likely be structurally and functionally different than the pre-disturbance forest. Moreover, successional trajectories following BBD disturbance will likely differ from successional patterns following other types of disturbance because of continued impacts of the disease. Arthropod, bird, and small mammal communities are all likely to be sensitive to these changes.

When considering responses to beech bark disease, positive and negative effects, in terms of increases and decreases of populations, may be evident. Some wildlife populations may increase (e.g. woodpeckers, salamanders, some fish species) because of increases in dead and dying trees and coarse woody debris, while

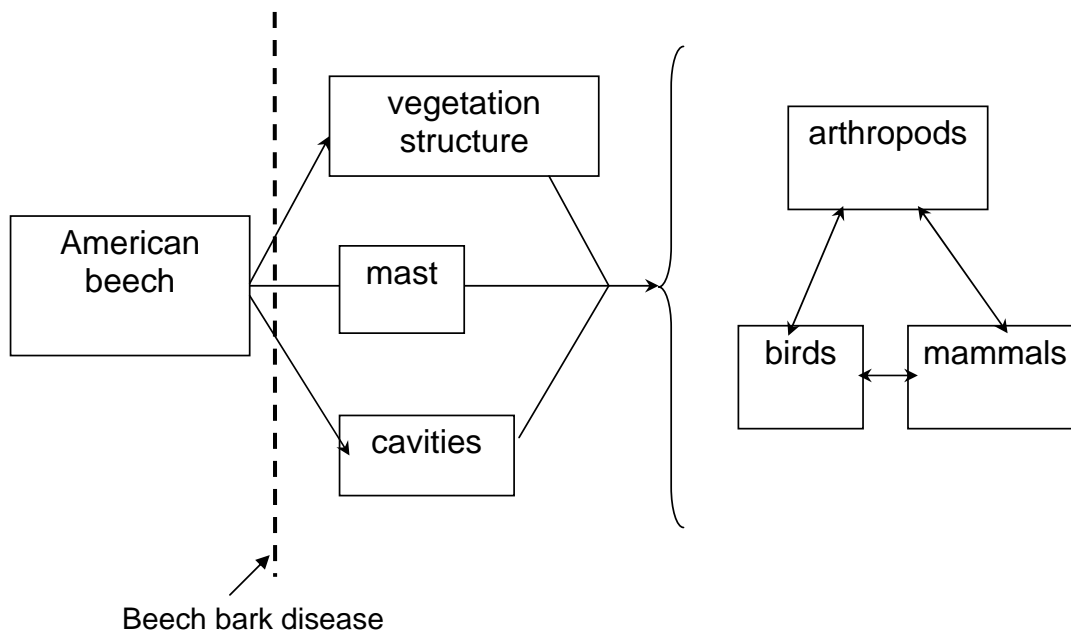


Figure 2.—Resources provided by American beech to arthropod, bird, and mammal communities. The dotted line represents the presence of beech bark disease which may change resource availability for these communities. Note: The interactions proposed in this figure are within the context of Figure 1, and the magnitude and direction of the interaction will vary, depending on the stage of infection in which the interaction occurs.

some wildlife species may decline (e.g. canopy nesting and foraging birds) because of the loss of a dominant canopy species. The changes that do take place in animal populations will depend upon how the specific resource they utilize is changed by BBD. That resource will likely be related to beech mast and vegetation structure. Whether populations increase or decline, both responses are the result of a non-natural disturbance agent and therefore should perhaps be considered to be negative. Diseased beech forests have reduced foliage and mast, and increased snags, coarse woody debris and invertebrates on the main stem. The potential long term effects of beech bark disease include the loss of a dominant or codominant tree species, the loss of major mast producing species in many areas, elevated coarse woody debris and altered tree community structure. Long term impacts on animal populations will depend upon the resilience of each population to the changes that occur as a result of BBD.

## Conclusion

Indirect impacts of exotic tree pathogens on wildlife are often difficult to measure and may be confounded by many other factors. However, some hypothesized effects

can be anticipated, and can thereby inform and guide research and management. More research is needed to characterize impacts on wildlife populations and to demonstrate the mechanisms underlying these impacts. An improved understanding of these impacts may be useful in policy decisions relating to exotic species introductions, and to the restoration of beech forests.

The current natural range of beech includes the eastern portion of the Upper Peninsula of Michigan, and contains uninfected areas as well as areas in the advancing and killing fronts. The absence of beech from the western part of the Upper Peninsula allows comparisons between sites with and without beech, as well as between sites with and without beech bark disease. We have research underway to examine the relative value of American beech vs. sugar maple seed to small mammals, to investigate if and how small mammal populations/communities are affected by the incipient invasion of BBD, and to determine the effects of beech bark disease on wood infesting insects, ground dwelling arthropods and other insect taxa that can be used in assessments of biodiversity.

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# ALTERNATE YEAR BEECHNUT PRODUCTION AND ITS INFLUENCE ON BEAR AND MARTEN POPULATIONS

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## Abstract

Wildlife managers in the northeastern USA are interested in determining the amount of American beech (*Fagus grandifolia*) needed on the landscape to support bear and other wildlife populations. The need to understand the dynamics between beechnut production and wildlife populations is heightened by the impact of beech bark disease and the increased use of intensive forestry practices on commercial forests in the Northeast. Long-term monitoring of Maine's black bear (*Ursus americana*) and marten (*Martes americana*) populations indicate that alternate year patterns in bear reproduction and marten harvest rates may be correlated to beechnut production. In northern Maine, 22% of the female black bears that were reproductively available reproduced following falls when beechnut production was poor. The proportion of reproducing females increased ( $P < 0.001$ ) to 80% following falls when beechnut production was high. After 21 years of a consistent alternate year pattern in bear reproduction, the pattern changed in 2003. In 2003, the proportion of females producing cubs did not increase as expected but rather increased in 2004, after a poor beechnut crop. For marten, trapping harvests rates exhibited a strong alternate year pattern, where harvest rates during odd-numbered years were double that of even-numbered years. Marten harvest patterns were similar ( $P < 0.001$ ;  $r^2 = 0.65$ ) in northern Maine and the Adirondacks of New York, and appeared to be inversely related to beechnut production. Beechnut production in the Adirondacks was cyclical (first order autocorrelation of -0.69) and fluctuated in an alternate year pattern from 1993 to 2003. We propose two hypotheses to explain the

variation in marten harvest rates. (1) Marten harvests decrease during years when beechnut production is good because of the decreased vulnerability of marten to baited traps. (2) Increased energy intake during a good beechnut year increases marten kit production or survival. This results in a large number of juveniles that may be trapped the following fall and increases the overall number of marten taken by trappers.

## Introduction

Throughout the range of American beech (*Fagus grandifolia*), beechnuts are an important food for many species of wildlife (e.g., Glover 1949; Nixon et al. 1968; Gysel 1971). However, it is in the northern most part of this tree's range, where other mast producing trees (e.g., oaks [*Quercus* spp.]) are scarce, that beechnuts may have their greatest influence on wildlife populations (McLaughlin et al. 1994, McDonald and Fuller 1994). In Maine, beech trees normally have crop failures every other year (i.e., on odd-numbered years) and good nut production on even-numbered years (Schooley 1990). This alternate year pattern of beechnut production may influence the behavior and population demographics of a number of wildlife species (e.g., McLaughlin 1998).

Wildlife managers in the northeastern USA are interested in determining the amount of American beech needed on the landscape to support black bears (*Ursus americana*) and other wildlife populations. Over the last 10 years, intensive forest management practices have increased the rate at which beech trees are being removed from commercial forests. In addition, beech bark disease remains prevalent in the Northeast, which may decrease the quantity of beechnuts produced over the lifetime of infected trees (but see McNulty and Master this proceedings). To insure that enough mature (40 yr +) beech trees are available for wildlife and that commercial forests remain productive, wildlife managers would like to develop science-based guidelines for foresters to use in managing beech as an important forest component. As a first step towards achieving this goal, we (1) reexamined beechnut production patterns in the Adirondack Mountains of northern New York and Maine, (2) tested the hypothesis that alternate year production of beechnuts influences black bear reproduction in northern Maine, and (3) examined the relationship between beechnut production and American marten (*Martes americana*) trapping harvests in Maine and northern New York.

Bears in the Northeast preferentially feed on high-energy foods, especially hard mast, such as beechnuts and acorns, when they are available (Hugie 1982; Elowe and Dodge 1989; Costello 1992; McDonald and Fuller 1994). Beechnuts have a protein content equivalent to corn (ca 11% dry mass) and a fat content (ca 17.3% dry mass) that is >5 times the fat content of corn (Elowe and Dodge 1989). The fat content of beechnuts may be particularly attractive to black bears. Black bears depend on internal fat deposits for the energy needed for hibernation and reproduction, and hence, feed on foods that maximize their caloric intake (Nelson et al. 1983; Harlow et al. 2002).

Food availability or nutrition is often the factor that limits the growth of black bear populations, with the reproductive success of females, being the most important factor influencing population growth (Garshelis 1994). Females that do not attain a certain mass threshold will not produce offspring (Elowe and Dodge 1989; Samson and Huot 1995), and the percentage of females producing cubs decreases during poor food years (Rogers 1976). Nutrition also influences the age of first reproduction (Rogers 1987). In states like Pennsylvania, where the variety of foods provides bears a high level of nutrition every year, females usually produce cubs by age 4 (Rogers 1987). In contrast, the mean age of first reproduction for female bears in northern Maine is 6 years, because one of their primary fall foods (i.e., beechnuts) is not available every year (McLaughlin et al. 1994). In addition to the effect nutrition can have on reproductive rates, nutrition may also affect cub survival (Rogers 1976, 1987).

The American marten is a forest dwelling species that opportunistically feeds on a variety of small mammals (e.g., red-backed voles [*Clethrionomys gapperi*], snowshoe hare [*Lepus americanus*], and red squirrels [*Tamiasciurus hudsonicus*]), fruits, and nuts (e.g., raspberries [*Rubus* spp.]; Martin 1994; Lachowski 1997). Although the use of beechnuts by marten has not been well described, fisher (*Martes pennanti*), a closely related species, will consume large amounts of beechnuts (Brown and Will 1979). Marten have high energetic requirements and little (5%) body fat (Buskirk and Harlow 1989); therefore, food availability readily influences their behavior and survival. Variation in beechnut production may affect prey abundance and availability, because many of the marten's prey species use beechnuts as a food

source. Beechnut production may also influence the vulnerability of marten to trapping. Marten are trapped for their fur in several jurisdictions in the Northeast using baited traps. In Maine, which has the largest population of marten of any state except Alaska, between 2000-5000 marten are trapped every year. The vulnerability of marten to bait is believed to change with food availability, and marten harvest rates appear to be inversely related to beechnut production.

## Methods

### Bear Reproduction

Information on black bear reproduction was collected on 3 study areas in Maine from 1982 to 2004. Study areas are described in McLaughlin et al. (1994) and Schooley (1990). The northernmost study area, Spectacle Pond, was located 27 km SW of Ashland, Maine. The area was >95% forested with spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) being the dominant tree species on lowland sites and a complex of sugar maple (*Acer saccharum*), beech, and yellow birch (*Betula alleghaniensis*) dominating the well-drained upland sites. The study area was representative of the region, which was primarily managed as commercial forestland for pulp production. During the fall, bears in this area primarily fed on beechnuts (Hugie 1982, McLaughlin et al. 1994), when they were available, and other hard and soft mast crops (e.g., beaked hazel [*Corylus cornuta*] and wild cherries [*Prunus* spp.]). The Stacyville site was located in north central Maine about 88 km SE of Spectacle Pond. The study area was about 80% forested with agricultural fields adjacent to wooded areas. Fall foods for bears in the Stacyville area included grain crops, soft mast, and hard mast (including beechnuts). The Bradford study area, the southernmost study site, was located in central Maine about 90 km SW of Stacyville. The Bradford study area was about 92% forested and interspersed with a mix of agriculture and residential areas. Bears in this study area primarily fed on grain and apple crops in the fall and some red oak (*Quercus rubra*) acorns in the fall. Beechnuts were uncommon in this area.

Bears were caught in foothold restraints, in late spring to early summer. Body size and mass were measured, and a premolar was extracted for age determination as described in McLaughlin et al. (1994). Female bears were radiocollared and monitored by fixed-wing aircraft throughout the year (McLaughlin et al. 1994). In January and February, crews located the females' dens and

chemically immobilized adult females for collar replacement and collection of morphometric and reproductive data. Cub production was determined from in-den counts of neonates (McLaughlin et al. 1994).

We tested the hypothesis that alternate year beechnut production has no influence on bear reproductive rates by comparing bear reproductive rates from Spectacle Pond, where bears heavily utilized beech, to bear reproductive rates from the Stacyville and Bradford study sites, where beechnuts make up a smaller component of their fall diet. If beechnuts had no influence on bear reproductive rates, we would expect reproductive rates to be equivalent among the three study sites and across years (i.e., no difference in reproductive rates among even- and odd-numbered years). Comparisons among study sites were limited to the period from 1983 to 2000, because 1983 was the first year all study sites had radiocollared bears and by 2000 the number of radiocollared females had declined to only 4 animals at the Stacyville study site (bears were no longer being collared at this site). We tested whether the proportion of reproductively available females (i.e., radiocollared females  $\geq 4$  yr of age that were not accompanied by offspring when they entered dens in the fall) that produced cubs differed among study sites during even- and odd-years using one-way Analysis of Variance (ANOVA). Female bears  $\geq 4$  yr of age were chosen for comparison because earliest reproduction occurred at 4 years of age in all three study areas (McLaughlin et al. 1994). Duncan's Multiple Range Test was used to isolate significant differences among means (Ott 1984). Differences in bear reproduction rates within a study site during even- and odd-years were compared using paired t-tests.

### **Marten Harvest Rates**

Marten harvest rates in Maine were determined from pelt tagging records from Wildlife Management Unit (WMU) 2. Maine's WMU 2 encompassed approximately 20,738 km<sup>2</sup> of northwestern Maine and included portions of Aroostook, Somerset, Penobscot, and Piscataquis counties. This WMU contained the best marten habitat in the state (MDIFW 1990, unpublished data, MDIFW). The landscape in WMU 2 primarily consisted of rolling hills to mountains dominated by spruce-fir forests interspersed with northern hardwoods (similar to the Spectacle Pond study site). Most of this WMU was privately owned and managed as commercial

forest. The marten trapping season, in Maine, ran from approximately November 1 through December 31. Marten trappers were limited to 25 marten/trapper/yr from 1990 until present. Prior to 1990, there was no limit on the number of marten an individual trapper could take in a season.

Marten harvest rates in northern New York were determined from pelt tagging records. Open trapping areas for marten included approximately 15,540 km<sup>2</sup> of Adirondack Park (WMU 5F, 5H, and 6J) in northern New York. Marten were trapped from the last week of October through mid-December (season length ranged 37-46 days). The marten harvest in New York was restricted to 6 marten/trapper/yr.

Marten trapping records from 1980 to 2004 from Maine's WMU 2 were used to investigate long-term patterns in marten harvest rates. We investigated the relationship between beechnut production and marten harvest rates in New York and Maine using linear regression (Zar 1984). Data from 1990 to 2002 were used for this comparison because Maine initiated a 25 marten harvest limit in 1990, and beechnut production data was not available for the Adirondacks until 1988.

### **Beechnut Production**

Beechnut production in New York was measured at the Huntington Wildlife Forest. The Huntington Wildlife Forest is a 6,000 ha research facility in the central Adirondack Mountains (74° 15' N, 44° 00' W) operated by the State University of New York, College of Environmental Science and Forestry, and is further described in McNulty and Masters (these proceedings). Beechnut production was measured at the stand level from 1988 to 2003 on fifty circular plots (McNulty and Master, this proceedings). From July to November each year, seed traps (13.9 L [5 gal] buckets) were located in the center of each plot. Seed production was estimated from each seed trap for northern hardwood and mixed conifer-hardwood stands (Adirondack Long-Term Ecological Monitoring Program Project #26: Seed Production Survey). We compared beechnut production at Huntington Wildlife Forest to beechnut production in other jurisdictions by characterizing beechnut production using the Durbin Watson statistical test for autocorrelation (SAS Institute 2001) and the first order autocorrelation output. The first order autocorrelation

output is equivalent to the lag 1 autocorrelation function used by Piovesan and Adams (2001) to characterize beechnut production cycles.

Beechnut production in Maine was noted at the Spectacle Pond study site and other sites in northern Maine each fall from 1982 to 2004. Beechnut production was classified as scarce or abundant based on observations by biologists and anecdotal reports.

## Results

### Bear Reproduction

The proportion of reproductively available females bearing cubs at the Spectacle Pond study site fluctuated in an alternate year pattern from 1982 to 2000 (Fig. 1). In 2001 and 1987, the alternate year pattern of cub production appeared to be attenuated. For both years, the attenuation in the alternate year pattern can be attributed to a large cohort of 4-year old female bears being included in the sample. Although female bears at this study site can reproduce at 4 years of age, they often delayed sexual maturity and first reproduced at 6 years of age (McLaughlin et al. 1994). Therefore, it is likely that most of the 4-year old females were sub-adults and not reproductively available. In 1987, 6 of the 15 reproductively available females  $\geq 4$  yr of age were 4-year olds. Excluding this cohort from the calculation, 100% ( $n=9$ ) of the available females  $\geq 5$  yr of age had cubs in 1987. In 2001, 8 of the 15 females that were  $\geq 4$  yr of age were 4-year old bears. Excluding this cohort from the calculation, 87% ( $n=7$ ) of the available females  $\geq 5$  yr of age had cubs in 2001, which is in line with the usual alternate year pattern of reproduction (Fig. 1). In 2003, the normal pattern of increased cub production did not occur. This was associated with a lower level of beechnut production than was expected in Maine fall of 2002. The proportion of females bearing cubs in 2004 did not follow the traditional alternate year pattern and was higher than expected (Fig. 1).

The proportion of reproductively available females bearing cubs differed ( $F = 6.64$ ;  $df = 2, 24$ ;  $P = 0.005$ ) among the three Maine study sites during even-years, i.e., years following falls when few beechnuts were produced (Fig 2). Post-hoc tests revealed that fewer ( $\bar{X} = 22\% \pm 0.07$  SE) females at the Spectacle Pond study site produced cubs following poor beechnut crops than females at the Stacyville or Bradford sites ( $\bar{X} = 58\% \pm 0.17$  SE;  $\bar{X} = 76\% \pm 0.05$  SE), respectively.

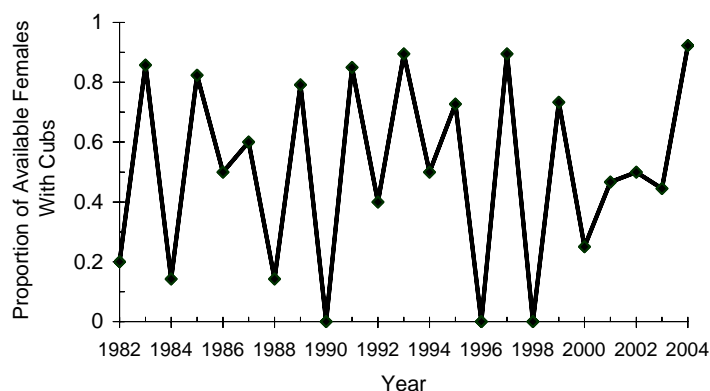


Figure 1.—Proportion of reproductively available female bears (i.e., radiocollared females  $\geq 4$  yr of age that were not accompanied by offspring when they entered dens in the fall) with cubs at the Spectacle Pond study site in Maine.

The proportion of females with cubs was not significantly different among the Stacyville and Bradford sites for those years.

The proportion of reproductively available females bearing cubs in odd-years, i.e., years following falls when beechnuts were abundant, did not differ ( $F = 0.318$ ;  $df = 2, 24$ ;  $P = 0.730$ ) among the three study sites (Fig. 2). The percentage of reproductively available females producing cubs at the Spectacle Pond, Stacyville, and Bradford study sites was ( $\bar{X} = 80\% \pm 0.03$  SE;  $\bar{X} = 88\% \pm 0.06$  SE;  $\bar{X} = 83\% \pm 0.11$  SE), respectively.

A significant difference in the proportion of reproductively available females bearing cubs from one year to the next was only seen at the Spectacle Pond study site ( $P < 0.001$ ) (Fig. 2). At Stacyville, where beechnuts were less abundant, the year-to-year difference in the proportion of reproductively available females bearing cubs was less evident ( $P = 0.116$ ), and there was no difference ( $P = 0.523$ ) at the Bradford study site where beech is uncommon.

### Marten Harvests

In Maine, the marten harvest in WMU 2 fluctuated in an alternate year pattern from 1980 to 2003 (Fig. 3). This alternate year harvest pattern persisted through a period of over-trapping (i.e., 1984 to 1989), appeared to be somewhat attenuated from 1990 to 1994 (in 1990 a trapping limit was imposed of 25 marten / trapper /yr) and resumed a normal pattern until 2002. In 2002, the marten harvest did not decline as much as expected, and

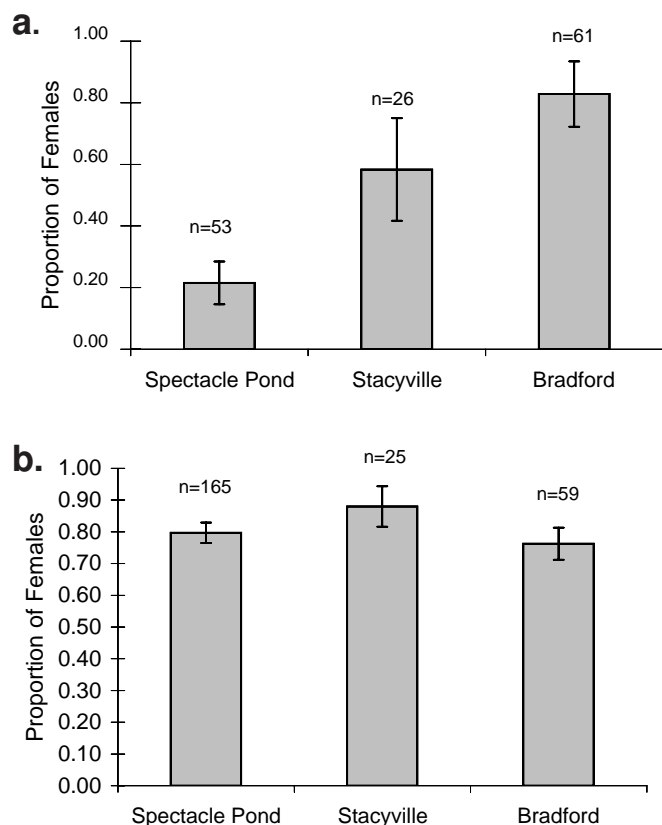


Figure 2.—Proportion of reproductively available female bears (i.e., radiocollared females  $\geq 4$  yr of age that were not accompanied by offspring when they entered dens in the fall) with cubs at the Spectacle Pond, Stacyville, and Bradford study sites in Maine during (a.) even-years that followed poor beechnut production and (b.) odd-years that followed good beechnut production from 1983 to 2000.

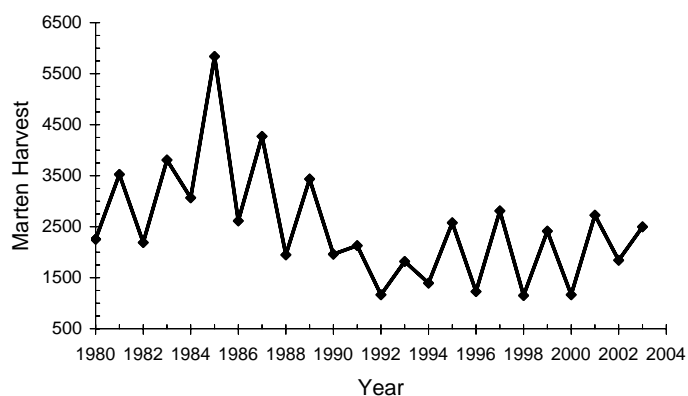


Figure 3.—Marten trapping harvest in Wildlife Management Unit 2 in Maine.

was the highest even-year harvest since the 25 marten limit was imposed. The 2003 harvest was similar ( $P = 0.487$ ,  $r^2 = 0.158$ ) to the past 4 odd-numbered year harvests from (1995 to 2003).

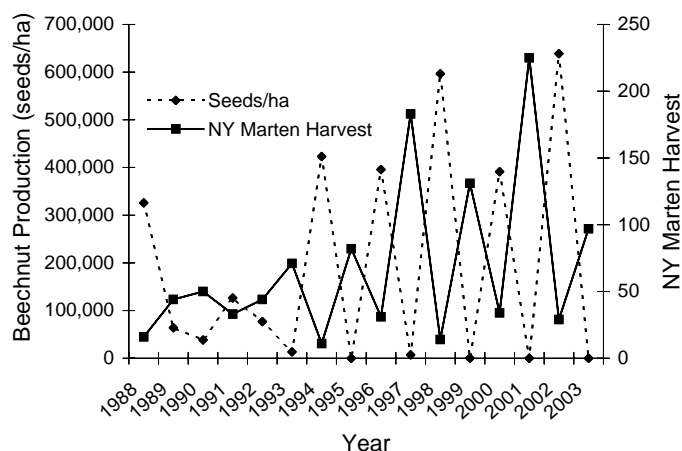


Figure 4.—Marten trapping harvests from Adirondack Park (Wildlife Management Units 5F, 5H, and 6J) in New York compared to beechnut production from the Huntington Wildlife Forest, central Adirondacks. Beechnut production was measured using seed traps on 50 circular plots.

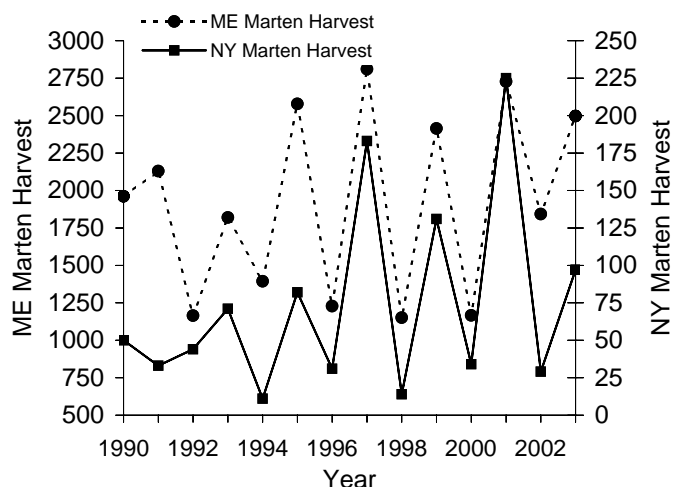


Figure 5.—A comparison of Maine's marten trapping harvests from Wildlife Management Unit 2, to New York's marten trapping harvest from Adirondack Park (Wildlife Management Units 5F, 5H, and 6J).

The New York marten harvest from 1990 to 2003 fluctuated in an alternate pattern from 1993 until 2003. For that period, the marten harvest pattern was inversely related to beechnut production in New York (Fig. 4). From 1988 until 1993, neither beechnut production nor the marten harvest fluctuated in an alternate year pattern. The New York marten harvest was correlated ( $P < 0.001$ ;  $r^2 = 0.65$ ) to the Maine marten harvest (Fig. 5), with the greatest disparity between the data sets occurring from 1990 to 1992, and in 2002 when the Maine harvest rate declined proportionally less.

## Beechnut Production

In the Adirondacks, beechnut production in hardwood forests fluctuated in an alternate year pattern starting in 1993, with the heaviest nut production occurring during the fall of even-numbered years (Fig. 4). Nut production ranged from complete mast failures, during 4 years, to an estimated high of 638,712 beechnuts/ha in fall 2002 (Fig. 4). Beechnut production during Fall 2004 was low, breaking the pattern of heavy nut production on even years. Year-to-year beechnut production in the Adirondacks was characterized as having a first order autocorrelation of -0.69 (Durban Watson = 3.26), which is indicative of a negative serial correlation (Ott 1984). That is, beechnut production in a given year was inversely related to beechnut production the following year.

In Maine, beechnut production appeared to fluctuate on an alternate year basis from 1982 to 2001 with abundant crops occurring in even-numbered years and less production in odd-numbered years. In Fall 2002, and through Fall 2004, beechnut production did not appear to follow the alternate year pattern of production observed the previous 20 years. In particular, beechnut production was notably scarce during Fall 2004.

## Discussion

We reject the null hypothesis that alternate year beechnut production does not influence black bear reproduction in northern Maine. At the Spectacle Pond study site, where beechnuts were an important fall dietary item for bears, the mean proportion of female bears producing cubs decreased to 22% when a denning period followed a poor beechnut crop. However, during denning periods following good beechnut production, 80% of the reproductively available females produced cubs. The proportion of females producing cubs did not differ among years at the other two study sites where beechnuts were a less important fall food item. At these study sites, bears utilized agricultural crops and soft mast, which are more dependable on a year-to-year basis (McLaughlin et al. 1994). Consequently, cub production at these study areas was more consistent on a year-to-year basis. During years of good beechnut production, the proportion of reproductively available females bearing cubs among the three study areas was equivalent. This indicates that bears at the Spectacle Pond site had the same reproductive potential as bears at the other study sites when food resources were plentiful.

McLaughlin et al. (1994) and McLaughlin (1998) proposed that the differential cub production rates among the study sites might be explained by the mass gain of mature females prior to hibernation. Following good beechnut years, the in-den mass of fully-grown females (i.e., females  $\geq 7$  yr of age that did not den with yearlings) was similar ( $\bar{X} = 67$  kg) among the three study sites (McLaughlin et al. 1994). However, following poor beechnut years, the mass of females  $\geq 7$  yr of age declined significantly at Spectacle Pond (from 69.8 kg to 53.8 kg) but not at the other study sites. The low mass of females, at Spectacle Pond following a poor beechnut crop, likely indicates that fewer females attained sufficient mass for reproduction.

Beechnut production in Maine appeared to follow a regular alternate year pattern from 1982 until 2001; however, as of Fall 2004, Maine had 3 consecutive years of sparse beechnut production. Despite the scarcity of beechnuts in Maine, a high proportion of reproductively available females produced cubs at the Spectacle Pond study site in 2004. This would appear to indicate that good cub production, in northern Maine, is not necessarily contingent upon good beechnut production the preceding fall. We do not have an explanation for why a high proportion of females produced cubs in absence of a good beechnut crop. Bears are opportunistic feeders and will exploit alternative foods if they are abundant. Since females must receive adequate nutrition for cub production to occur, we have to assume that sufficient alternative foods were available in 2003. The mass of females  $\geq 7$  yr of age that denned without yearlings was similar (i.e.,  $65.6 \pm 4.7$  kg and  $64.5 \pm 4.0$  kg) in 2003 and 2004 at Spectacle Pond. Their mass was somewhat higher than the mass ( $53.8 \pm 12.8$  kg) of females (same class and location) that denned following poor beechnut crops from 1982 to 1991 (McLaughlin et al. 1994). The higher mass of denning females in 2003 and 2004 raises the question of whether an alternative food source became more prevalent in recent years. Unfortunately, Maine's Department of Inland Fisheries and Wildlife did not collect enough detailed information on hard and soft mast production to determine whether an alternative food was particularly abundant those years, or whether the distribution of foods has been altered with recent changes in forest harvesting practices. Currently, states in the Northeast are considering a region-wide mast production survey. We strongly support such initiatives and hope this study serves as an example

of how mast production information can be integral to understanding the dynamics of wildlife populations.

The sparse beechnut production in Maine in 2002 and 2004 is not known to be related to any particular climatological event, and may be within the normal variation expected for beechnut production. In other regions (e.g., Michigan; Gysel 1971), beechnut production did not follow the consistent alternate year pattern we observed. High levels of beechnut production are usually associated with a wet period, 2 years prior to the masting event, followed by a hot dry summer, 1 year prior to the masting event (Piovesan and Adams 2001). Maine and other areas in the northeast experienced drought conditions in 2001 and 2002. Although beechnut production at the Huntington Wildlife Forest in New York was the highest in 15 years in 2002, beechnut production was not high in Maine. We do not know why beechnut production in the Adirondacks during the late 1980's and early 1990's differed from the alternate year pattern reported in Maine.

Beechnut production, as measured at the Huntington Wildlife Forest in the Adirondacks, appears to alternate between years in a cyclical pattern similar to other beech populations (e.g., Piovesan and Adams 2001). Beechnut production in the Adirondacks was characterized as having a first order autocorrelation of -0.69. This level of autocorrelation was similar to the level calculated for beechnut production in Michigan (-0.74) from 1959-1968 but higher than what was reported in New Hampshire (0.05 and -0.48) for 1971-1981 and 1976-1981 (Piovesan and Adams 2001). Based on data from New Hampshire (i.e., Graber and Leak 1992) and northern England, Piovesan and Adams (2001) proposed that beech at the northern limits of their range did not cycle, and produced few beechnuts because of the stresses associated with cold climates. We question this conclusion based on beechnut production at the Huntington Wildlife Forest and in Maine. The Adirondacks and northern Maine are well known for cold, severe winters and yet have strong beechnut cycles and abundant nut crops. The disparity between the conclusions of Piovesan and Adams (2001) on beechnut production in northern latitudes and our data emphasizes the need to exercise caution when comparing beechnut production rates among studies. For example, the highest nut production (in 2002) at Huntington Wildlife Forest was 64 nuts/m<sup>2</sup>, which might be

interpreted as evidence of a very low nut production rate as compared to the 658 nuts/m<sup>2</sup> Gysel (1971) reported in Michigan. However, the measurement of 64 nuts/m<sup>2</sup> represents beechnut production in northern hardwood and mixed conifer/hardwood stands, while the measurement of 658 nuts/m<sup>2</sup> represents nut production under individual beech trees (Gysel 1971).

Harvest rates for marten in Maine and the Adirondacks varied in an alternate year pattern and were highly correlated to each other. This year-to-year variation in marten harvest rates appears to be inversely related to alternate year patterns in beechnut production. Similar variations in marten and fisher harvests have been observed for over 100 years, although the periodicity of low and high harvests is not clear. Hardy (1899:526) wrote, "When in the fur trade, I used to buy 175 to 200 [fisher] skins annually. While these were not all taken in Maine, I think, from the best data I could get, that the annual catch of Maine was 150 to 300. The catch varies greatly in different years, just as that of Sables [marten] does, as some years both take bait better than others."

We propose two hypotheses as to why marten harvest rates varies inversely with beechnut production. The first hypothesis is an offshoot of the observations Hardy made 100 years ago, i.e., marten harvests decrease during years when beechnut production is good because their vulnerability to baited traps decreases. We hypothesize that during good beechnut years, small mammals will make heavy use of beechnuts and are easily preyed upon by marten. This increase in prey availability and the consumption of beechnuts by marten lowers the attractiveness of baited traps to marten. Secondly, we hypothesize that increased energy intake during a good beechnut year may increase marten kit production or survival, which results in a large number of juveniles being available for trapping the following fall. This large cohort of juveniles would increase the overall number of marten taken by trappers. We recognize that these two hypotheses may not be mutually exclusive.

The need to understand the dynamics between beechnut production and wildlife populations is heightened by the impact of beech bark disease and increased use of intensive forestry practices on commercial forests in the Northeast. Further work is needed to determine the alternative foods bears rely on when beechnuts are not available, and whether recent changes in forest harvesting

practices have affected the availability of these foods. This work is necessary if wildlife managers are to make recommendations to landowners on the amount of mature beech needed on the landscape. Additional studies are needed to understand how alternate year beechnut production affects the community dynamics of northern forests.

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# INVERTEBRATE BIODIVERSITY IN NORTHERN HARDWOOD ECOSYSTEMS UNDER VARYING DISTURBANCE REGIMES

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## Abstract

During 2003-2005 we are investigating the effects of forest type, forest stand characteristics, beech bark disease (BBD) and mechanical thinning on the biodiversity of ground-dwelling arthropods in northern hardwood stands in Michigan. This study is also examining the relationship between downed woody debris and invertebrate biodiversity within a forest stand. The goal of this research is to help explain the complex relationships and interactions between ground-dwelling arthropods, forest stand characteristics, and disturbances in Michigan's northern hardwood forests. Specific research questions being asked include: (1) What is the relationship between downed woody debris and ground-dwelling arthropod diversity?, (2) What is the relationship between forest type and ground-dwelling arthropod diversity? and (3) What is the effect of BBD and thinning on biodiversity of ground-dwelling arthropods? We are collecting ground-dwelling arthropods using unbaited pitfall traps in 48 northern hardwood stands in Michigan based on forest type, presence/ absence of mechanical thinning, and presence/ absence of BBD. Ground beetles (Coleoptera: Carabidae), camel crickets (Orthoptera: Gryllacrididae) and sowbugs (Crustacea: Isopoda) are identified to the species level and are the focal groups of this study. All other ground-dwelling arthropods are grouped and quantified by taxonomic group. A better understanding of the factors affecting diversity of ground-dwelling arthropods is important for management, conservation and the preservation of biological diversity.

## Introduction and Literature Review

Biodiversity of ground-dwelling arthropods is influenced by both abiotic and biotic factors at multiple scales from global latitudinal patterns to local microhabitats within a forest stand. Generalizations can be made about patterns of species distributions and diversity on a continental scale, but each taxonomic group examined will have specialized requirements and slightly different factors influencing its persistence in the environment.

Disturbances, both natural and anthropogenic have been shown to influence arthropod distributions, and certain invertebrate groups have been used to study the impacts of these disturbances and to make recommendations for management of disturbed areas (Davis 2000; Werner and Raffa 2000; Lewis and Whitfield 1999; Rodriguez et al. 1998; Niemela et al. 1993; Pearson and Cassola 1992; Lenski 1982).

Invertebrates dominate many forest ecosystems in terms of species richness and biomass, and influence ecosystem processes such as predation, decomposition, nutrient cycling, and pollination (Werner and Raffa 2000; Price 1997). Many studies have used ground-dwelling arthropods as indicators because of the large sample sizes that can be obtained with relatively unbiased methods, short generation times, low dispersal ability which makes them susceptible to disturbance, and sensitivity to microsite changes (McGeoch 1998; Kremen 1994; Kremen et al. 1993).

Downed woody debris (DWD) serves as an important habitat component for many invertebrate and vertebrate groups (Hunter 1990). Structural diversity provided by DWD has been shown to increase biological diversity in forested stands (McGee et al. 1999). Several studies have been conducted to quantify the amount of DWD present in forest ecosystems (Muller 2003; Hagan and Grove 1999; Goodburn and Lorimer 1998; Guby and Dobbertin 1996). Although the importance of the downed wood resource to plants and animals in these ecosystems is assumed, most studies do not directly examine the relationship between DWD and organism use. Managing for DWD has become recognized as necessary for maintenance of biodiversity; management activities such as thinning can heavily impact amounts of DWD in a forest stand (Hagan and Grove 1999).

## Methods

This study examines the factors influencing diversity of ground-dwelling arthropods and is investigating invertebrate biodiversity under varying disturbance regimes in northern hardwood stands in Michigan. Forty-eight northern hardwood stands are used in this study; 24 stands are located in the northern Lower Peninsula (LP) and 24 stands are located in the eastern Upper Peninsula (UP) (Figure 1). Dominant overstory tree species include American beech (*Fagus grandifolia*

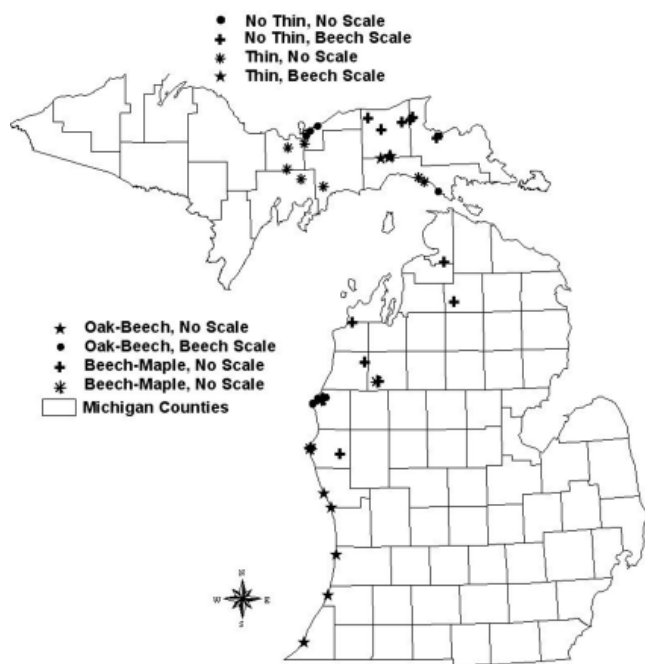


Figure 1.—Location of research stands in the biodiversity study in Michigan.

Ehrh.), sugar maple (*Acer saccharum* Marsh.), northern red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.). Treatment types in this study involve a combination of two factors: (1) presence or absence of exotic beech scale and (2) forest type (maple-beech, oak-beech) (LP) or silvicultural treatment (two levels: no silvicultural treatment, selection cut (5 years prior to data collection) (UP)).

Ten unbaited pitfall traps are placed 40 m apart along transects within each stand. Traps are opened for 3 days each month during mid-June, mid-July and mid-August. Collected organisms are counted and grouped by major taxa. The ground beetles (Coleoptera: Carabidae), camel crickets (Orthoptera: Gryllacrididae) and sowbugs (Crustacea: Isopoda) are further identified to the species level. Spiders (Araneae), millipedes (Diplopoda), centipedes (Chilopoda) and land snails and slugs (Gastropoda) are identified to the family level.

For the downed wood study, piles of wood found naturally in a stand are used. Piles are chosen based on four classes of DWD that vary by volume and decay class (Table 1). Pitfall traps are placed as close to the center of the DWD as possible and trap catches are compared among the different classes of DWD. Five replicates of each of the classes are chosen within each stand and eight

Table 1.—Downed woody debris (DWD) sampling classes

DWD class	Quantity/ Quality of DWD
0	Very low volume of DWD (small branches and twigs)
1	One large tree (> 20 cm DBH, >3 m long) in early decay stages
2	One large tree (> 20 cm DBH, > 3 m long) with advanced decay
3	Two large trees (> 20 cm DBH, > 3 m long) in early decay stages
4	Two large trees (> 20 cm DBH, > 3 m long) with advanced decay

stands in the UP were selected for this part of the study. Four of the stands have heavy BBD where mortality of overstory beech has already occurred and four stands are not infested with BBD. Pitfall trap catches will be compared between the different DWD classes to determine if different invertebrate groups and/or species are utilizing different volumes and decay classes of downed wood.

## Preliminary Results and Discussion

Significantly more individual arthropods were caught in pitfall traps in August compared to June and July (Figure 2). No significant differences were found between the number of arthropods in plots with and without beech scale. In the Lower Peninsula oak-beech stands without

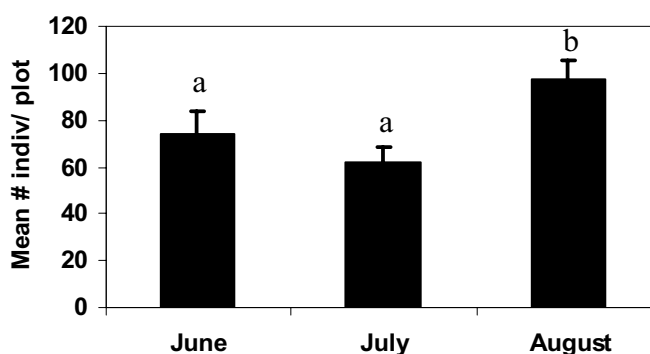


Figure 2.—Mean number of individual arthropods per plot in June, July and August 2003 in Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different among months.

beech scale present had significantly more arthropods compared to oak-beech stands with beech scale and maple-beech stands with and without beech scale (Figure 3). In the Upper Peninsula no significant differences were found between the number of arthropods in thinned or unthinned stands with and without beech scale.

Significantly more carabid beetles were caught in pitfall traps in August compared to June and July (Figure 4). No significant differences were found between the number of carabid beetles in plots with and without scale. In the Lower Peninsula no significant differences were found between numbers of carabid beetles in oak-beech or maple-beech stands with or without beech scale. In the Upper Peninsula significantly more carabid beetles were found in unthinned stands compared to thinned stands (Figure 5).

## Conclusion

This research is continuing through 2006. Preliminary results show no effect of BBD or mechanical thinning on number of arthropods caught in pitfall traps. Once individuals are identified to species, we will determine if species shifts occur as a result of habitat changes due to BBD or thinning. Research during summer 2005 will focus on ground beetles, camel crickets and sowbugs at the species level and the relationship between arthropods and downed woody debris.

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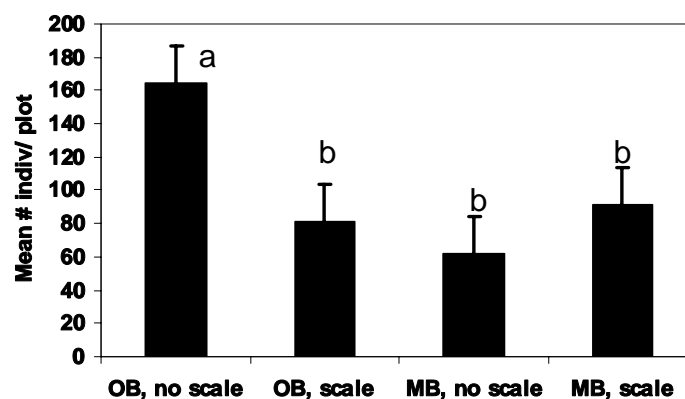


Figure 3.—Mean number of individual arthropods per plot in oak-beech (OB) and maple-beech (MB) stands with and without beech scale present in Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different within each scale rating and forest type.

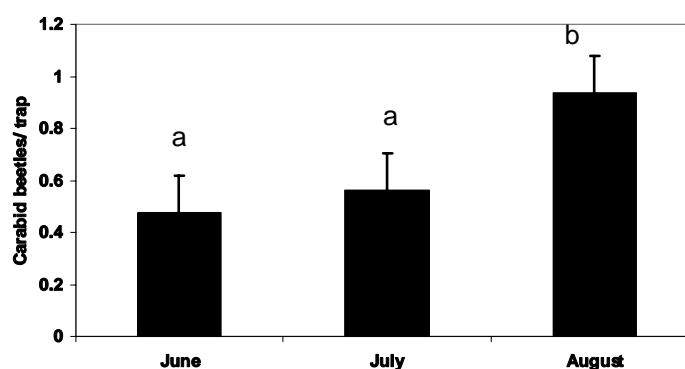


Figure 4.—Mean number of carabid beetles (Coleoptera: Carabidae) per plot in June, July and August 2003 in Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different among months.

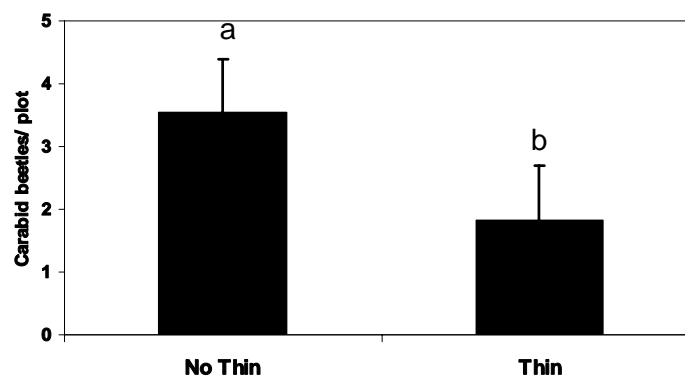


Figure 5.—Mean number of carabid beetles (Coleoptera: Carabidae) per plot in June, July and August 2003 in Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different by treatment.

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# IMPACTS OF BEECH BARK DISEASE ON WILDLIFE RESOURCE ABUNDANCE IN MICHIGAN

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## Abstract

Beech bark disease was discovered in Michigan in 2000 and will likely kill at least 50% of mature American beech trees. Our study was designed to determine how wildlife resource abundance will be affected as beech bark disease spreads and intensifies throughout Michigan. We assessed the potential impact in forest stands with varying beech densities (low, moderate, and high) and abundance of *Cryptococcus fagisuga* (absent, light, and heavy). Variables were measured in 62 stands throughout the Upper and Lower Peninsulas of Michigan in 2002 and 2003. Beech snags were significantly more abundant in stands with heavy *C. fagisuga* abundance than in stands with absent or light *C. fagisuga* abundance. Coarse woody debris volume and beechnut mass were highest in stands with heavy *C. fagisuga* abundance, although means were not statistically different.

## Introduction

Beech bark disease (BBD) was discovered in Michigan in 2000, although evidence suggests it had been established for at least 10 years prior to identification (McCullough 2001). Spreading from its origins in Luce and Mason Counties, BBD is now confirmed in at least eight counties in both the Upper and Lower Peninsulas. The impacts of BBD specific to Michigan's forests are largely unknown, but will likely include changes in understory species composition. Michigan State University (MSU) is working in conjunction with the University of Michigan on a long-term research project to investigate the impacts of BBD as it spreads in range and intensifies throughout the state. The objectives of our research at MSU are to *i*) assess abundance of wildlife resources in stands with varying levels of beech bark disease and beech densities and *ii*) compare baseline wildlife resource abundance with long-term data of stands affected by beech bark disease.

## Study Area

Research was conducted in 62 permanent plots in the Lower and Upper Peninsulas of Michigan. Stands were selected in a two-factorial design and grouped by beech density and *C. fagisuga* abundance. Beech density was classified by absolute basal area of beech as low ( $< 9 \text{ m}^2/\text{ha}$ ), moderate ( $9\text{-}18 \text{ m}^2/\text{ha}$ ), or high ( $>18 \text{ m}^2/\text{ha}$ ). Abundance of *C. fagisuga* in a  $100 \text{ cm}^2$  sample area was estimated on 12 beech trees on the north and south sides of the main bole at 1.3 m on upslope side. Trees were considered "heavily infested" if *C. fagisuga* covered greater than 30% of the area on at least one azimuth. Stands were classified according to the number of trees heavily infested with *C. fagisuga* within the plot boundary as absent (zero), light ( $< 2$ ), or heavy ( $> 2$ ).

## Methods

Coarse woody debris volume and snag density were measured in stands along two perpendicular transects of 51 m length. Volume of coarse woody debris greater than 7.6 cm diam. within 0.5 m of each transect was measured. We determined snag density by counting and identifying all dead trees greater than 12.7 cm dbh within 5 m of each transect. Beechnuts were collected from four seed traps set in stands ( $n=36$  in 2002,  $n=51$  in 2003) between 15 August and 7 December. Traps were  $1 \text{ m}^2$ , standing approx. 70 cm off the ground (varying with terrain), and constructed from industry standard  $3/4"$  pvc pipe and 40% shade cloth. All seed samples were sorted to species, oven-dried at  $38^\circ\text{C}$  for 72 hours, and weighed.

## Results and Discussion

Coarse woody debris volume was greater in stands with beech bark disease, although means were not significantly different likely due to the limited number of stands with heavy *C. fagisuga*. Coarse woody debris volumes have been shown to increase in stands affected by beech bark disease and exceed volumes of  $166 \pm 42 \text{ m}^3/\text{ha}$ , whereas unaffected stands contain  $15\text{-}45 \text{ m}^3/\text{ha}$  (McGee 2000, Carbonneau 1986). While means were variable, volumes ranged from  $43\text{-}167 \text{ m}^3/\text{ha}$  in stands with heavy *C. fagisuga*.

Beechnut mass was not significantly different among stands with absent, light, or heavy *C. fagisuga* abundance, nor among stands with low, moderate, or high beech density. Linear regression of beech basal area ( $\text{m}^2/\text{ha}$ ) and

beechnuts (g/m<sup>2</sup>) was significant ( $p = 0.035$ ) but explained only 9.8% of the variance. Long term monitoring will account for any changes in beechnut production as BBD progresses.

Mean density of total species of snags did not significantly differ among stands with low, moderate, or high beech density and absent, light, or heavy *C. fagisuga* abundance. Mean density of beech snags was highest in stands with high beech density ( $p=0.008$ ) and in stands with heavy *C. fagisuga* ( $p=0.022$ ). The interactive effect between beech density and *C. fagisuga* abundance was significant ( $p=0.011$ ). Linear regressions of number of beech snags and beech basal area were significant ( $p=0.009$ ), but only explained 10% of the variance. These results suggest beech bark disease has increased the density of standing dead beech trees.

## Acknowledgments

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# WOOD-INFESTING INSECT ABUNDANCE AND COMMUNITY STRUCTURE IN RELATION TO BEECH BARK DISEASE

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The impacts of non-native forest insects and diseases on host tree species are measured extensively, yet impacts on other forest organisms are rarely quantified. The purpose of this research was to measure changes in wood-infesting insect communities in relation to beech bark disease. Beech bark disease causes mortality of American beech, producing a large increase in dead wood quantities within a stand in a relatively short time period. We propose that wood-infesting insects, as well as other insects collected when trapping wood infesting insects, may serve as useful study organisms for measuring changes in animal communities brought about by tree mortality associated with exotic pests and pathogens. Fifteen study sites were used during the summer of 2003; five sites each in beech forests with beech bark disease, beech forests without beech bark disease, and forests without beech in the Upper Peninsula of Michigan. Six flight intercept panel traps baited with ultra-high release ethanol lures were deployed in each study site. Traps were run from late May to early September and were emptied every two weeks. Trap contents were sorted into family groups for wood-infesting insects (Coleoptera: Scolytidae, Cerambycidae, Curculionidae, Buprestidae; Hymenoptera: Siricidae). In addition, another taxon consistently caught in these traps was also counted (Coleoptera: Elateridae). Preliminary data analyses revealed significant differences in scolytid abundance among site types, with beech bark disease sites having the lowest abundances over the course of the summer. In contrast, elaterids tended to be more abundant in sites with beech bark disease. Differences in wood-infesting insect abundances among site types are likely due to changes in dead wood quantity and quality brought about by beech bark disease caused tree mortality. Scolytids may be limited in their use of dead beech trees because of the presence of *Nectria* initiated cankers and necrotic tissues. Species identification is ongoing to further elucidate the impacts of beech bark disease on the community structure of wood-infesting insects.

# **DISRUPTION OF MAST PRODUCTION IN AMERICAN BEECH (*FAGUS GRANDIFOLIA*) AND EFFECTS ON SMALL MAMMAL COMMUNITIES RESULTING FROM BEECH BARK DISEASE**

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It is thought that the incipient incursion of beech bark disease (BBD) into the Upper Peninsula (U.P.) of Michigan may lead to changes in the mast ecology of American beech (*Fagus grandifolia*). Although the short-term impact of BBD remains to be seen, any disruptions in mast production could eventually lead to population and community level changes in organisms that exploit beech seed. We measured beech seed production across the U.P. in both healthy and BBD-infected (advancing and killing front) forests in an ongoing attempt to describe the relationship between BBD, beech, and native small mammal communities. We characterized small mammals at both the population and community levels in the same forests in which we measured mast production, as well as in nearby forests that are similar but do not contain beech. To date, we have found evidence suggesting that mast production does not differ significantly between healthy and infected forests. Small mammal trapping has provided evidence that small mammal species diversity is higher in the healthy beech forests than either the BBD forests or the no beech forests. Additionally, population estimates for the southern red-backed vole (*Clethrionomys gapperi*) were significantly higher in the no beech forest than in either of the beech forests; this species was never found in healthy beech forests, but was found in low numbers in BBD infected forests. Together, these patterns suggest that some interesting processes are occurring in the beech forests of the U.P. Continued effort in these pursuits, as well as additional methods to investigate the relative value of beech seed to small mammals will help to further our knowledge of how native mammal communities are affected by this exotic forest pest complex.

## Knowledge Gaps and Research Priorities

### *Knowledge Gaps*

- What is the beech mast foundation information/baseline (i.e. periodicity of mast crops, nut quality, individual tree vs. stand level)?
- What are the effects of beech mast production on wildlife (i.e. viability, which species use beech nuts)?
- Is beech only locally important to wildlife (especially bears)?
- Which invertebrate communities rely on coarse woody debris?
- Does the change of vegetation structure affect nesting resources (birds)?
- Could the changes in mast and vegetation structure affect bird migration?
- What is the forest structure influence on insectivores (vertical structure change and cavities)?

### *Research Priorities*

- Determine how BBD affects the periodicity of mast crops and nut quality (resistant trees vs. susceptible trees).
- Identify how important regional beech mast production is to wildlife.
- Recognize all species utilizing coarse woody debris.
- Determine the quantity of nutrient structure and nutrient cycling and the quality of decay rates.
- Determine the viability of the beech mast production across beech range.
- Identify the effects of bird behavior in the presence of BBD.

## **Section 4:**

### **Beech Genetics and BBD Resistance**

## THE GENETICS OF RESISTANCE OF AMERICAN BEECH TO BEECH BARK DISEASE: KNOWLEDGE THROUGH 2004

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### Introduction and Background

In stands long affected by beech bark disease (BBD), a small percentage of American beech trees (*Fagus grandifolia*) remains disease free. Trials using an artificial inoculation technique have indicated that these trees are resistant to the scale insect (*Cryptococcus fagisuga*) portion of the disease complex (Houston, 1982, 1983). In many cases, resistant trees were observed to occur in close proximity to one another. A study of the patterns of disease-free trees in two stands in Nova Scotia demonstrated that the majority of resistant trees within these stands were located in groups (Houston 1983). Based on the spatial arrangement of these resistant trees, Houston and others concluded that these groups “suggest a genetic resistance transmissible both vegetatively and sexually” (Mielke et al. 1986). However, in the 1986 study, it was not determined if the resistant clusters of trees were from root sprout or seed origin. Similar findings were reported in stands located in Massachusetts, West Virginia, Prince Edward Island, Maine, New York and New Hampshire (Houston and Houston 1994, 2001). All the stands included in these studies were selected based on the presence of at least one group of disease-free trees.

### The Search for a Marker Correlating with Resistance

In northern hardwood stands that have been long affected by BBD, large numbers of severely deformed American beech trees persist. To further complicate stand management practices, root sprout initiation can be stimulated by the large number of trees in decline due to BBD, resulting in the formation of “thickets” of diseased, deformed beech sprouts. To improve stand quality, silvicultural approaches are needed to reduce the number of susceptible trees and increase the number of resistant beech trees. Such approaches rely on the ability to distinguish between resistant and susceptible trees. One difficulty forest managers encounter in carrying out recommended treatments is that even in heavily infested areas, trees that remain free of scale may be escapes and

not truly resistant. In the initial stages of infestation, larger, more mature trees are attacked first while smaller juvenile trees do not show scale build-up until later phases of infestation. Currently, the only known method to test for resistance is the artificial infestation method developed by Houston (1982). Drawbacks to this method include the minimum 1-year wait for results and the reliance on live scale eggs, which could result in spread of the scale insect if this method were used in areas where the scale was not yet found. Identification of a marker correlating with resistance would be beneficial not only as an aid to management of the disease, but also in genetics research.

Houston and Houston (1994, 2001) used isozyme analysis to assess the genetic structure of several BBD affected stands. Individual trees were analyzed using nine polymorphic enzymes to generate an isozyme profile. Based on these isozyme profiles, an indication of relatedness of individuals (either clonally or by family structure) could be estimated. Although many resistant individuals located within the same stand shared an identical isozyme pattern, there was no distinct pattern that correlated to resistance. In fact, there were cases where resistant individuals were shown to have the same isozyme pattern as a susceptible individual. In searching for a marker correlating to resistance, the number of isozyme loci that can be scored is limiting and a system that generates a larger number of polymorphic loci will be required.

We used RAPDs (randomly amplified polymorphic DNA) (Williams et al. 1990) to analyze subsets of the individuals that Houston and Houston (1994, 2001) had included in their isozyme analysis. This polymerase chain reaction (PCR)-based technique relies on short (10 base) primers to detect random polymorphisms in the genomic DNA. One hundred and forty-four individuals were screened with 24 different primers to uncover 34 reliable polymorphic loci (Carey et al. 2001). Using this technique, we were able to show that some individuals with identical isozyme profiles were not truly clonally related. An estimate of the probability of misidentifying two individuals as clonal was generated by taking the inverse of the product of the frequency of the most prevalent phenotype. The phenotype in this case is referring to whether a particular band is present or absent at each of the 34 polymorphic loci. Based on this

calculation, there is only a 1 in 49,500 chance of clones being inaccurately identified using these loci. Although the numerous polymorphic loci that can be assessed quickly using RAPDs are more sensitive in determining clonal relationships than the limited number of isozyme loci, there was still no specific RAPD pattern or band that was associated with resistance. To identify a marker linked to resistance, a more informative marker system will be required.

Amplified fragment length polymorphism (AFLP) is a molecular marker generated by a combination of restriction enzyme digestion and PCR amplification (Vos et al. 1995). This technique is more powerful than RAPDs because a large number of polymorphic loci can be generated in a single amplification. To date, we have screened 80 primer pairs using subsets from the original stands described by Houston and Houston (1994, 2001). This has identified 274 polymorphic loci, or about three times as many polymorphisms per primer as compared to RAPDs. These AFLP primers were used to screen “bulks” consisting of equal quantities of DNA from 10 different individuals. For two different stands in Maine and one in Nova Scotia (Houston and Houston 2001) a bulk of resistant trees was screened along with a bulk of susceptible trees, for a total of six bulks. Three of the 80 primer pairs showed bands that were present only in the resistant bulks and not in the susceptibles. However, when these primer pairs were used to screen an expanded population of individuals (N = 144), the relationship with resistance did not hold.

Even though the 80 primer pairs screened did not produce a marker that correlates to resistance, we believe that using AFLPs is currently the most efficient way to search for such a marker. In populations where the relatedness of individuals is not absolutely clear, the search for a marker is very much like looking for a needle in a haystack. Nevertheless, due to the ease of generating large numbers of polymorphisms with AFLPs, in combination with the low sample number for screening by using bulks, it should be possible to screen through thousands of markers. With such high numbers, the odds of success increase. However, by using this semi-random population approach, any marker that is potentially linked to resistance would have to be confirmed through breeding and studies of inheritance.

## **Controlled Cross-Pollinations in American Beech**

Without question, looking for markers correlated with resistance should ideally be done through breeding so the segregation pattern of the phenotype (resistance) can be assessed directly in comparison to the marker to determine if the marker co-segregates with the phenotype. However, generating a full-sib family using resistant American beech parents is not a simple task for many reasons. First, the estimated minimum age for seed production in American beech is 40 years, and a beech tree of that age can reach heights of 70 to 120 feet (Rudolf & Leak 1974). Second, flowers are usually most prevalent in areas of the canopy that are in direct sunlight, generally toward the top of the tree. Third, flowering in beech is variable and flowers are extremely susceptible to spring frost. In general, good beech seed crops are produced every 2 to 8 years (Rudolf and Leak 1974).

Fortunately, we were able to identify scale-free trees that were very near a paved campground roadway in Ludington State Park, MI. The site is located in a killing front, so the disease pressure was high enough to be able to select “clear” trees with reasonable confidence that they were resistant. The parent trees were tested for resistance using the artificial infestation technique. An 8 ½ x 11 ½ inch foam pad failed to enhance the formation of scale colonies underneath after being in place for a year on all parent trees. The following year, 300 eggs were placed under the foam pad. Again, little to no scale insects colonized underneath the foam. In cases where insects were found under the foam, there was no evidence of egg production. Susceptible control trees also were tested in a similar manner, and in these cases the foam alone was sufficient to detect an enhanced scale population on the tree.

Details of the methods used to perform controlled crosses are outlined in Koch and Carey (2004a). Crosses were performed between two resistant (R) parents, between a resistant and an intermediate (I) parent (initially thought to be scale free, but eventually developed low level infestation) and between a resistant and susceptible parent. The reciprocal cross between the susceptible (S) and resistant parent was also performed.

**Table 1.—Controlled Cross-Pollinated Seed**

Cross (♀ x ♂)	Seeds						Germinative Capacity	Number of Plants
	Full	Germinated	Rotten	Empty	Total	% Full		
1506 (S) x 1504 (R)	11	84	0	146	241	39	81 %	77
1504 (R) x 1506 (S)	49	31	10	585	675	13	12 %	11
1504 (R) x 1501 (I)	35	0	0	98	133	26	37 %	13
1505 (R) x 1504 (R)	28	33	0	170	231	26	84 %	51

Individual seeds were dissected from their seed coats to determine if they were full, germinated (radicle evident), rotten (including a small percentage that showed evidence of insect damage), or empty. The germinative capacity is the percent of full seeds + germinated seeds that once sown resulted in a seedling. *Table from Koch & Carey (2004b)*

**Table 2.—Open-Pollinated Seedlings.**

Parent Tree	Number of seeds	% full	Germinative capacity	Number of plants
1506 (S)	802	35	60 %	168
1504 (R)	2081	28	8.5 %	49
1511 (S)	478	24	2.6 %	3
ME (R)	283	75	53 %	149

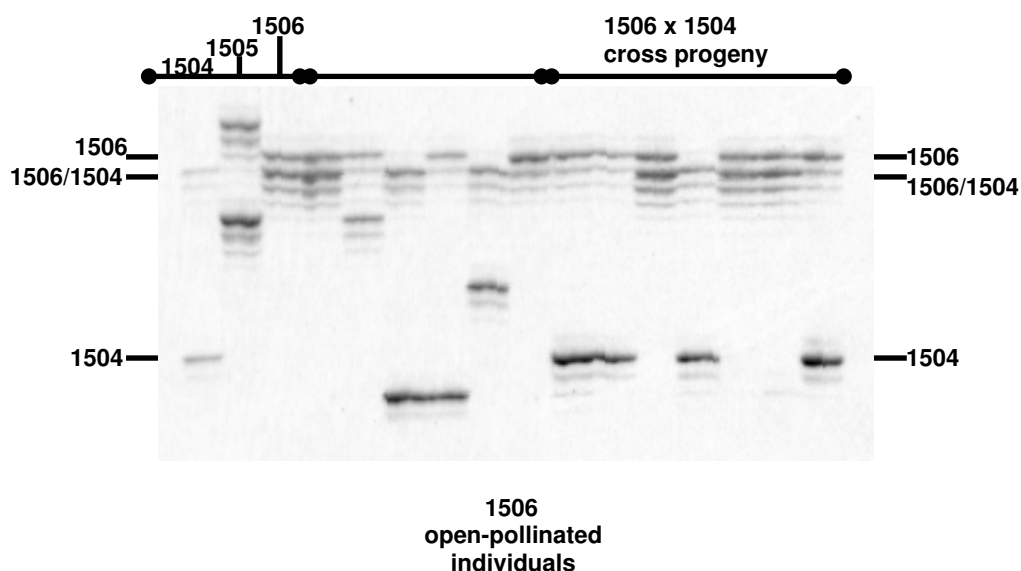
The germinative capacity is defined as the percent of full seed + germinated seeds that once sown resulted in a seedling. *Table from Koch & Carey (2004b)*

The results of the controlled cross-pollinations are listed in Table 1. The amount of full seed ranged from 13 to 39 percent. The germinative capacity (the percent of sound seed that germinated) varied from 12 to 84 percent, providing some evidence of mating incompatibilities . The susceptible tree 1506 was used as both a pollen donor and a maternal parent along with the resistant tree 1504. Interestingly, when 1504 was used as a pollen donor with both 1506 and the resistant tree 1505, seeds with a high germinative capacity (81 and 84 percent) were produced. But when 1504 was used as a maternal parent with either 1506 pollen or 1501 pollen, the seeds produced had germinative capacities of 12 and 37 percent, respectively. For tree 1506, the opposite pattern was observed; this tree was more successful as a maternal parent than a pollen donor (Koch and Carey 2004a).

As a control, open-pollinated seed was collected from two of the parents used in the crosses, the resistant tree 1506 and the susceptible tree 1504. Open-pollinated seed also was collected from 1511, a susceptible tree in the same part of the Ludington State Park (LSP) campground, and from a tree in Maine that was part of a 150 acre stand where all susceptible trees have been

removed (Table 2). The open-pollinated seed collected from LSP was similar to the cross-pollinated seed in the range of the percentage of barren seed observed. This similarity between the germinative capacities of cross-pollinated seed compared to open-pollinated seed from the same parent (1504, 1506), indicates that the pollination bagging process did not negatively effect seed development. Overall, 24 to 35 percent of the seeds collected from trees at Ludington State Park (1506, 1504, and 1511) were full. This figure is only slightly higher than the reported 13 to 29 percent of sound nuts collected from 20 trees in East Lansing, MI (Gysel 1971). Interestingly, the percentage of sound seeds collected from the ME tree was much higher (75 percent) than those collected from Ludington State Park. This value was comparable to those reported by Leak and Graber (1993) for seed collected from beech in the White Mountain National Forest. Over a 6-year period of time seeds from White Mountain were consistently between 75 and 88 percent sound.

Although some steps were taken to minimize self-fertilization during the controlled cross-pollination experiments, including forcing pollen production for use



**Figure 1.—Confirmation of parentage using SSRs.** Only the alleles observed in the 1504 and 1506 parents on the left are also seen in the cross-progeny, indicating that each of the individuals was pollinated by 1506. Two of the open-pollinated individuals have alleles present that are also from either 1506 or 1504, indicating that some of these individuals may be the result of a cross between 1506 and 1504. Other individuals, as expected, have bands not seen in 1506 or 1504. To confirm parentage, each individual must be screened with several different SSR markers. The data shown here is a preliminary indication of parentage. To confirm parentage, a larger number of markers will be used.

in crosses prior to natural pollen release, we did not emasculate flowers. Experiments looking at self-pollination in American beech indicated a high degree of self-sterility (Koch and Carey 2004a). In addition to controlled crosses being contaminated by self-pollination, there is also always the small possibility of other sources of pollen contaminants, such as entering through a small tear in the pollination bag. To confirm the parentage of the cross-progeny and rule out contaminating pollen donors, we have begun working with SSRs (simple sequence repeats). These markers consist of tandem repeats of sequence units usually less than 5 bp in length (Bruford and Wayne, 1993). They differ from both RAPDs and AFLPs in that they are codominant and therefore can identify heterozygotes, which greatly simplifies parentage analyses. One disadvantage is in the extensive process involved in screening for microsatellites. However, once they have been identified and primers developed, the PCR-based protocol is relatively simple. Several microsatellite loci have been identified in several *Fagus* species, including *F. crenata*, *F. japonica*, *F. sylvatica* and *F. orientalis* (Tanaka et al. 1999; Pastorelli et al. 2003), so we started by screening these for informativeness in *F. grandifolia*. To

date, the nine primers developed in *F. crenata* have been screened and five have been found to amplify polymorphic bands in *F. grandifolia*. We have begun screening all of the cross-progeny and parents with these primers, and the preliminary data (Figure 1) has revealed no evidence of contaminating pollen.

## Methods

### Screening for Resistant Seedlings

The artificial infestation method developed by Houston (1982) was used to test both the full- and half-sib families for resistance to the beech scale insect. To collect insect eggs, polyurethane foam traps measuring 21 ½ cm x 28 cm and backed by masonite were affixed to susceptible trees at the Holden Arboretum (Kirtland, OH) in the summer of 2002. One year later, the pads were peeled back to reveal an enhanced scale population underneath. Using a paintbrush, the eggs were brushed off the tree and into a one gallon plastic ziplock bag. The eggs were kept on ice and stored at 4° C. Prior to use, the eggs were sieved through 200 µm nylon mesh to separate them from debris and adult insects. Using a dissecting microscope, individual eggs were counted out and 150 eggs were placed on pieces of moistened polyurethane

**Table 3.—Results of Scale Challenge Tests**

Seedling source	Number of resistant	Number of susceptible	Total	Hypothesized Ratio Tested	P
1505(R) x 1504(R)	21	26	47	(9:7) <sup>a</sup> 4:5 <sup>b</sup>	(.110) .974
ME(R), Open-pollinated	31	40	71	(9:7) <sup>a</sup> 4:5 <sup>b</sup>	(.033) .893
1506(S) x 1504(R)	12	41	53	(9:7) 1:3 <sup>c</sup>	(<.0001) .692
1506(S) Open-pollinated	22	67	89	(4:5) 1:3 <sup>c</sup>	(.0014) .950
1504(R) Open-pollinated	7	26	33	1:3 <sup>c</sup>	.616
1510(S) Open-pollinated	3	22	25	1:3 <sup>c</sup>	.133

<sup>a</sup>Ratio is derived from a dihybrid cross between two heterozygous individuals where a single dominant allele for each gene is required for resistance, yielding a 9:7 ratio.

<sup>b</sup>Ratio derived from a dihybrid cross resulting in a 9:7 ratio, but if the homozygous, dominant condition for either of the genes is assumed to be lethal, the resulting ratio is 4:5.

<sup>c</sup>Ratio is derived from assumption that R tree must again be heterozygous for both genes and S tree is homozygous for both genes.

R = resistant, S = susceptible

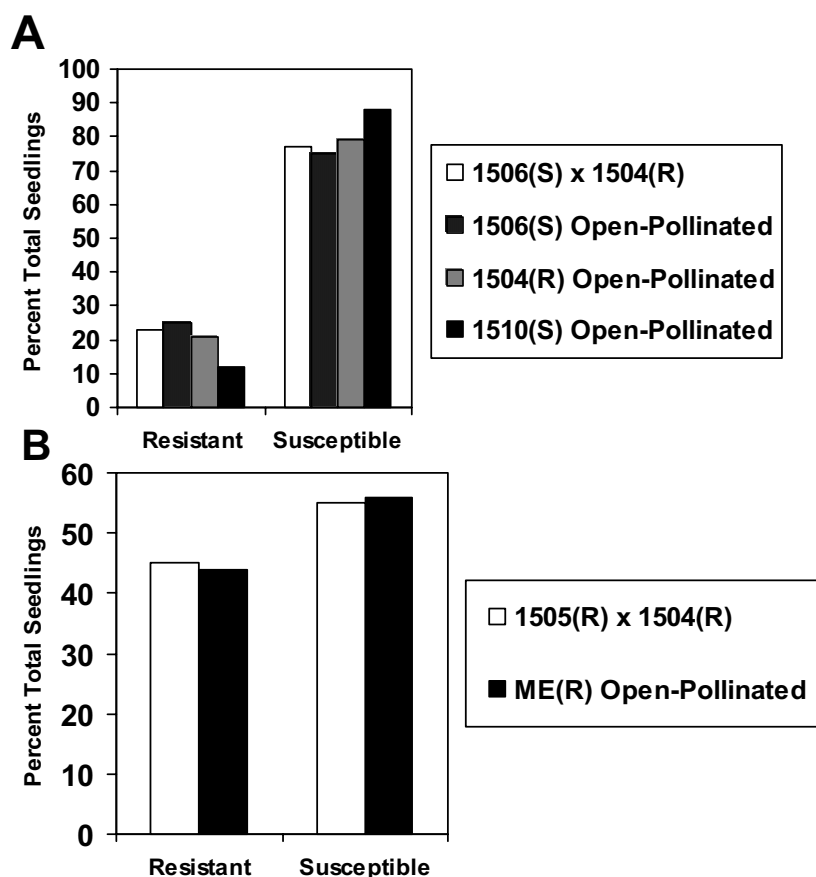
foam measuring 3 cm x 7 cm. The foam was affixed to the stem of the seedlings using plastic coated wire, with the eggs facing directly against the bark. The potted seedlings were kept in a lathe house and fertilized weekly with a 12-12-12 fertilizer throughout the growing season and brought into a cold storage facility (4° C) from November to April. In July of 2004, the foam pads were removed and the number of insects that had established on the bark under the pad were counted using a 10 X hand lens. Individual trees with five or fewer insects were deemed resistant. Two size classes of scale were observed and in all cases where five or fewer insects were observed, they were of a smaller size class compared to those observed on susceptible trees. Many times they also appeared brown and shriveled, not round and yellow as observed on susceptible trees. Chi-square analysis determined the goodness of fit with the hypothesized ratios. The probability (P) was determined using the chi-square to P calculator at <http://faculty.vassar.edu/lowry/tabs.html>.

## Results

The results of the scale counts are summarized in Table 3. Seedlings challenged included those resulting from the R

x R cross and seedlings from the S x R cross. The resistant pollen donor in each of these crosses was the same individual, tree 1504. Seedlings were called susceptible if they had five or more scale insects present. In most cases, when five or fewer scale insects were observed, they were a smaller size class than what was observed in susceptible individuals with five or more scale insects present. Forty-five percent of the seedlings resulting from the R x R cross were resistant based on these criteria. In comparison, 44 percent of the open-pollinated seedlings from Maine were resistant. In this case, the stand of the maternal tree had been managed for BBD by removing all of the susceptible trees 10 years earlier (Trial, personal communication). It is probable that the pollen donors were all resistant. Consequently, the ME open-pollinated seedlings are the result of several different R x R crosses and it is not unexpected that the proportion of resistant progeny is similar to the proportion observed in the R x R controlled cross (Figure 2B).

Twenty-three percent of the individuals from the S x R cross were resistant according to the scale challenge assay.



**Figure 2.—Proportion of Resistant Seedlings. A.** Comparison of the proportion of resistant to susceptible seedlings obtained from an S x R cross, an open-pollinated resistant tree and two open-pollinated susceptible trees. **B.** Comparison of the proportion of resistant to susceptible seedlings obtained from an R x R cross and an open-pollinated resistant tree.

The open-pollinated seedlings from the same resistant tree used as the pollen donor in the controlled crosses were 21 percent resistant. The similarity between these open-pollinated seedlings and the seedlings derived from the S x R cross is not surprising because theoretically the open-pollinated seeds are the result of many different R x S crosses (Figure 2A). The maternal parent, 1504, is resistant and it is probable that most of the potential pollen donors were susceptible. In contrast, the susceptible maternal parent, 1506, also produced 25 percent resistant open-pollinated seedlings. It was expected to produce fewer resistant offspring than the half-sib family derived from the resistant parent 1504. However, upon closer inspection, it was determined that a putatively resistant tree was located within 10 feet of 1506 and in fact, the crown of this tree actually touched the crown of 1506. This tree had no visible scale colonies and has since been challenged using the artificial infestation technique. The majority of the open-pollinated seedlings from 1506 were possibly the result of an S x R cross with this nearby resistant tree.

Open-pollinated seedlings from tree 1510, a susceptible tree, yielded 12 percent resistant individuals. The closest known resistant tree is 700 feet away from 1510, yet several other susceptible trees are located nearby. It is likely that the majority of pollen donors in this case are susceptible, but a percentage of seeds resulting from a resistant pollen donor cannot be ruled out. In future experiments, true S x S controlled crosses will be performed, using tree 1506 if possible.

## Discussion and Conclusions

The percentage of resistant seedlings resulting from the R x R cross (45 %) was about a 4-fold increase over the percentage of resistant progeny from the open-pollinated susceptible tree 1510 (12 %). The higher proportion of resistant progeny observed in the R x R cross compared to the S x R cross provides the first genetic proof that resistance to the beech scale insect is a heritable trait. Although the data presented here is from a preliminary trial, the result of only a single year of challenge testing, the fact that the same proportion of resistant progeny was observed in both the full-sib family (R x R) and in the ME half-sib family provides support for the validity of

the data and the challenge test. Further support is seen in the similarity of the proportion of resistant progeny observed in both the S x R controlled cross and in the half-sib family derived from the R parent. Using the chi-square goodness of fit test, the ratio of resistant to susceptible individuals resulting from both the R x R and S x R crosses does not fit either the 3:1 or 1:1 ratios that would be expected from these crosses, respectively, if resistance were a single gene trait. The chi-square goodness of fit test was also used to test the 9:7 ratio that would be expected to result from a classic dihybrid cross. The R x R cross was found to fit this ratio, but with a very low P value of .110 (Table 3). The ME open-pollinated seedlings were found not to fit this ratio with  $P = .033$ .

Previous work by Wargo (1988) concluded that there is a correlation between high levels of scale infestation with higher levels of bark amino nitrogen. If the genes involved in resistance are somehow related to nitrogen metabolism, it is possible to imagine that if the homozygous dominant state of one of the genes results in a complete block of a metabolic pathway, not just a reduction, that lethality could be observed. If the assumption is made that the homozygous dominant condition for either of the two genes is lethal, the expected ratio for the dihybrid cross is 4:5. The chi-square goodness of fit test for this ratio gave a very high P value of .974 for the R x R cross and .893 for the ME open-pollinated family (Table 3). The resistant-to-susceptible ratio generated by the S x R cross did not fit the 9:7 or 4:5 ratios, providing support for the observation that the ratios produced by crossing two resistant individuals are different from the ratio produced by a S x R cross. However, the S x R family ratio was found to fit a 1:3 ratio ( $P=.692$ ), which is the ratio that would be expected in a dihybrid cross between a resistant individual who is dominant heterozygous for both genes and a susceptible individual that is homozygous recessive for both genes.

The data presented are from a preliminary trial with a relatively small sample size. The two-gene model suggested may be an oversimplification and is presented here as a starting point, a model to be tested in future work. Furthermore, use of a biologically based assay introduces a degree of variability that could potentially result in false positive or false negative results, skewing the ratio of resistant to susceptible individuals. To

determine to what extent variability within the insect challenge assay may influence the data presented here, we have repeated the insect challenge test on all of the full- and half-sib families. Data will be collected in August of 2005. In fall of 2005, we hope to establish a field planting of the cross-progeny to confirm the results of the artificial infestation experiment and to assess traits such as growth rate, form, and long-term durability of resistance. Other efforts under way include grafting of all cross-progeny as a means of preserving the germplasm and to produce replicates for further experimentation. Finally, efforts are ongoing to expand the pool of resistant parents used in genetic studies as a way to survey mechanisms involved in resistance and their mode of inheritance.

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## AMERICAN BEECH VEGETATIVE PROPAGATION AND GENETIC DIVERSITY

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### Abstract

Work is underway in two regions of North America to develop the protocols and knowledge required to conserve genetic resources and restore populations of disease resistant beech. The work builds on years of research by Houston and others within the US Forest Service. Two aspects of this work include developing vegetative propagation techniques and understanding patterns of genetic diversity. Although American beech regenerates readily from root suckers under natural conditions, efforts to vegetatively propagate the species have met with limited success. There are no reports in the published literature of successful production of rooted cuttings, micropropagation from buds, or somatic embryogenesis. Grafting is somewhat more successful. Barker and others (1997) and Simpson (2001) were able to develop rooted plantlets through micropropagation of buds but neither were successful in over-wintering them. Present studies focus on reducing incidence of contamination, improving root formation, and maintenance of plantlets after transfer to a soil medium and understanding causes of inability to survive a dormant period. Both Simpson (2001) and Koch (personal comm.) have had success with rooting but none of the rooted cuttings have flushed after over-wintering. Grafting appears promising as a tool for resistance screening and developing seed orchards.

Understanding patterns of genetic diversity within and among populations of resistant and susceptible trees is important for carrying out gene conservation. Genetic parameters including diversity were estimated for populations located throughout the range of beech bark disease (Houston and Houston 1994 2000). They reported that susceptible trees had higher heterozygosity than resistant trees. A study has been initiated to examine the distribution of genetic diversity for 10 populations in a restricted geographical area in New Brunswick, Canada.

## Introduction

The American beech component of forests in north-eastern North America has been devastated by beech bark disease caused by the introduced insect-disease complex, *Cryptococcus fagisuga*, a soft-bodied scale, and *Nectria* fungi species (most commonly, *N. coccinea* var. *faginata* and, less commonly, *N. galligena*). In the Maritime provinces of eastern Canada, where the disease was first discovered, beech forests have been reduced to scrubby stands with no commercial value, and much reduced ecological value.

Natural resistance to beech bark disease apparently exists with a low frequency in all areas where the disease occurs and this resistance is believed to have a genetic basis (Houston 1983). The disease is caused by initial infestation by the beech scale and subsequent infection by the *Nectria* fungus. In the absence of beech scale, the disease rarely occurs. Restoration of beech in mixed wood or tolerant hardwood forest ecosystems depends on genetically-based resistance to the disease (or to the scale insect).

Conservation of the resistant gene pool and restoration of disease-free beech requires vegetative propagation techniques and knowledge of genetic structure of populations. Several studies have reported on genetic diversity over the range of the disease. Understanding the resistance mechanism or mechanisms and genetic mode of inheritance (number of genes involved, penetrance, additive or dominant gene action) is essential for developing a program for breeding resistant genotypes.

American beech is notoriously difficult to propagate by vegetative means, in spite of the high frequency of root sprouting commonly observed after disturbance. Cuttings have been successfully rooted and micropropagation has yielded apparently healthy plantlets, both at low success rates, but subsequent development of the plants, especially over-wintering poses the biggest problem.

The purpose of this paper is to provide an overview of current and previous work in vegetative propagation including rooting cuttings, micropropagation, grafting; and in genetic studies including population genetic structure of infected stands and levels of genetic diversity among resistant and susceptible trees.

## Vegetative Propagation

Reid (1984) described attempts to produce rooted cuttings from stump sprouts. He used softwood cuttings with a mist enclosure and successfully rooted 10% of the cuttings but they did not over-winter. Simpson (2001) used softwood cuttings derived from root suckers collected from forest stands and from suckers produced in a greenhouse from roots collected in the field and kept in damp peat until suckers were produced. He tried many different culture combinations and found that with a mist enclosure, cuttings that had been dipped in a 5000 ppm IBA solution rooted well (75% of trees tested produced some rooted cuttings), but all died over winter. Simpson reported that his success varied by date of collection, genotype, diameter of the tree from which roots had been collected and the IBA concentration.

Work on rooting cuttings continues in two labs: Koch and Carey (2004a) have achieved a reasonable rate of success with cuttings but the over-wintering problem has not been solved. Ramirez, a Masters student at the University of New Brunswick, has attempted various cultural approaches to rooting cuttings, including a hydroponics system, without success.

Similarly, attempts to produce plantlets by tissue culture of buds or stem segments have met with some success but no plantlets have successfully over-wintered. Barker *et al.* (1997) worked with seedlings, shoot tips from root sprouts, and buds from mature trees with varying success but none survived the transfer to soil. Simpson (2001) worked with buds from mature trees and buds from 47% of trees produced some rooted plantlets; however, none over-wintered. Beech buds are difficult to sterilize and contamination was an on-going problem in both projects. Incomplete rejuvenation may account for the inability of plantlets to survive the transition to soil and break dormancy after winter. Plantlets develop buds and shut down when they are still very small, and their roots are not well-developed.

One of us continues to work on micropropagation using both buds from mature trees and stem segments from root suckers produced in the greenhouse as explants (Fig.1). She has tried culturing epicormic shoots induced in a greenhouse, as well. The contamination is

higher with buds than with stem segments because of the layering of bud scales and the impossibility of eliminating all sources of contaminants that may be stuck between bud scales (Fig. 2a and 3a). Green, non-woody stem segments (1 cm in length) excised from suckers, produced by greenhouse-cultured, meter-long sections of beech roots (ranging from 1 - 3 cm in diameter) in peat moss were easier to sterilize, but no more successful in terms of rejuvenation (Fig 2b and 3b).

Currently, Ramirez is examining the roots from plantlets cultured in standard AC growth medium to determine whether they are structurally different from those of seedlings.

Grafting has proven more successful. In New Brunswick, scions were collected in late February and early March in 2003 from 20 undiseased and 5 diseased trees, and were grafted onto rootstock produced from seed collected from undiseased trees. The success rate was approximately 33% and varied by genotype (Fig. 4a). More significantly, success varied by diameter of the rootstock stem; the smaller the rootstock, the greater the difficulty in matching with a scion of similar size (Fig. 4b).

## Genetic Structure and Diversity

Understanding the genetic structure and distribution of genetic diversity is important before embarking on gene conservation and restoration activities. For example, it is important to know whether all resistant trees in a stand are likely to be related or even if they are ramets of the same clone, before deciding if the gene pool of resistant selections will be increased by sampling more than one tree per stand. It is also important to know whether the levels of genetic diversity are consistent among resistant and susceptible genotypes, i.e. whether resistant trees across populations are deficient in genetic diversity. If this is the case, susceptible trees may be needed to retain natural levels of genetic diversity within the resistant gene pool.

If the restoration of beech attains sufficient importance to merit the development and implementation of a breed strategy, it will be important to know whether genetic diversity is distributed evenly across the species range.

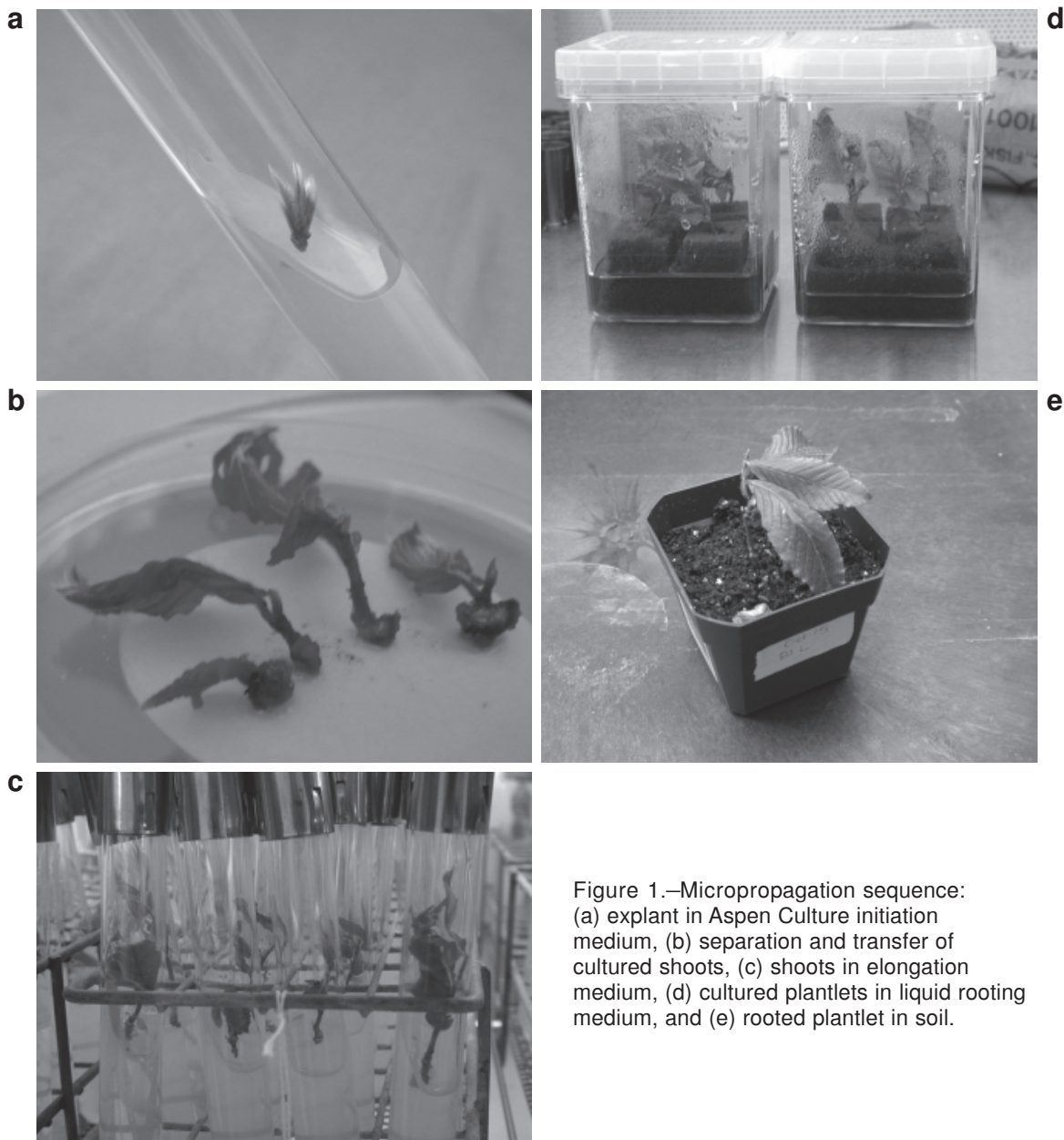


Figure 1.—Micropropagation sequence: (a) explant in Aspen Culture initiation medium, (b) separation and transfer of cultured shoots, (c) shoots in elongation medium, (d) cultured plantlets in liquid rooting medium, and (e) rooted plantlet in soil.

Houston and Houston (1994) reported on allozyme diversity in two mapped stands; one in Massachusetts with 173 trees and the other in West Virginia, looking at 152 trees. They found very little difference in genetic diversity parameters between the two populations. Both appeared to be clonal mosaics. In general they found high expected and observed heterozygosity, although the West Virginia population exhibited a heterozygosity deficiency (observed was lower than expected).

Kitamura and others (2000, 2001) evaluated allozyme diversity in several studies examining the substructuring

of beech populations, particularly comparing populations with and without regeneration by root suckers. In one study, 21 populations were sampled and 12 allozyme loci were scored (Kitamura and Kiwano 2001). They reported a very high  $G_{ST}$  value (0.168), indicating a strong degree of differentiation between populations. Mean expected heterozygosity was relatively low at 0.186. Thirteen polymorphic loci were scored in another study by Kitamura *et al.* (2000), which compared populations having varying amounts of regeneration by root suckers in Quebec and Pennsylvania. They reported similar levels of genetic diversity among populations. The final study

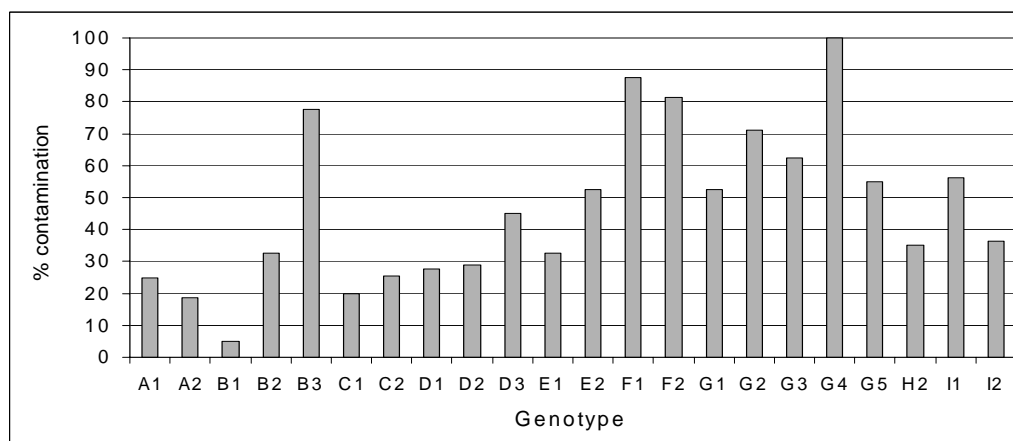


Figure 2a.—Percent contamination of bud cultures by genotype for buds from 22 trees representing 9 locations (A to I) in southern New Brunswick.

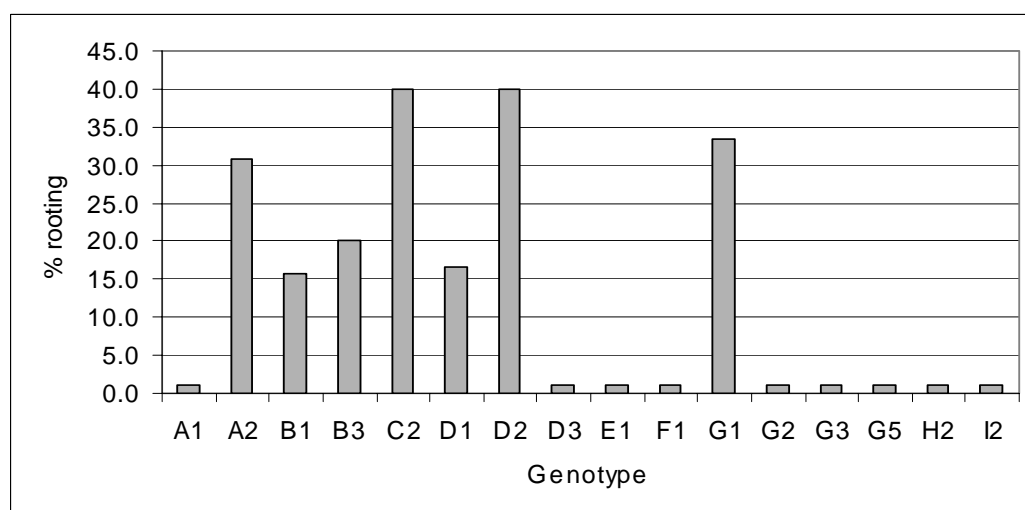


Figure 2b.—Percent of cultured shoots that produced roots by genotype for buds from 16 trees that proliferated shoots in culture.

(Kitamura *et al.* 2001) compared populations with and without vegetative regeneration by root suckers, and found a homozygote excess in the three populations with clonal reproduction and a heterozygote excess in the population that originated only from seed.

Houston and Houston (2000) sampled 9 stands from Prince Edward Island in eastern Canada to West Virginia and they mapped the susceptible and putatively resistant trees in four stands. They scored 23 allozyme loci and found that though the levels of diversity were within the range expected for forest trees, they were lower than reported for most other hardwood species. Resistant and susceptible subsets of populations were very similar in most diversity measures; however, resistant trees exhibited a deficiency of heterozygotes.

## Resistance Screening and Breeding

Recently, small-scale programs have been initiated in Ohio (Koch and Carey 2004b) and in New Brunswick at the Canadian Forest Service Atlantic Forestry Centre, to screen disease-free mature trees for resistance to the scale insect, and to produce crosses for challenge tests and genetic analysis. Grafted stock has been screened at both locations using the technique developed by Houston (1982) (Fig. 5). Results of challenge tests on grafted trees in New Brunswick are preliminary (only one year of data is available yet) but indicate strongly that most disease-free trees in natural stands are genetically resistant.

The results of challenge tests on seedlings produced by controlled crossing among resistant and susceptible trees carried out in Ohio are reported in these proceedings (J.

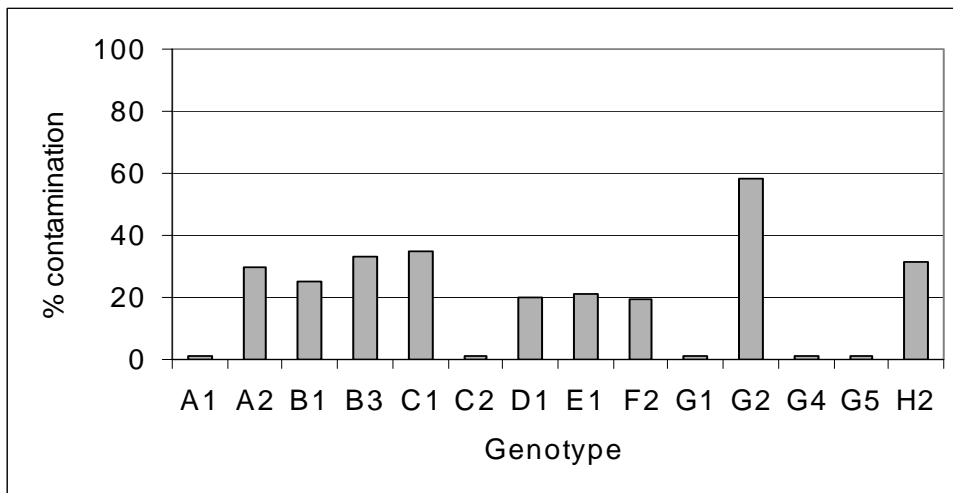


Figure 3a.—Percent contamination of stem section cultures by genotype for suckers produced in a greenhouse from 14 trees representing 8 locations (A to H) in southern New Brunswick.

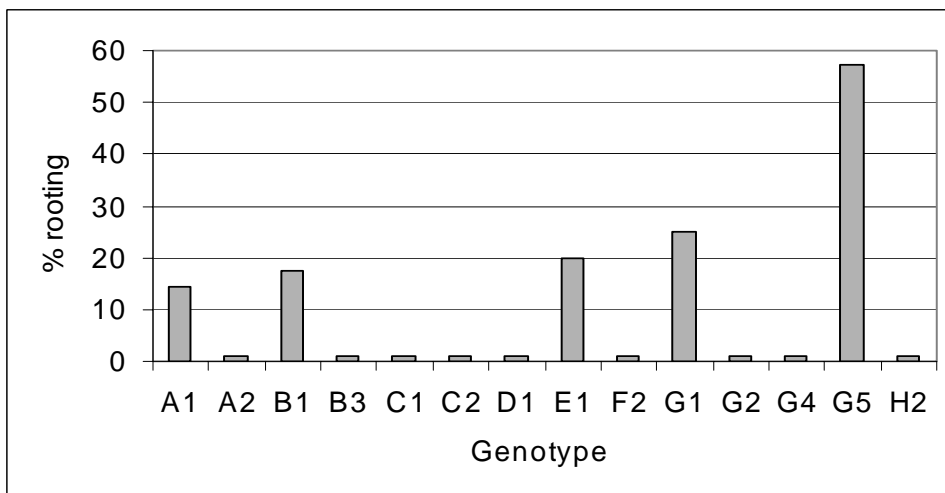


Figure 3b.—Percent of cultured shoots that produced roots by genotype for stem sections from 14 trees that proliferated shoots in culture

Koch). Controlled crosses were conducted in New Brunswick as well, using four resistant and two susceptible trees at each of two locations in spring 2004. Seed was set for all crosses but results are not yet available. Resistance screening will be carried out starting in summer 2005, with results expected in summer 2006.

## Conclusions

None of the conventional vegetative propagation techniques work well for beech. Cuttings have been successfully rooted but the challenge of over-wintering remains. Micropropagation works best with shoot segments from root sprouts but rejuvenation remains problematic, and none have successfully over-wintered.

Grafting is a useful technique for resistance screening and developing seed orchards. It is not a solution for mass production of scale-resistant genotypes.

Several general conclusions may be drawn from the body of existing literature and recent results of studies. Any two resistant trees in a beech stand may be identical or closely related, emphasizing the need to sample broadly in a breeding program for resistance. It appears that sufficient genetic diversity exists in resistant trees, scattered across populations, to conduct a breeding and restoration program. Initial indications imply that populations differ sufficiently to require sampling over broad geographic areas for conservation of the resistant

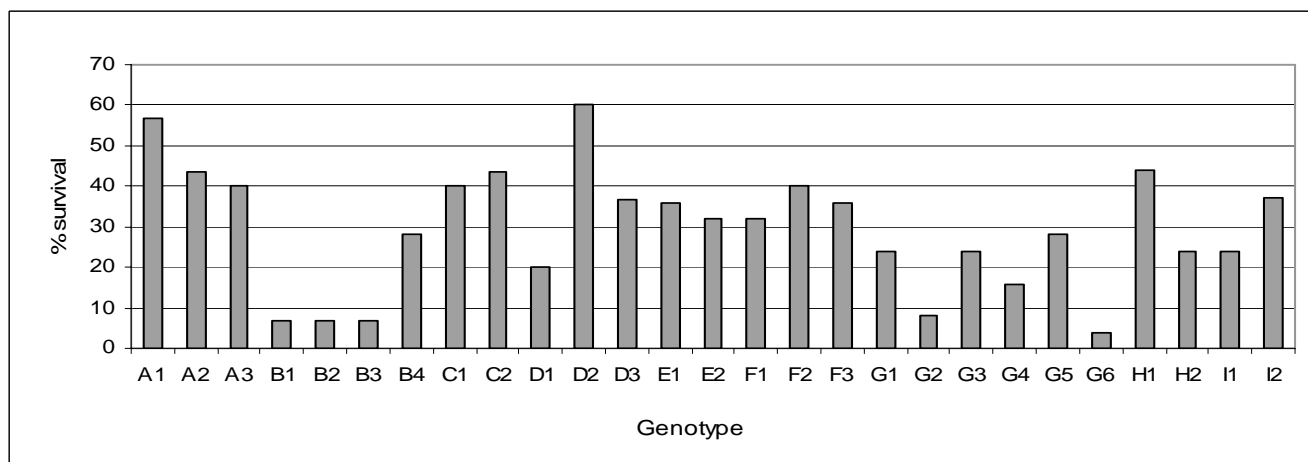


Figure 4a.—Grafting success for 22 genotypes representing nine locations (A — I) in southern New Brunswick.

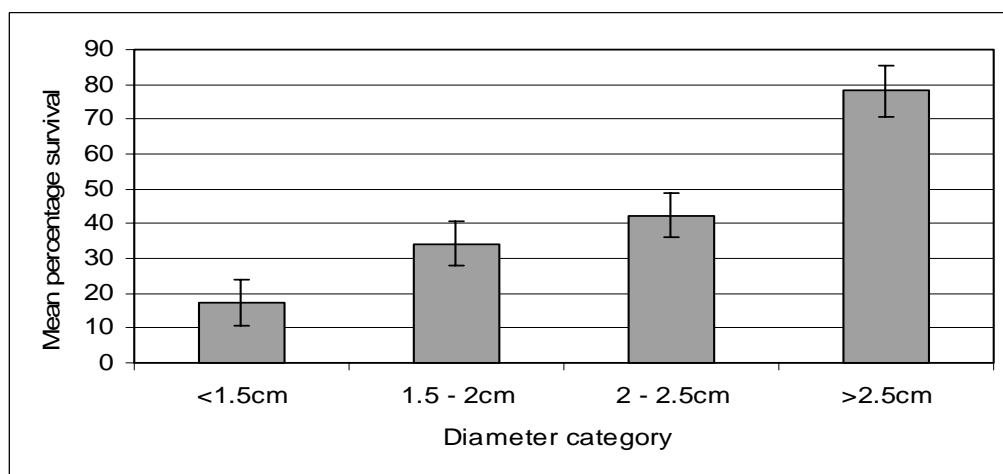


Figure 4b.—Survival of grafts with scions of different diameters; grafting success appears to be related to scion diameter.

gene pool. We know little, however, about genetic structure over intermediate geographic distances. Gaps and discrepancies between studies results imply a need for further work.

Breeding for resistance to the beech scale appears to be technically feasible, but more complete results of challenge tests on recently completed crosses are required before embarking on a breeding program. The parallel and complementary work undertaken in the two research programs (Ohio and New Brunswick) will enable comparison of genetic control of resistance near the point of introduction and near the new killing front of the disease.



Figure 5.—Beech bark disease screening on grafted stock from disease free mature trees.

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## Knowledge Gaps and Research Priorities

### *Knowledge Gaps*

- What is the mode of inheritance?
- What are the mechanism(s) of resistance?
- What is the durability of resistance (temporal/spatial)?
- What are the requirements to establish resistant seed/propagates?
- What are the best methods of restoring resistant beech populations and introducing them to forests?
- What is the genetic diversity of host, scale and *Nectria* sp.?

### *Research Priorities*

- Develop database for reporting resistant trees, management of disease and share research results.
- Retain diverse collection of resistant germoplasm over biogeographic range of beech.
- Identify genetics and mechanisms of resistance and tolerance of the BBD complex as a whole.
- Use knowledge gained by determining mechanism(s) of resistance to develop tools for identifying resistance.
- Assess genetic diversity of resistance and other desirable traits. Examples: drought resistance, correlations between traits (resistance and deleterious traits).
- Develop methods of propagation, both vegetative methods and seed production.
- Return resistance to the field.
- Education program for BBD, resistance conservation.

## **Section 5:**

### **Modeling the BBD system**

# USING MODELS TO IDENTIFY FORESTS AT RISK OF MAJOR STRUCTURE AND COMPOSITIONAL CHANGE DUE TO BEECH BARK DISEASE

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## Abstract

Relatively few models have been developed to predict changes in forest structure as a result of BBD. A lack of understanding of the critical factors that control the severity of the disease in forests, and at what spatial scale these factors act, continues to limit our ability to predict changes in forest structure and composition following the establishment of BBD. However, historical data sets combined with new measurements across a spectrum of northeastern forest stands may allow us to model the characteristics of uninfected forests that put them at risk of a significant state change of descending into the undesirable condition that has been characterized as 'beech hell'. We propose to test for hypothesized drivers of this state change by combining measurements of forest structure and dynamics with historical patterns of abundance in the scale insects and fungus that cause BBD. Forest management could benefit from models that identify (1) stands that are at risk of undesirable state change, and (2) key factors that drive the transition. Models may suggest strategies for directing the transition toward more desirable outcomes in aftermath forests. In particular, we hope that empirically based models can be developed to predict the location and attributes of forests that will retain beech nut production in the presence of BBD.

## Introduction

Beech bark disease (BBD) is a result of co-infection of beech trees (*Fagus grandifolia* Ehrh.) by an ascomycete fungus (*Nectria coccinea* var. *faginata*) and the beech scale insect (*Cryptococcus fagisuga* Lindinger) (Ehrlich 1934). Because initiation of the disease requires some fissures in the bark, many trees do not become afflicted until they have attained a size where establishment and reproduction by the insect is possible. Also, disease

progression is very slow relative to some other forest pathogens such as Dutch Elm Disease or Chestnut blight; infected trees may die within several years or may require a decade or more to die. These two details have consequences for the demographics of infected beech populations because they allow persistence of beech even within forests where virtually every tree becomes infected, and virtually every infected tree eventually succumbs to the disease.

In New England and New York State, over 100 years after the introduction of the beech scale - *Nectria* fungus complex to North America, BBD is still a significant factor affecting forest stand structure and composition. McGee (2000) reported that the disease-killed trees accounted for approximately 22% of coarse woody debris in Adirondack northern hardwood forests. A study in central New York reported that beech trees made up 52% of the gaps in the northern hardwood forest while they represented only 26% of the canopy trees (Krasny and Whitmore, 1992). In an examination of changes in forest structure over a 15-year time period (1985-2000) at one northern hardwood forest site, Forrester *et al.* (2003) found that while beech was still a dominant component of the forest canopy, there was a shift toward greater importance of sugar maple. In New Hampshire forests, growth of severely infected trees was shown to have been reduced by 40% relative to healthy beech trees (Gavin and Peart, 1993). Biogeochemical implications of these changes in forest structure have been suggested, but have yet to be shown consistently.

Contrary to early hypotheses that BBD would lead to widespread replacement of beech by sugar maple and yellow birch, beech has persisted, although with a dramatically altered size distribution that includes large numbers of saplings and small trees, and none of the large trees that were once common. In fact, forest managers commonly report that infected beech stands actually preclude regeneration of economically valuable timber species and that this condition seems to be self-perpetuating (because infected trees tend to produce copious root suckers before dying, which out-compete the seedlings of birch or maple; e.g., Hane, 2003). Also, loss of mature trees, and the dramatically reduced beech nut crops, have negatively affected many wildlife species. Foresters lack any practical tools for remediating stands that have descended into "beech hell".

Models that will provide tools to identify stands that are at risk of this undesirable state change, and identify key factors of forest dynamics and epidemiology that drive the transition are required. Outcomes of such models may suggest strategies for preventing the transition before it occurs. Models must be based on empirical data and be developed to predict the location and attributes of forests that will retain beech nut production in the presence of BBD.

### Using Models to Predict Future Disease Impacts

The limited number of models that have been developed to predict the future of northern forest structure due to BBD is likely due to a combination of factors including: 1) Initial lack of interest in beech as a merchantable species and, 2) the fact that beech basal area does not appear to be declining, though the size structure of beech in forests is altered (Forrester *et al.*, 2003). Researchers and managers who have maintained an interest in BBD have now generated enough data to show that the disease, though not eliminating beech from the forest, has serious implications for forest structure and composition, changes in coarse woody debris, and wildlife species dependent upon beech nuts and large trees. All of these threats may affect the economy and ecology of northern forest communities.

Twery and Patterson (1984) developed a matrix using transition probabilities that were based on within stand comparisons between data they collected in Massachusetts and New Hampshire in 1981 and 1982, and historically collected data from those sites in the 1960's (MA) and the 1930's and 1950's (NH) respectively. The goal was to examine potential long-term successional trends in stands of various composition that had been influenced by BBD. The major successional implications from that relatively qualitative model were that 1) stands where hemlock was dominant would tend toward a loss of beech from the canopy and hemlock dominance, (perhaps with an increased red maple or yellow birch component) due to the high beech mortality evident in those plots, 2) beech-dominated stands would remain beech-dominated since some mortality of larger trees will be replaced by advanced regeneration of young beech, and 3) stands co-dominated by beech and sugar maple would also tend to retain their composition. The authors concluded that BBD was a "partial disturbance which acts slowly over a long time period causing a

reduction in growth" (Twery and Patterson, 1984). The authors suggested the need to understand how the relative proportions of resistant and susceptible beech might change over time as a function of intraspecific competition. They suggested that over time the proportion of resistant beech in a stand might increase in the absence of growth inhibition by the disease.

Le Guerrier *et al.* (2003) developed a SORTIE model to examine potential long-term scenarios for the structure of forests containing beech and hemlock (*Tsuga canadensis*). Therefore, all stands included hemlock, and resistance to BBD was not included in any scenario. The recruitment submodel in SORTIE was not altered since studies had shown that adult vigor does little to change sprout production and survival if the adult tree is alive (Jones and Raynal, 1987). Their models, based on hypothetical stand structure and parameterized with information from the published literature suggest that, over a 300 year time scale, larger beech will again be present in stands where there was high mortality due to the disease complex. Additionally, like Twery and Patterson (1984), they report that hemlock trees benefit from beech mortality in their model scenarios.

Twery and Patterson (1984) and the more recent LeGuerrier *et al.* (2003) model corroborate each other fairly well and confirm patterns that have been observed from published field studies particularly with respect to the short-term changes in stands and the response of plots with a high hemlock component (Runkle, 1990). They, however, do not explicitly incorporate interspecific competition in the understory, or dynamics that might result from differences in reproductive strategies or success of susceptible versus resistant individuals (mast/seed production, physiology of root sprouts versus seedlings). In addition, a recent study by Hane (This Proceedings) found that, contrary to Jones and Raynal (1987), there was a significant positive relationship between disease severity and the number of root sprouts produced by adult beech. This suggests that future demographic models for forest structure and composition need to include this relationship. Finally, research has yet to clearly identify abiotic or topographic variables that strongly correlate to the level of disease in a given stand. Griffin *et al.* (2003) found that disease severity was correlated with beech density at spatial scales of 60 - 1000 ha but not at the stand (1 ha.) scale. Twery

and Patterson (1984) found no singular relationship between aspect, solar radiation index, soil type and habitat type and disease severity among plots. Using a multiple regression approach, the best relationship included hemlock basal area, proportion of beech, the proportion of total density in beech, and slope position. The influence of hemlock may be direct (competition for soil moisture) or indirect (influence on air temperature and relative humidity in the canopy).

There is a critical need to continue modeling approaches with the use of current empirical data from experiments and long-term data sets from stands that have been historically measured. Results of these future models may have value in managing forests within the regions that are already infected, and could be useful in projecting the potential impacts in forests that have yet to be infected. Because northeastern forests are currently in all the stages (as described by Shigo, 1972) of the disease progression, we have the opportunity to develop hypotheses using dynamic models parameterized from aftermath forests that have been severely altered by the disease and those that have experienced less beech mortality and/or subsequent community structure changes, and test the hypotheses in stands that are at an earlier stage of the disease (such as stands in Michigan or Maryland). It is clear that future modeling efforts must incorporate data collected in forests from across the range of the disease because the spatial scale at which factors that affect disease severity are still relatively unknown.

## Future Modeling Efforts

Beech bark disease can apparently trigger a state change from diverse, productive forests to nearly monotypic, self-perpetuating, stands of scrub beech, colloquially known as “beech hell” (Figure 1). However, some stands long afflicted with BBD seem to have stabilized in a condition that is far less affected, with retention of most size classes of multiple tree species, and continue to support much of the native biodiversity. This suggests that forests may be resilient to BBD until some disturbance threshold is reached (Figure 2), beyond which there is rapid, lasting degradation of forest structure and function. We can test these hypotheses, and develop predictive models of BBD impacts, through

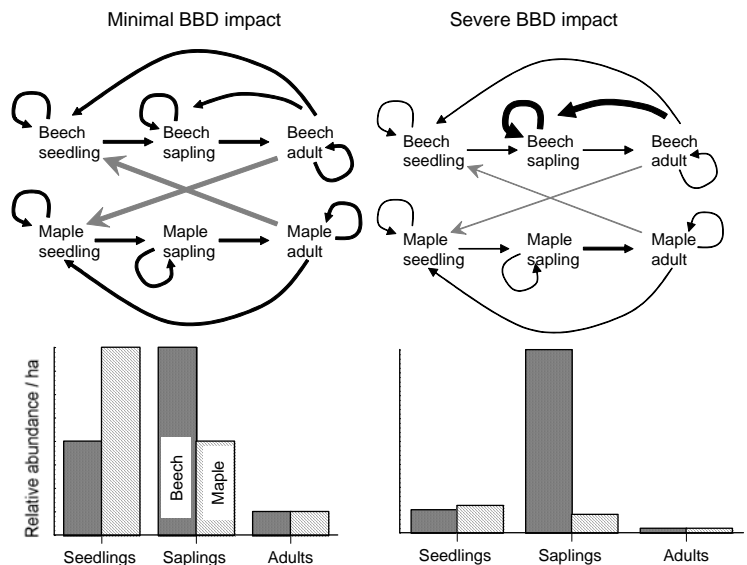


Figure 1.—Graphical model of alternative states that appear to exist in northern hardwood forests afflicted with beech bark disease. Black arrows represent demographic transitions. Gray arrows represent replacement of one species by another species at that spot in the forest. Change in line thickness between states indicates change in transition probabilities. Lower figure indicates relative abundance of species and size classes in natural and impacted forests. Research will test predictions derived from this model and evaluate the expected consequences for dynamics and equilibria of plausible changes in transition probabilities.

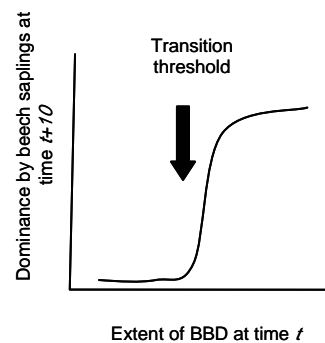


Figure 2.—Hypothesized relationship between BBD and forest state. The alternative states depicted in Fig. 1 may be separated by a rather abrupt threshold.

measurements of stand composition and dynamic trajectories in multiple hardwood stands scattered throughout the northeast. Data that can be used in the model are (1) from forest stands that already have historical baselines of annual measurements of BBD and (2) long-term plots from the USDA Forest Service’s Forest Inventory and Analysis (FIA) surveys, and other large data sets, collected from hardwood forests in the eastern United States with varied histories of BBD.

Using stand structure data from two cycles (approximately 10+ years apart) of sampling in FIA/FHM plots within regions with a long history of BBD (New England states), a shorter history of BBD (mid-Atlantic states), and little or no history of BBD (Midwestern states) will allow the testing of model predictions and identify the conditions under which forests do and do not become low diversity stands dominated by beech saplings. Data on changes in beech age and size structure from intensive study sites can be integrated into models to strengthen the validity of models that evaluate the consequences of different scenarios of BBD using FIA data. The model above will allow one to test changes in transition probabilities that can yield an abrupt state change in forests, as hypothesized in Figure 2, and if so, which specific demographic attributes are most critical, and where response thresholds could be expected. Data from other sites not used to generate the model will be used to test hypotheses developed with historical data, particularly with respect to coarse-scale spatial variables (vegetation type, soil, elevation, etc). These models will provide a tool for forest managers to identify sites that are at risk in the near future, and may suggest strategies for minimizing risks of degradation on a longer time frame. Model outcomes can be compared to those developed using hypothetical scenarios (Le Guerrier *et al.*, 2003).

The goal of these predictive models should be to forecast future forest structure based on (1) the historical abundance of scale insects and fungi that produce BBD and (2) easily measurable stand characteristics that may reasonably influence BBD or those that have been identified by the literature as possible correlates with disease severity (i.e. previous density and dispersion of mature beech, previous size distribution of co-dominant tree species, soil type, and climate). Once developed and validated, these models will provide a tool for forest managers to identify sites that are at risk in the near future, and may suggest strategies for minimizing risks of degradation on a longer time frame.

The hypothesis that BBD can induce a state change in forest dynamics predicts that the dominance of beech saplings in 2004-2006 is a threshold function of BBD severity 10-20 years previously (as in Fig. 2). Resampling historical sites will allow us to estimate the current abundance of scale insects and fungi for comparison with old data. This will permit a test of the hypothesis that

there are geographic hotspots in the abundance of scale insects and *Nectria* that are temporally stable, vs. the alternative that high intensity of BBD in one decade leads to reduced abundance of scale insects and *Nectria* in the next decade (perhaps because of depletion of suitable host trees). If the latter, this would be a form of delayed negative feedback that could produce predictable multi-decadal oscillations in forest structure. We will also be able to evaluate several other hypotheses to explain spatio-temporal patterns in the abundance of scale insects and *Nectria*. If abundance is strongly influenced by climatic patterns, there should be high spatial correlations (e.g., abundances in NH and VT should tend to go up and down in approximate synchrony). If instead, abundance of scale insects and *Nectria* is strongly influenced by local abundance of mature, susceptible, host trees, there should be little spatial correlation (stands with low and high abundances should be interspersed), and average abundances should be positively correlated with the density of large infected beech trees (many of which will now be dead, but still evident as deadfalls or logs). We may also be able to test for effects on BBD severity of soil types, site index, and the frequency of putatively resistant beech genotypes.

## Products of this Modeling Approach

1. Improved ability to identify stands in the northeast and beyond that are at risk of severe BBD impacts. Such stands would be candidates for preventive silvicultural treatment before transition and may warrant special attention for monitoring and protection along advancing fronts.

2. Characterization of long term trajectories in stands with a range of infection severity. If severely afflicted stands appear destined to grow out of it, patience may be prudent, but if they enhance the infection of other stands, sanitation may be warranted. We will be able to compare our model predictions with those of others (i.e. LeGuerrier *et al.*, 2003).

3. Improved ability to identify stands that may retain significant beech production. This would aid wildlife managers and conservation efforts.

4. Identification of manageable forest attributes that promote beech nut production and minimize transitions to an undesirable state. This may suggest strategies that can be applied to forest landscapes to improve forest health.

5. Refinement, and knowledge transfer, of standardized cost-effective monitoring programs for BBD in the northeast and beyond. The protocol developed by Houston for quantifying BBD severity may have general utility for forest health assessments. Surprisingly, there is presently no standardized program for monitoring the spread and intensity of BBD in U.S. forests.

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# POPULATION AND LARGE-SCALE DISPERSAL DYNAMICS IN THE BEECH SCALE INSECT *CRYPTOCOCCUS FAGISUGA*

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## Abstract

Pathogens and parasites play important roles in ecological communities and their influence is meaningful when they represent a newly arrived invader. At geographic scales, invading tree pests have caused major disruptions of terrestrial ecosystems. The bark disease of American beech (*Fagus grandifolia* Ehrl.) is an example of a disease invasion that has had a major impact on forest composition throughout northeastern North America in the past 50 years. The combined infestation of the European beech scale insect *Cryptococcus fagisuga* Lind., and the subsequent invasion of fungi (*Nectria* spp.) have substantially altered the structure of American beech populations. Because the scale insect must precede the fungus, it is the key component of disease spread. Despite this, there is little ecological research in North America on the beech scale insect. I examined the population and local dispersal dynamics of the beech scale insect on American beech populations in continuous forest inventory plots within the Edmund Niles Huyck Preserve in eastern New York State. Range maps of the insect's dispersal were re-interpreted to model the diffusive spread of the beech scale insect. Results indicate that geographic dispersal does fit a diffusion model, however estimated velocity was less than expected.

## Introduction

The limiting component in the spread of beech bark disease is the spread of the scale insect (Houston et al. 1979), because the attack by the scale predisposes the beech tree to an invasion by the *Nectria* spp. (Burns and Houston 1987). Without the scale, the fungi are unable to invade and the disease cannot progress. Knowledge of the patterns of scale reproduction and dispersal would help in understanding the disease's persistence in the aftermath zone of North America and would be beneficial to research on the original host, European

beech (*Fagus sylvatica*), for which mortality from the disease can be high on a local scale (Wainhouse et al. 1988).

The specific objective of this study was to quantify the spread of the beech scale insect over the past 100 years through the diffusive spread model. An understanding of the dynamics of the spread can help predict future spread of the disease, which has so far extended across less than half of the American Beech's geographic range (Houston 1994).

The diffusion coefficient  $D$ , can be calculated using  $mt$ , the mean squared deviation at time  $t$ , where  $mt = 2Dt$ . At time  $t$ , dispersing individuals are normally distributed about the release point with a mean of zero and a variance of  $2Dt$ . The mean square deviation of the distribution of the individuals is the variance of the normal curve and will increase linearly through time with a slope of  $2D$  (Kareiva 1983, Dwyer 1992).

Velocity of the expansion front of an invading species (Skellam 1951),  $V$ , is constant and can be calculated as

$$V = 2\sqrt{rD}$$

where  $D$  is the diffusion coefficient and  $r$  is the intrinsic rate of increase. This is the speed that the population front moves outward from the origin. Expansion results from both population growth and diffusion (Shigesada and Kawasaki 1997).

## Methods

To determine the diffusion coefficient,  $D$ , distance measurements were taken from the point of insect introduction in Halifax, Nova Scotia, to the extent of spread for each time interval delineated on published contour maps. Measurements were performed on my own digital projection of maps from Houston et al. (1979) and Houston (1994). Two sets of measurements were performed, one of maximal and one of minimal distances from the source introduction. Dispersal range boundaries limited by Atlantic coastal shores within the beech range were not included. In addition, satellite populations in Ohio and West Virginia were not included in diffusion coefficient measurements because their spread was apparently not due to diffusion, but possibly facilitated by human vectors (Houston 1994).

**Table 1.—Mean fecundity for *Cryptococcus fagisuga* (eggs per adult) by host infestation level with corresponding minimum and maximum values. 100 colonies were sampled weekly (40 from low and 60 from high density infestation)**

Density (colonies/cm <sup>2</sup> )	Mean fecundity (eggs/adult)	SD	Maximum eggs/adult	Minimum eggs/adult
High = 15 trees	12.93	4.56	22.61	7.31
Low = 10 trees	10.30	2.22	14.30	7.02
Total (25 trees)	11.88	3.96		

(T 21.5 = 1.917, p = 0.069)

In order to determine the demography of the beech scale insect, I sampled a series of randomly selected colonies collected from the same 25 trees, in four different forest plots in the E.N. Huyck Preserve in Rensselaerville, NY. Each tree was first sampled in early spring (March) and once a week during the reproductive period of the insect's life cycle (June through October). Each weekly random sample consisted of four individual colonies from each tree, stratified into four major compass directions to take into account any microclimate variations due to colony orientation on the tree. Of the 25 adult beech trees that were sampled, fifteen trees were of relative high density ( $2.09 \pm 1.14$  colonies/cm<sup>2</sup>) (mean  $\pm$  SD) and ten were of lower density ( $0.43 \pm 0.184$  colonies/cm<sup>2</sup>). For each colony, I recorded the number and size of adults, numbers of eggs and numbers of first instar (crawler) larvae.

In order to accurately estimate insect fecundity, I needed to account for all the eggs laid throughout the season. This required a reliable measure of adults present within a colony, along with an estimate of the cumulative egg total for a colony. A cumulative egg total was calculated by summing the weekly egg count with the cumulative egg count from the same tree 25 days earlier. This method takes into account both eggs present in the current sample and eggs that have hatched into crawler larvae. The estimate of the total eggs produced for each tree was calculated by averaging the cumulative egg total from the last 6 weeks of sampling. The mean egg total was then divided by number of mean adults per colony (calculated by averaging the number of adults per colony for each tree for the entire sample period before the presence of eggs) to determine a mean insect fecundity value for each tree.

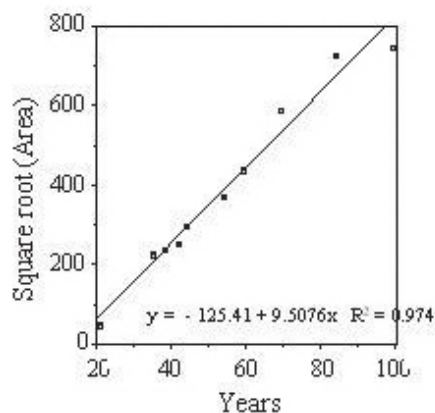
## Results

The linear relationship between the square root of the area and time indicates, for the most part, a constant velocity in the spread of the insect (Figure 1).

To calculate the velocity with which the beech scale insect spreads over space, the diffusion coefficient and intrinsic rate of increase were used. Substituting my estimate for  $r$  (2.47)(Table 1) and  $D$  (0.571 to 1.97 km<sup>2</sup>/year )(Figure 2) into the equation for velocity of the spread of the organism, the velocity of the insect was calculated to be between 2.38 to 4.41 km/year.

## Conclusions

There was not a significant difference in fecundity among insects located on high infested and low infested trees. Results indicate that geographic dispersal does fit a diffusion model, however estimated velocity was less than



**Figure 1.—Square root of the area occupied by the beech scale insect (*Cryptococcus fagisuga*) in years following 1890 introduction. The straight line is the least-squares fit.**

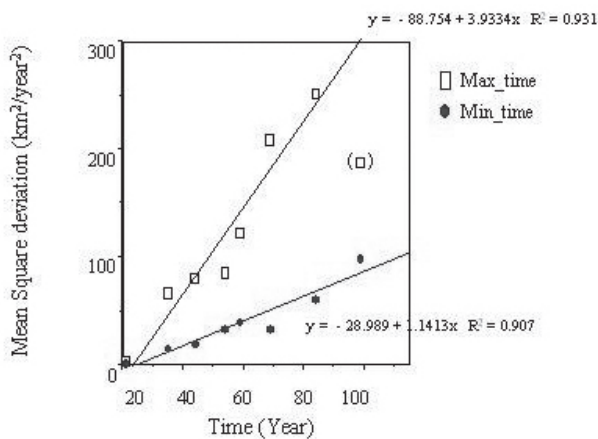


Figure 2.—Mean squared deviation of the maximum dispersal distance of the beech scale insect in North America vs. the time since release. The straight line is a least-squares fit, with the exclusion of the data point in brackets.

expected. These reduced velocity estimates could be from potential differences in insect growth rates between the advancing front and the aftermath zone. They could also result from the convergence of insect populations from multiple introduction points or, most likely, from the influence of human vectors.

### Acknowledgments

This study would not have been possible without the assistance of Dr. Tom Caraco and Dr. George Robinson and the financial support of the Edmond Niles Huyck Preserve.

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## THE BIOGEOGRAPHY OF BEECH BARK INVASION OF N. AMERICA

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Beech bark disease was accidentally introduced to Nova Scotia from Europe around 1900 and has since spread southwestward into New England, New York, Pennsylvania, and West Virginia. Spatial analysis of historical records of the disease spread in N. America indicates that it has maintained an average radial rate of spread of  $19.3 \text{ km/year} \pm 0.82 \text{ km/year}$ . This slow rate of spread is presumably due to the limited dispersal capabilities of beech scale insects. The geographical distribution of American beech was mapped via krigging of ca. 20,000 forest inventory plots. The greatest concentration of beech is in the Adirondack Mountain region of New York though smaller concentrations existed in Maine, New Hampshire, Vermont, West Virginia, and northern Pennsylvania. Beech also exists at very low levels over a large range extending through most forested regions of the eastern U.S.A. There is no evidence that beech bark disease spreads faster in portions of N. America with higher concentrations of host trees. Comparison of forest inventory data with historical records of beech bark disease expansion indicates that the proportion of beech basal area that is dead or dying is greatest in newly infested stands; after the disease has been present in a stand for many years, beech mortality rates tend to diminish slightly.

## Knowledge Gaps and Research Priorities

### *Knowledge Gaps*

The challenge of modeling is to develop model systems that include critical components, yet are not over complex. These models must be parameterized and a great deal of information is not yet available. A lack of information on the statistical nature of relationships or transition probabilities between model components will lead to many assumptions. Modeling efforts may be most useful in this context when they can be used to generate hypotheses that can be tested in the field using either intensive field studies or broad geographic data sets depending on the types of questions asked and hypotheses generated. In this way models can be linked to research designs and the empirical data collected can feed back into the model in an iterative way.

### *Research Priorities*

- Determine research questions that will benefit from and also provide data to parameterize explicit models.
- Determine management questions that will benefit from explicit models.
- Identify types of models that generate useful information for managers or hypotheses that can be tested to improve our knowledge, some examples follow:
  - o Long-term Stand Dynamics Tests
    - \* For Alternate Stable States with respect to size structure and abundance of beech.
    - \* How stand attributes may influence disease dynamics over time.
  - o Human dimensions models that include perception, value of beech, economic constraints, land use history and current management.
  - o Landscape-scale dynamic models including potential effects of habitat fragmentation and regeneration history (seed versus clonal).
  - o Scale insect population dynamics, host and site influences, scale-fungus interactions.
  - o Range expansion and adaptation of BBD tests for long range and large scale dispersal patterns.
    - \* The significance of satellite populations, long range vectors.
    - \* Landscape factors that accelerate or reduce spread.
    - \* Genetic factors that accelerate or reduce spread.
    - \* Management opportunities to limit spread.
    - \* Effects of forest fragmentation on BBD dispersal.
    - \* Modeling potential evolutionary changes in specific (host-parasite, parasite-parasite) interactions as range expands.
  - o Modeling Management Strategies For BBD Tests For the Potential to Manage Stand Health.
    - \* Quantifying outcomes of beech density management.
    - \* Designing means of enhancing resistance in populations.
    - \* Quantifying outcome of various sanitation strategies at large and small scales.

## **Section 6:**

### **Silviculture and Management to Address BBD**

## MANAGING BEECH BARK DISEASE IN MICHIGAN

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### Abstract

The year 2000 discovery of beech bark disease in Michigan's Upper and Lower Peninsulas marked the beginning of a major shift in the ecology of its northern hardwood forests. Michigan has 7 million acres of beech containing forests. About one-half of these forests have  $\geq 20\%$  beech basal area. Estimates place initial killing front losses at 7.5 million pole size and larger beech, or 22.7 million cubic meters of sawtimber. Management strategies are influenced by the basal area and size of beech trees, and distance from BBD advancing fronts. Keeping a minor beech component ( $<1 \text{ m}^2$  basal area) minimally affects stand vulnerability and productivity, and offers an extended period of mast production. All heavily scale infested trees are considered a high risk of beech snap and are removed if they pose a threat to human safety in parks and campgrounds. Information from evaluation monitoring plots established throughout the state will quantify and help predict short and long-term impacts of beech bark disease on forest composition, productivity, and wildlife values. Scale and BBD spread rates are also being evaluated. Newly detected, isolated scale infestations far in advance of the advancing front are being removed to evaluate potential impacts on spread rates. Not moving infested beech logs or firewood to or through uninfested beech areas from August to snowfall when crawlers are active is being promoted. Michigan is cooperating with national and state efforts to discover and define resistance to BBD, and to hopefully produce a source of resistant seedlings.

### Introduction

The year 2000 discovery of beech bark disease (BBD) in Michigan's Upper and Lower Peninsulas marked the beginning of a major shift in the ecology of its northern hardwood forests. The forest management guidelines presented in this paper will hopefully assist forest resource professionals and recreation managers as we react to and prepare for this unfortunate and difficult ecological transition. As with all guidelines, this is a work-in-progress. We have much to learn as this new

exotic pest begins altering our beech resource in its many habitats and forest associations.

### The Beech Resource

American beech (*Fagus grandifolia*) is the only native species of this genus in North America. It is a slow-growing, common, deciduous tree that attains ages of 300 to 400 years. 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 glacial period. Michigan is at the extreme northern and western edge of American beech range.

The American beech is easily recognized even in dense, complex forests by its thin, smooth, light gray bark. Unlike most other hardwood trees, it retains this smooth bark throughout its mature years. The smooth bark of the American beech presents a tempting surface for the carving of initials and names. Carvings into the beech bark persist for the life of the tree, as do bear claw marks produced as black bears forage for nuts in the fall.

Beech is an important nut producer in the northern hardwood type. The distinctive triangular nuts are eaten by people and are an important food for wildlife. Beech mast is palatable to a large variety of birds and mammals, including mice, squirrels, chipmunks, black bear, deer, foxes, ruffed grouse, ducks, and blue jays.

Beech wood is excellent for turning and steam bending. It wears well, is easily treated with preservatives, and is used for flooring, furniture, turned products and novelties, veneer, plywood, railroad ties, baskets, pulp, charcoal, and rough lumber. It is especially favored for fuelwood because of its high density and good burning qualities.

The 1993 USDA Forest Service Survey reports that Michigan has 7.16 million acres of Maple-Beech-Birch type containing 1.67 billion board feet of beech, or 138 million trees in all size classes. This includes 15 million beech trees greater than 9 inches in diameter at breast height (dbh), and 0.9 million greater than 21 inches dbh.

### Hazard Tree Management

Michigan's state parks and state forest campgrounds were the first areas impacted by the beech bark disease. The

disease was first detected at Ludington State Park on the west shore of Michigan's Lower Peninsula, and at Bass Lake State Forest Campground just south of the southern Lake Superior shoreline in the Upper Peninsula. Both areas have abundant large, old beech trees. BBD infected beech began to structurally fail in these areas when stressed by high winds.

Many trees that are partially girdled by *Nectria* and often further weakened by ambrosia beetle galleries are broken by high winds. This breakage is called "beech snap." This creates a hazard situation to people and personal property where beech trees occur in campgrounds, other recreation areas or near homes. Hazard rating guidelines were developed recognizing this new threat to people and property. We currently recommend that heavily infested beech be removed if structural failure could cause personal or property damage. This does not presuppose visible signs of tree decline. If tree decline is associated with heavy scale infestation, the tree is removed immediately, or the area is closed until tree removal. This is a conservative, proactive approach. Heavily scale infested trees will eventually die or fail. This guideline reduces chances of missing hazard trees which quickly succumb to scale and BBD; helps ensure a safe environment for visitors, staff and property; and forces us to sooner face imminent tree loss and forest restoration issues.

## Loss and Impact Estimates

The first wave of BBD in northern Pennsylvania forests killed roughly 50% of the beech trees larger than 25 centimeters in diameter at breast height (dbh). Another 25% of the trees lived, but were infected by *Nectria* (McCullough, et al., 2002). These live infected trees were weak, grew slowly and had patches of dead tissue. The remaining 25% of the trees either escaped scale infestation or *Nectria* infection, or were at least somewhat resistant.

It is estimated that once the Killing Front spreads throughout Michigan, we will have lost 7.5 million beech pole size and larger beech. This represents 800 million board feet of sawtimber.

## Review of Factors Influencing Disease Development and Damage

The age, density (e.g. basal area) and size of beech trees, and stand tree species composition affect BBD

establishment rates and stand vulnerability. Older forests with a high component of large beech are most vulnerable. Management options should take into account the beech tree's thin bark which renders it highly vulnerable to injury by fire (large shallow roots are especially vulnerable), sunscald, logging, pruning, and disease.

If beech is a minor component of the overstory, mortality of beech trees may simply function as a selective thinning with little loss of timber value. Mortality of scattered large beech may actually increase the habitat available for birds, mammals and other wildlife. Beech is the only nut producer in the northern hardwood type. Thus, keeping a minor beech component offers an extended period of mast production and eventual habitat for cavity nesters and dens.

Growth of other tree species associated with beech will be enhanced as BBD removes beech from competition. Analysis of DNR Forest Health Monitoring plot data indicates that BBD spread rates are lower in stands with lower beech basal areas. Thus, the loss of beech basal area may be more gradual, and have less impact on stand stocking levels where there are fewer, more scattered beech.

## Management Strategies

Management strategies are influenced by the amount of American beech in a stand and the distance from the BBD Advancing Front. Distance is used to estimate the amount of time before BBD impacts a stand. Estimates from northeastern forests suggest that the advancing front spreads at a rate of 6 miles per year. In addition, once scale reaches a new area, it often takes several years of scale infestation before *Nectria* is abundant. This is particularly true when a new scale infestation is a long distance from the Killing Front.

Management guidelines are presented for scale infested and uninfested beech stands. Guidelines for uninfested stands are suggested for areas projected to have more than five years before BBD related tree decline and mortality. The scale may arrive within this window, but again, it takes a few years before *Nectria* begins impacting tree growth and survival. Guidelines for uninfested beech are applied to stands greater than 40 kilometers from the Advancing Front. This figure may be modified as our understanding of rates of scale and *Nectria* movement are

enhanced via monitoring plots and yearly surveys. A current year map of the BBD advancing and killing fronts is published on the MDNR Forest Health Website at <http://www.mcgi.state.mi.us/foresthealth/>.

### **Uninfested Stands > 40 kilometers from the Advancing Front of Beech Bark Disease**

Management plans for beech containing stands anywhere in Michigan should now consider BBD vulnerability. Stands dominated by beech ( $\geq 20\%$  basal area) are highly vulnerable to damage. This is especially true if large trees ( $>25$  cm dbh) are abundant.

American beech is not always evenly distributed in stands which have a minor American beech component. Hardwood stands often have inclusions of almost pure beech groves. In these cases, percent basal area may not accurately reflect overall stand vulnerability or susceptibility.

In general, these guidelines reduce the basal area of large diameter beech and increase tree species diversity in stands with a significant beech component. This reduces within stand rates of spread of the beech scale; reduces negative impacts on stand stocking levels; and provides more management options via non-host species abundance.

### **Management Guidelines**

- 1) Consider reducing the amount of overstory beech present in the stand. For purposes of BBD management it is not necessary or desirable to eliminate beech from a stand. However, increasing tree species diversity provides more management options and may reduce rates of beech scale spread.
  - a. Discriminate against large, over mature trees with rough bark and signs of decay. These trees will be the first lost and will offer the fewest advantages in terms of prolonged mast production or survivability. Reduce stand to 70 -100 sq. ft. of basal area. There is time before BBD impacts beech growth and survival for stands to add basal area in expected increments relative to site quality and stand vigor.
  - b. Consider short-term and long-term impacts on wildlife food availability and habitat. Leaving scattered snag or den tree beech to enhance

wildlife habitat does not significantly increase the risk of tree loss. Oak or other mast producing tree species should be considered to replace beech where beech density is high.

#### 2) Retain vigorous trees with smooth bark.

Identification of potentially resistant trees is important for decreasing the long-term susceptibility and vulnerability of the beech resource to BBD. Vigorous trees with smooth bark are most often found to be resistant to beech scale establishment.

#### 3) Use harvest systems that minimize injuries to beech root systems.

Root injury is the primary cause of root sprouts in beech. Spring root injuries maximize sprouting response.

#### 4) Survey stands regularly to detect the arrival of beech scale.

Knowing when scale enters a stand will establish a rough timetable for future expected beech snap and tree mortality. Beech snap creates hazard, and can be responsible for large volume losses before salvage harvests are scheduled. Trees susceptible to snap do not always show signs of decline.

#### 5) Favor regeneration of other tree species via selection or planting in canopy gaps.

Some of the principal associates of beech are sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), American basswood (*Tilia americana*), black cherry (*Prunus serotina*), eastern white pine (*Pinus strobus*), and several hickories (*Carya* spp.) and oaks (*Quercus* spp.). On poorer, lighter soils conifer components (*Tsuga*, *Picea*, *Pinus*) are more common.

Beech is relatively shade tolerant and is often out-competed by other species in large canopy gaps where the ground is exposed to sunlight during much of the day. Birch, black cherry, red maple or other shade intolerant species will grow faster and overtop beech reproduction. However, beech is avoided by browsing deer which may decrease successful regeneration of more favored species in areas with high deer numbers.

The Michigan Department of Natural Resources currently recommends 30-foot average canopy gaps, and 60-ft. gaps to encourage intolerant tree species. Using 100-ft. gaps for group selection when intolerants are present (cherry, yellow birch, oak, ash) is also an option

to increase diversity. Regeneration success relies on placing gaps in areas of good advanced regeneration and seed source. Without this, gaps may become raspberry patches. With canopy gaps as big as 100 ft. it is very difficult to get an “accurate” BA reading, thus group selection may be the best choice.

### **Uninfested Beech Stands < 40 Kilometers from the Advancing Front**

Management guidelines in this section address the influence of beech abundance within the following context:

- 1) Beech Stands without Scale
- 2) Beech Stands within the Advancing Front (e.g. with scale insects)
- 3) Beech Stands within the Killing Front (e.g. with decline, beech snap and/or tree mortality)

#### **Beech Stands without Scale**

Within 40 kilometers of the BBD Advancing Front, there is a risk of losing beech basal area during the current harvest cycle. This translates into less or no opportunity to improve tree species diversity prior to significant BBD impacts. Translated to forest management terms, there is a significant risk of BBD impacts reducing stand basal area to below minimum stocking levels. This is especially true in patches or stands with high densities of beech.

The only guidance for selecting residual beech to retain is to favor smooth barked, healthy, vigorous trees. Keep in mind that 50% of trees with a  $\geq 25$  cm dbh will be lost in the first few years as these stands enter the Killing Front. Many of the first trees to succumb will be less healthy and rough barked.

#### **Beech Stands within the Advancing Front (with Scale Insects)**

- 1) Identify, mark and retain resistant trees. In stands that are infested with beech scale, look for trees with few or no beech scales, especially when these trees are growing near heavily infested trees. These trees should be clearly marked, protected and reported to the Michigan DNR Forest Health Program for inclusion into tree resistance research. (Note: We train resource professionals to recognize resistant trees and provide a Cooperative BBD Resistance Tree

Survey Form which details tree marking and reporting details.)

Resistant trees may be found in groups due to root sprouting habits of beech. Identify and protect all trees in such groups. Sprouts and possible seed source from these trees offers an opportunity to regenerate a BBD resistant resource.

- 2) Identify trees for salvage. Discriminate against trees that are heavily infested with beech scale. Select large, over mature trees with rough bark, trees with evidence of decay, broken tops or other injuries first.
- 3) Maintain some beech basal area. Retain some large beech for wildlife habitat. This will not significantly affect the spread or impact of BBD. These trees will die first and most quickly, so should not be used in calculating minimum stand basal area.  
Generally, increasing species diversity and shifting the beech component towards smaller, more resistant size classes will reduce the impact of BBD. This will help prolong the beech resource's ability to produce mast. In stands where oak, hickory or hazel are abundant, beech mast may be less important.
- 4) Favor regeneration of other tree species via selection or planting. Consider trees suited to the habitat type with special consideration for mast producing species.
- 5) Do not transport scale infested beech firewood or logs to or through beech areas outside the Advancing Front between August and late Fall. The mobile life stage of the beech scale known as crawlers are mobile in the fall. They are readily dispersed by birds and strong winds. Moving recently harvested wood from infested areas risks spreading beech scale to new areas at greater than expected rates.

#### **Beech Stands within the Killing Front (with decline, beech snap or tree mortality)**

Once beech begins declining, snapping and/or dying, BBD impacts progress at a rapid pace. Resistant trees will be more apparent. Once a large portion of the mature beech resource has been lost, beech stands enter the final stage of BBD impact known as the Aftermath Forest.

Management choices will depend on site productivity, habitat type, residual stocking levels and residual tree species. Heavily impacted stands may require artificial regeneration to restore acceptable stocking levels and/or acceptable tree species.

### Statewide Education and Outreach

A high quality Michigan BBD Bulletin was created to inform and educate forest resource professionals and the general public (See McCullough et al., 2002). Many forest health training sessions have featured BBD biology, detection, evaluation, protection of putatively resistant trees and management guidelines. This has the added advantage of increasing the likelihood of detecting new BBD infestations as they appear in new areas, ahead of the advancing front. This is important when applying management guidelines which are dependant on years of BBD free growth. The statewide network of evaluation monitoring plots is, of course, the primary source of such information.

Fortunately, we have federal cost share programs to assist landowner reforestation efforts. Approximately 2,000 acres in the Upper Peninsula killing front were salvaged in 2004. Many of these hardwood acres were on lower quality hardwood sites. These poorer sites were replanted with oak, hemlock, red pine, white pine and hemlock with assistance for our Wildlife Divisions Landowner Incentive Program.

### Conclusion

Management tactics will likely change as we gain new understandings of scale spread rates, BBD disease progression in different forest associations, and BBD forest resource impacts provided by yearly detection surveys and Michigan's extensive network of evaluation monitoring plots. We will continue to support efforts to produce resistant planting stock. We will work ahead of the BBD advancing front to increase the tree species diversity of forest resources dominated by American beech. Hazard tree training for park and campground managers has gone from an occasional session to several sessions per year. Much of our beech resource is unaffected by BBD, so many Michigan residents have yet to experience or understand the implications of having BBD in the neighborhood. The loss of these majestic, old trees baring the initials of their predecessors and the claw marks of grateful bears... of this unique, unparalleled,

park-like old growth forest is in Michigan's not too distant future.

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# MANAGEMENT OF BEECH BARK DISEASE IN AFTERMATH FORESTS

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## Abstract

From two lines of investigation, it is apparent that on sites typical of the north-central and eastern regions in Maine, where beech bark disease has been present for over seventy years, achievement of a balanced species composition will be difficult to realize. The first line of inquiry was followed using an historical approach. Stands subjected to varying harvesting intensities were evaluated 20 to 30 years after the harvesting. Documentation of changes in beech composition and growth was recorded. The second study comes from a direct application of treatments, with species changes documented as time progressed. Initially a USDA Forest Service study, this project was evaluated again after a period of ten years. In both studies, beech continues to be a dominant and sometimes aggressive occupier of sites, regardless of harvesting treatment. While some data show that beech presence can be statistically different initially, depending on harvesting treatment, significant biological gains in maintaining or improving a balanced species composition will likely take several cutting cycles, if not rotations. The clear implication is that, in order to efficiently recover the productivity potential of these sites in a timely manner, additional silvicultural techniques need to be applied to the standard harvesting regimens currently practiced.

## Introduction

The beech bark disease, a disease complex resulting from the interaction of an insect, *Cryptococcus fagisuga* Lind., and one of several fungal pathogens of the genus *Neonectria*, has been occurring on American beech (*Fagus grandifolia* Ehrh.) in North American forests for approximately 100 years. Three stages of disease progression have been characterized by Shigo (1972). The first stage is described as an advance front, where the presence of only the beech scale insect occurs. Following the development of high populations of scale, and usually after a period of approximately ten years or more, a killing front stage occurs. In the killing front, *Neonectria* fungi invade bark tissues predisposed to infection by the feeding activities of the beech scale. Widespread beech

mortality then often occurs. Forest areas that have experienced the killing front stage, and have continued to develop for a long time period in the presence of both the scale insect and the pathogenic *Neonectria* fungi, are often referred to as aftermath forests. Aftermath forests are structured differently than pre-disease forests (Houston 1975). Most large, susceptible beech have been killed by the disease, leaving canopy gaps of various sizes, depending on the distribution of the beech in the original stand. Root systems of beech stems killed by the disease can sprout into dense thickets, thereby perpetuating the susceptible genotypes. Usually, scale populations are much lower than populations that occur in advance and killing front zones. As a result, beech stems that are small and highly defective characterize aftermath forests. These stems have numerous localized cankers of the beech bark disease. Usually these lesions are deep, since cankers were initiated when stems were small, and persist throughout the life of the trees, which typically survive for decades. Often, the percentage of beech in disease-affected stands increases as a result of the root sprouting capacity of the species (Houston 1975). This shift in species composition tends to leave stands in aftermath areas less biologically diverse, with stems of much lower value occupying considerable stand growing space. The end result is that stands affected by beech bark disease eventually support a decrease in overall stand productivity and value, placing a considerable cost on forest management to modify or correct the problem.

In Maine, the disease has been known to occur for over 70 years, with the killing front occurring throughout much of the region during the 1940's and 1950's. Early attempts to manage the disease were largely restricted to sanitation or salvage cutting of beech in disease-affected stands. Forests in northern and eastern Maine regions have experienced the most severe damage from the disease (Laustsen *et al.* 2003). This is based on current field observations of the degree of stem cankering on existing beech, beech mortality, and the relative proportion of beech in the stands.

The proportion of beech in many hardwood stands has increased over the past several decades. Manipulation of species composition is often a desirable goal of stand harvesting activities. Finding suitable harvesting protocols that allow foresters to control beech regeneration and beech thicket development could greatly reduce the effect of beech bark disease in future

stands. This report summarizes information from two specific studies on effects of harvesting intensity and harvesting season on silvicultural success in improving species composition in hardwood stands. The use of some intermediate silvicultural practices on controlling stem abundance of susceptible beech is also included. The findings are most applicable to sites and stands considered typical the north-central and eastern regions of Maine, but the management dilemma may be typical to other areas where aftermath forests have developed.

## Methods

Overstory density effects on growth of American beech were studied in the eastern region of Maine by Patton (1997). In this study, twenty sites were chosen from continuous forest inventory (CFI) plots that had been established in the 1950s, and measured every five years. The twenty sites were grouped into four treatments each representing one of the following harvest level intensities: light partial harvest, heavy partial harvest, clearcut, and an uncut control. Harvest intensity was described by residual overstory basal area per acre (BA/A) immediately following the harvest from data supplied by the CFI records. Light harvests had greater than 60 ft<sup>2</sup> BA/A, heavy harvests had between 21 – 59 ft<sup>2</sup> BA/A, clearcuts were commercial clearcuts, where some unmerchantable trees were left, but where residual basal area was less than 5 ft<sup>2</sup> /A. Drainage class was determined for each site based on soil depth to mottling, as described by Briggs (1994). Three plots per site were used to assess current overstory density using a 10-factor cruising prism, and an additional three 0.01 acre circular plots were used to characterize the understory at each site. The circular plots were centered on the prism plot centers. Species, diameter at breast height (dbh), crown class, and total height were recorded for all understory trees and overstory trees.

The second study was established by the USDA Forest Service in 1991 in a beech stand in north-central Maine. Details of this study have been described by Houston (2001). The study area is dominated by American beech, but also includes some sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), striped maple (*Acer pensylvanicum* L.), and white ash (*Fraxinus americana* L.). While initial total basal area varied between plots, beech represented between 70 to 85 percent of the basal area. The study consists of 15 ten-acre forest blocks to which

various harvest treatments were applied. Three blocks received a winter partial harvest, three received a summer partial harvest, three were clearcut in winter, three were clearcut in summer, and three were left as uncut controls. Overstory and understory data were also collected by standard sampling methods, as described (Houston 2001).

In 2002, ten growing seasons after the initial harvest treatments were conducted, the original overstory and understory plots were located and again measured for forest stand and tree characteristics by Farrar (2003). Data on overstory composition and structure were obtained using point samples centered on five points in a diagonal transect set across each 15-acre plot. Data on understory regeneration were obtained from nested 1-m and 2-m (39 and 78 in. diameter) plots centered on the middle three sample points of each transect.

## Results and Discussion

Harvesting methods that could reduce or discourage beech regeneration from developing in managed hardwood stands would allow increased productivity and improved overall health of aftermath forests. Using a historical approach at the eastern Maine sites, Patton (1997) found that harvest intensity had little effect on beech establishment and subsequent species composition percentage from twenty to thirty years after the harvest. The following percentage of beech, averaged across five sites in each of the four harvest intensities examined, showed the following: uncut stands, 26 percent; light partially harvested stands, 21 percent; heavy partially harvested stands, 29 percent; and in clearcuts, 22 percent. Although there was some variation from site to site within treatments, no clear trend can be drawn for making a case that harvesting intensity alone has a significant management effect on subsequent beech regeneration and development. Although most eastern Maine sites examined were moderately-well to well drained, drainage class was variable on sites within treatments, so no trends could be surmised. However, general soil and site conditions may have a significant influence on the aggressiveness of beech regeneration. One hypothesis is that the more fertile, moist but well-drained sites can more readily support higher value hardwoods, such as yellow birch, sugar maple, and white ash. Site relationships in aftermath forests, and in other regions of the range of beech as well, could provide useful insights in predicting the likelihood of significant composition changes following beech bark disease.

In the experimental approach used by Houston (2001) at the north-central Maine site, a similar finding regarding harvesting effects was reported. Four years after study initiation, differences in beech regeneration of seedlings and root sprouts between the harvest treatments had disappeared. In general, beech regeneration developed more abundantly in the summer clearcut harvest, but had lower survival rates than those that developed after the winter clearcut harvest. Thus, total numbers appeared to equalize. Farrar (2003) found that ten years after harvest, beech understory survival in winter clearcut blocks was 41 percent, and in winter partial cut blocks was 48 percent, a difference that was not statistically significant. However, beech survival in the summer clearcut blocks was 27 percent, compared with survival of 36 percent in the summer partial cut blocks. Thus the trend of higher mortality occurring in summer clearcut blocks appeared to continue throughout the ten-year period. Unfortunately, while these values were statistically different, survival of 27 percent of beech stems still provides a more than adequate supply of regeneration to dominate as the principal stand component over time. Clearcutting does provide, however, the opportunity for faster growing shade intolerant species to develop, such as paper and yellow birch (Patton 1997). While beech may be a significant component of these stands, the shade intolerant stems can out-compete the beech in height growth, and will improve stand species composition to some degree.

If clearcutting can marginally influence species composition by reducing beech regeneration, other silvicultural precautions need to be considered. In particular, Farrar and Ostrofsky (*manuscript accepted and in revision*) have described some unintended consequences of leaving beech resistant to the beech scale in stands that were subsequently clearcut. Leaving beech resistant to the beech scale is recommended to preserve a relatively reliable source of mast for wildlife interests, as well as to preserve the resistant genotypes in the landscape. Resistant American beech of high vigor left in clearcuts without the protection of surrounding trees were highly susceptible to decline and death from exposure. The results of this study have shown that in clearcut blocks, resistant trees that were left standing suffered mortality ranging from 67% - 78% by the end of the ten-year period. There was no mortality of resistant trees left standing in any of the partially cut blocks or in the no-cut control blocks. Management

guidelines to characterize minimum buffer requirements for leaving resistant trees in clearcuts, and even in heavy partial cuts, would be an important addition to management of hardwood stands in aftermath forests.

Based on these studies, and from other field observations of the aggressive nature of beech regeneration following a wide range of harvesting alternatives, it is clear that the use of harvesting protocols alone will not realistically improve the long-term composition of the aftermath forests in Maine. As further indication, Bohn and Nyland (2003) have reported that the likelihood is low of changing understory composition in stands with high proportions of beech, a characteristic of aftermath forests, following partial cutting in uneven-age stands in New York. Filip (1978) reported little change in overstory representation of beech following several cutting cycles of a selection system applied in New Hampshire, as well.

Additional, intermediate silvicultural methods are likely to be more efficient and cost-effective in the long run. Timber stand improvement work using herbicides or mechanical methods have been shown to be effective vegetation management alternatives (Horsley and Bjorkbom 1983, Kochenderfer *et al.* 2001, Ostrofsky and McCormack 1986, Ostrofsky and Houston 1988). While initial costs will be higher than when managing stand composition strictly with harvesting methods, the benefit of reclaiming lost site productivity within a single rotation may far outweigh the costs.

Stand conversion practices, heavy cutting prescriptions, and the use of herbicides can help shift stand composition away from defective beech towards more favorable species (Mielke *et al.* 1986). However, such practices are not acceptable alternatives in all stand situations, or for all ownerships. Individual stem treatment methods offer good potential for improving beech-dominated stands that have not yet been severely degraded in composition. This approach may also prove useful in stands where relatively high numbers of resistant beech occur. The selective removal of only the most susceptible and most debilitated stems requires a method that can be applied on a stem-by-stem basis. Direct mechanical stem girdling has been shown to be an effective way to kill small (up to 5 in. diameter) beech stems (Nyland 2004). Mechanical girdling may be most efficient when used on beech stems that have not had

extensive localized cankering of the bark. In aftermath areas of Maine, most beech stems, including small saplings one inch in diameter or less, often support extensive, deep cankering. Stems with deep cankers may require more effort to girdle mechanically, requiring a deeper cut, or effectiveness may be reduced.

Stem girdling with the use of heat is another alternative. Heat applied to the bark of undesirable stems will kill cambial tissues, resulting in girdling and tree death. This method has been tested in eastern Maine. One hundred beech stems in each of two diameter classes (0.5 in – 2.5 in.; 2.6 in. – 4.5 in.), and 75 beech stems 4.6-6.5 in. diameter at each of two sites were girdled in mid-March using a propane burner. The burner consists of a commercially available propane torch, with a backpack-mounted tank. Stems were girdled at about three feet from the ground. Observations have shown that treated trees die over an extended period of time. Virtually all treated trees produced leaves during the spring of treatment, and most re-foliated again the following spring, as well. When a sample of girdled stems was inspected by removal of bark, all trees were effectively girdled. Most showed evidence of stem swelling above the girdle, and epicormic sprouting immediately below the girdle. There was no observed root sprouting resulting from the treatment for up to three years following the treatment, the duration of the study.

Control was most effective in the smaller stem size classes. One explanation for the lack of root sprouting observed was that because the trees re-foliated, energy reserves stored in the roots were slowly depleted. These reserves could not be replaced due to the interruption of phloem at the girdle. In addition, the occurrence of a “slow kill” may be beneficial in small woodlot ownerships, or where aesthetically sensitive sites need treatment. The technique does offer an alternative to the use of herbicides, which some landowners find unacceptable. Drawbacks of the method include the labor-intensive application of the treatment, especially in large areas, or where sprout stems of beech are too numerous. Further testing seems warranted.

## Acknowledgments

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re-measurement and further research. Maine Bureau of Parks and Lands, and the Georgia-Pacific Corp. are gratefully acknowledged for allowing access to the study sites, for willingly sharing CFI data, and for offering other field assistance.

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# THE EFFECTS OF LAND-USE HISTORY ON BEECH BARK DISEASE SEVERITY

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## Abstract

While an increase in American beech (*Fagus grandifolia* Ehrh.) sapling density has been noted throughout the northeast, few studies have examined the causes of the increase. To examine the role of beech bark disease in the increase of beech sapling density, I assessed adult beech trees for beech bark disease damage, and measured beech sapling density surrounding the adult. I also investigated the effects of land-use history on beech bark disease severity and beech sapling density. Adult beech trees with more severe damage from beech bark disease had more saplings around them. Former sugarbushes had less damage from beech bark disease and lower densities of beech saplings than areas that were formerly logged, and beech was mostly absent from former agricultural sites.

## Introduction

Since the introduction of beech bark disease, American beech (*Fagus grandifolia* Ehrh.) has declined in overstory abundance but increased in dominance in the understory of many affected stands in the northeastern United States and southeastern Canada (Twery and Patterson 1984, Houston 1994). The formation of dense understory thickets of beech is in part due to physiology of the species, and in part due to the aftereffects of beech bark disease. The ability of beech to sprout from root suckers can lead to areas of very high density in the understory. Generally the suckers are thought to form after the parent tree incurs an injury on a shallow root due to freeze-thaw cycles or logging practices (Jones and Raynal 1986, Jones *et al.* 1989). The prolific sprouting can also follow in the aftermath of beech bark disease, as canopy trees are decaying and dying (Houston 1975, Fahey 1999). Beech physiology in the form of shade tolerance also contributes to the formation of dense thickets, as beech is extremely shade tolerant and can survive for decades in deep shade (Canham 1988). Beech sapling density is an important component of forested areas, particularly because increased competition from beech root suckers can suppress the survival of other desirable species in some forests (Hane 2003).

Few studies have been done to determine the factors that contribute to both the severity of the disease and the subsequent formation of these understory thickets, though management of the thickets has been examined (Bohn and Nyland 2002). Beech density has been shown to impact the disease severity at the landscape level, but not on the level of the individual stand (Griffin *et al.* 2003). Due to the wide variation in stand site conditions, controlling for factors such as aspect, slope, elevation, and soil can be difficult and each of these factors may contribute to disease impact. Additionally, human land-use impacts on the stand may also be highly variable. To date, no studies have been done to investigate the effect of past land-use on the severity and impact of beech bark disease. The main interaction of land-use and beech bark disease is likely to be through the impacts of variable land-use on beech density and subsequent variation in infestation of beech bark disease. In forests with land-use histories that result in compositions with limited representation of beech, the effects of beech bark disease are likely to be limited.

## Questions:

- 1) Do more heavily damaged trees have more vegetatively reproduced saplings?
- 2) Does land-use history have an effect on the severity of beech bark disease and the density of the resulting beech suckers?

## Methods

### Site descriptions:

Both formerly logged areas and former sugar bushes were utilized for this study. Sugar bushes are areas that have been selectively cleared to encourage growth and regeneration of sugar maple for tapping for maple sugar production. While the boom for the sugaring industry in New England was between 1790 and 1840, many farms in northern New England had sugar bushes as part of their income into the late 1800's (Hamburg 1984, Waldbauer 1999). The land-use impacts are very much like those of selective cutting, with the caveat that sugar maple was selected for rather than removed, and regeneration of the species was encouraged. Thus, in areas that were once used for sugar bushes, today we see a greater proportion of sugar maple, and much lower densities of beech.

Seven sites across the southwestern White Mountain National Preserve (NH) were selected. I chose sites based

**Table 1.—Sites used in this study, along with their land-use history, age and location**

Site	Land-use	Age	Location	Coordinates
Hubbard Brook Exp. Forest	Logged	80	West Thornton	43° 56' N, 71° 45' W
Hubbard Brook Trail	Logged	100	Warren	43° 57' N, 71° 49' W
Shadow Lake	Logged	85	Lincoln	44° 52' N, 71° 41' W
Bald Mtn	Sugarbush	70	Campton	43° 51' N, 71° 41' W
Chickenboro Brook	Sugarbush	100	Campton	43° 52' N, 71° 35' W
Goose Hollow	Sugarbush	80	Thornton	43° 53' N, 71° 35' W
Bowl Research Natural Area	None	mature	Sandwich	43° 56' N, 71° 23' W

**Table 2.—Results from the mixed-model ANOVA, which examine the effects of Beech Bark Disease Damage severity and Land-use History on beech sapling density**

Effects Test	P-value
Beech Bark Disease Damage Score	<0.001
Land-use History	0.047
BBD x Land-use history	0.113

on uniformity for age, elevation, soil, slope and aspect. All sites were last cut > 70 years before the study, and the Bowl Research Natural Area was never cut.

### Inventory:

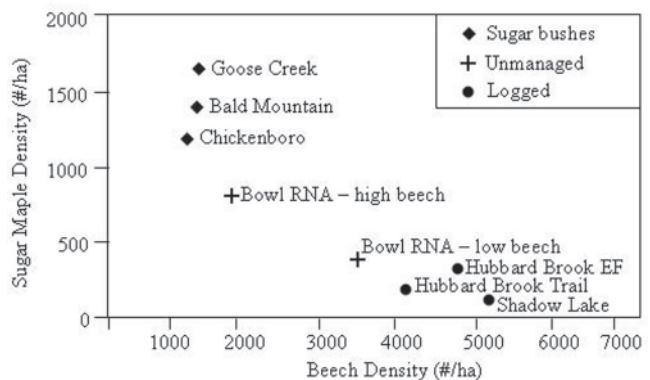
At each site, an inventory of trees, saplings and seedlings was done. At each site, a total of sixteen 25 m x 25 m plots for trees (> 10 cm dbh) were inventoried. Within each of these plots, two 2 m x 25 m transects were done for saplings (< 10 cm dbh, > 2 cm dbh). Within each plot, we also examined seedling populations in five 1 m x 1 m subplots. Seedlings were identified as either germinants (with cotyledons still attached) or > 1yr old seedlings. In the Bowl Research Natural Area, we surveyed two distinct areas, one with sugar maple as the dominant in the overstory and one that was dominated by beech. These two areas are designated as “low beech” and “high beech” in the results.

At each site, 20 isolated beech trees (> 20 m from nearest conspecific) were identified and assessed for damage from beech bark disease using a 0-3 scale (Houston and O'Brien 1983). I also counted and identified the seedlings and saplings within a 5.6 m radius of each adult beech tree.

## Results

I found that beech sapling density was predicted by the severity of beech bark disease ( $p < 0.001$ ; Table 2). Trees with the highest degree of damage had the highest densities of saplings around them (2300/ha), while undamaged trees had much lower densities (800/ha).

Additionally, land-use history had an effect on beech sapling density ( $p = 0.047$ ; Table 2). Trees in areas that were formerly managed as sugarbushes have fewer beech saplings than logged areas (Figure 1). Furthermore, beech in sites that were formerly sugarbushes had less severe damage from beech bark disease than sites that had been previously logged ( $p = 0.03$ , Figure 2). There was also a negative relationship between beech understory density and sugar maple understory density (Figure 2). Stands with dense thickets of beech, largely previously logged stands, had many fewer sugar maple saplings than stands without dense thickets.



**Figure 1.—Beech vs. sugar maple densities at sites with two different land-use histories (sugar bush or logged), and two areas of a site that has not been heavily impacted by human use (virgin).**

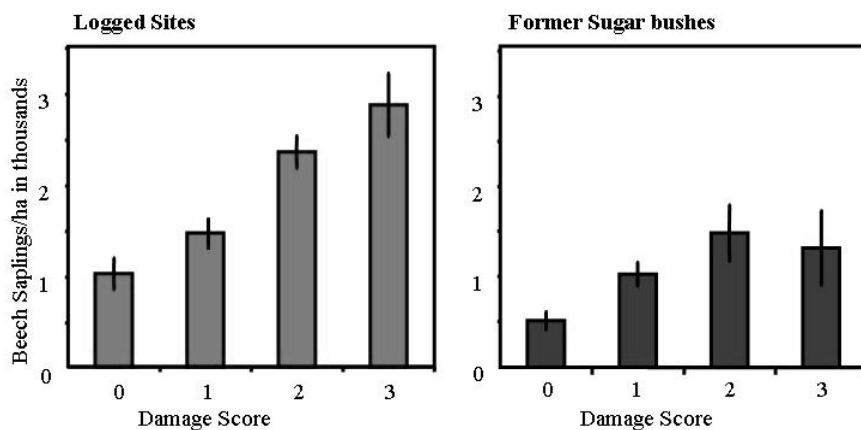


Figure 2.—Density of beech saplings as predicted by damage class in each land-use type. Damage class was assessed visually following methods from Houston and O'Brien (1983). The categories ranged from 0 (undamaged) to 3 (severely damaged).

## Discussion

Disease severity appears to vary by land-use history in the northern hardwood stands I examined (Fig 2), and in turn, the disease severity seems to contribute to higher beech sapling densities (Fig 1). Land-use is particularly interesting as a predicting factor, because management practices from > 80 ybp have an effect on the patterns of regeneration that we see today. The removal of species other than sugar maple has resulted in stands with reduced beech density, which results in both less damage from beech bark disease and lower beech sapling densities.

As predicted, the sugarbushes had much higher densities of sugar maple saplings than forests with high levels of beech present (Fig 1). The sugarbushes examined had similar elevation, slope, aspect, and time since disturbance to the logged areas, however whether sugarbushes were randomly distributed on the agricultural landscape is unknown (Waldbauer 1999). The results of the survey demonstrate that the presence of beech in the overstory has an apparent impact on the density of young sugar maple in the understory. The sugarbushes had higher regeneration of sugar maple than any other area, and also had the lowest density of beech saplings of any area, although the relationship may also be related to greater seed sources in areas of high maple density.

In forests with land-use histories that result in compositions with limited representation of beech, the effects of beech bark disease appear to be limited. These areas have little root suckering or canopy thinning in the form of branch or individual tree death. At the Bartlett

Experimental Forest, the severity and impact of beech bark disease varied with species composition and stand age, both strongly influenced by the logging history of a site (Twery and Patterson 1984). Older stands with more mature beeches had a higher mortality rate than stands with smaller, younger trees. This result is not surprising, given that tree age plays a key role in determining susceptibility to beech bark disease. In the logged stands in this study, beech was a major component of the overstory (trees > 10 cm dbh; 39-43% by density) and made up the largest proportion of the understory regeneration. Beech recovered in these stands from the effects of logging, and beech bark disease and its subsequent effects are evident in all three stands. In contrast, nearby younger stands have much lower densities of beech, many of which are not yet large enough to be infected with the disease (trees need to be approximately  $\geq 15$  cm dbh), and stands logged < 60 years before had only minor effects from beech bark disease. Therefore, areas that have been previously logged and are now mature are susceptible to beech bark disease and ice damage, and the indirect effects of these factors are contributing to the reduction of regeneration of sugar maple in these areas.

Due to the absence of mature beech on former plowed sites, even after 55-60 years of forest succession (Hamburg 1984), the incidence and impact of beech bark disease on sites with such a land-use history is likely to be minimal. However, the stand may be infected later, if a new outbreak occurs after beech has established itself in the stand. In the three abandoned sugarbushes (year of abandonment approx. 50-70 years ago), density of adult (> 10 cm dbh) beech was less than half that of

undisturbed or logged forests of comparable age and soil type. In addition many of the beech present were not yet large enough to be affected by the disease. The very few large (> 20 cm dbh) adult beeches that were present did have evidence of beech bark disease, but the areas of root suckers were confined to the areas around individual infected trees, rather than pervasive through the understory, as they are in some undisturbed and logged forests. The density of sugar maple saplings (< 5.0 cm dbh) was higher than densities in undisturbed or logged forests (Figure 1). This difference further indicates that the decline in sugar maple regeneration noted elsewhere (Twery and Patterson 1984, Jenkins 1997) is likely due, at least in part, to competitive effects due to the presence of beech and the effects of beech bark disease (Hane 2003).

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# REGENERATION OF AMERICAN BEECH (*FAGUS GRANDIFOLIA* EHRH.) IN MICHIGAN: INTERACTIONS OF BEECH BARK DISEASE AND MANAGEMENT PRACTICES

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## Abstract

Distribution and origin of American beech (*Fagus grandifolia* Ehrh.) regeneration is being studied as part of the Michigan Beech Bark Disease Monitoring and Impact Analysis System. As overstory basal area of all species decreased in stands, the amounts of beech regeneration and total regeneration increased. Both beech regeneration and regeneration of all species were more abundant in the Upper Peninsula compared to the Lower Peninsula. The majority of beech regeneration in Michigan was of seed origin. Also, more beech regeneration and total regeneration were present in mechanically thinned stands as compared to unthinned stands. As overstory beech trees are killed by beech bark disease and overstory basal area decreases, both beech regeneration and total regeneration will probably increase in affected stands. Currently, stands with beech bark disease have lower beech regeneration and total regeneration; this is likely a result of management practices that have led to the maintenance of high basal areas since many of these stands are in state parks. Structural and compositional changes in regeneration are expected to be observed in infected stands once beech bark disease has been present for a greater length of time, overtaking the effects of past management practices.

## Introduction and Literature Review

The major objectives of this regeneration study are to: (1) determine location and size distribution of beech regeneration and regeneration of other overstory species in Michigan's northern hardwood stands, (2) monitor changes in beech regeneration and total regeneration in relation to beech bark disease, (3) determine origin (seed or sprout) of beech regeneration in Michigan and (4) study influences of management practices on beech regeneration and total regeneration. American beech can reproduce either by seed or vegetatively by root sprouts; the extent of each type has been little studied (Jones and Raynal, 1986; Held, 1983; Ward, 1961). In the absence

of disturbance sexual reproduction is thought to be the most common form of reproduction throughout most of its range.

Asexual reproduction of beech occurs mainly in the beech gaps of the Smoky Mountains (Russell, 1953) and in more severe environments in the northern and western parts of its range (Ward, 1961). Beech sprouts generally occur when the roots are injured, causing adventitious buds to form, although sprouts can occur where injury is not evident (Tubbs and Houston, 1990; Held, 1983). Beech sprouts are more abundant on exposed south-facing slopes where freeze and thaw activity can damage shallow roots and stimulate sprouting (Held, 1983). Although beech sprouts have high mortality rates, they also have rapid growth and there is continual production of new sprouts, ensuring that the mechanism of asexual sprouting contributes significantly to individuals reaching the sapling stage (Forcier, 1973).

## Methods

The 61 forest stands used in this study were part of the Beech Bark Disease Monitoring and Impact Analysis System (Thompson and Witter, 2002) (Figure 1). In each stand regeneration plots were placed at every other prism point beginning with the first, for a total of 15 regeneration plots per stand. Plots were 2m X 10m, with the prism point centered on one short edge and the long sides extending out in the direction of the next prism point. Each plot was divided into 4 quadrants.

Within each regeneration plot, all trees >90 cm in height and <12.5 cm in diameter at breast height (DBH) were identified to species and tallied by height class: (1) 0.91-1.20 m, (2) 1.21-1.50 m, (3) 1.51-1.80 m and (4) >1.80 m. Presence or absence of American beech ≤ 90 cm in height was recorded for each quadrant, and overall beech seedling density (low, <10%; medium, 10-25%; high, >25%) was determined for each regeneration plot based on the percentage of the plot area covered by American beech seedlings and then an average density per stand was calculated (Figure 1).

Origin (seed or sprout) was determined for 60 beech stems (four stems per regeneration plot) ≤ 90 cm tall within each stand. If the regeneration plots did not contain enough individuals, origin was determined for stems outside the plots but within the stand. Origin was



Figure 1.—Location of research stands and regeneration density in Michigan. Overall beech seedling density (low, <10%; medium, 10-25%; high, >25%) was determined for each regeneration plot based on the percentage of the plot area covered by American beech seedlings and then an average density per stand was calculated.

determined by removing debris from the base of the stem and searching for lateral roots, which easily distinguished seed or sprout origins.

## Results and Discussion

Beech regeneration was more abundant in stands that had lower overstory basal area, whether from natural disturbances or anthropogenic factors. Lower growing season, higher precipitation, and absence of beech scale were important factors in explaining where high amounts of beech regeneration were found. Stands located in close proximity to Lake Michigan and Lake Superior had the longest growing seasons (Albert et al., 1986). Beech and all species regeneration was more abundant in the Upper Peninsula (UP) compared to the Lower Peninsula (LP) (Figure 2). The stands with the highest amounts of beech regeneration were along the coast of Lake Superior, and some were in areas that had been thinned. Stands thinned in the late 1980's and early 1990's are likely to have higher amounts of advanced regeneration (stems > 1.8m) 10 to 20 years later. A combination of the lake-moderated climate along with the presence of thinning may explain the higher amounts of beech regeneration in these areas.

Significantly more beech regeneration is present in stands dominated by sugar maple and American beech or compared to stands with a strong northern red oak (*Quercus rubra* L.) component (oak-beech) (Figure 3).

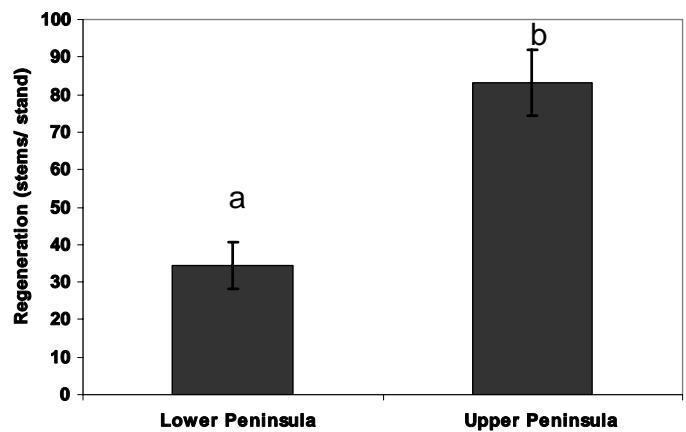


Figure 2.—Mean amounts of beech regeneration in the Lower and Upper Peninsulas of Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different.

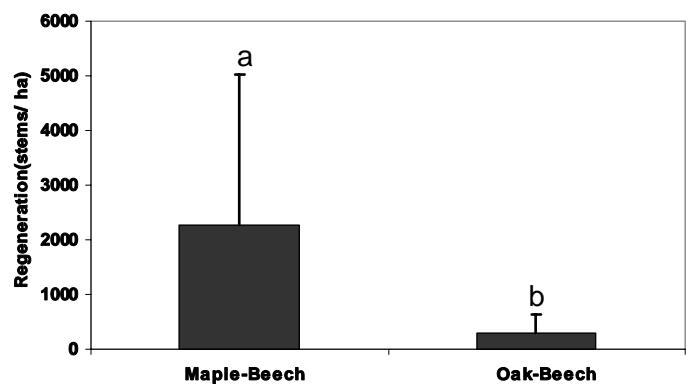


Figure 3.—Mean amounts of beech regeneration in two forest types in Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different.

Amounts of beech regeneration were lowest in the oak-beech stands due to their lower productivity and lower moisture availability.

As BBD progresses throughout Michigan, the gaps created by the death of overstory beech will likely be dominated by beech and sugar maple regeneration (Forrester and Runkle, 2000; Woods, 2000; Barnes et al., 1998; Barnes, 1991). These are the most common species currently present in the understory of the northern hardwood stands that were studied; both of these species respond positively to canopy gaps. The dense canopies found in northern hardwood forests often exclude regeneration of other tree species. Twery and Patterson (1984) predicted that the beech-sugar maple forest type would be very successful after BBD moves

through a stand. Houston (1975) found that while the structure of forests in Maine were very different after BBD moved through than before this disease was present, beech was still a very important component in terms of both relative numbers of stems and basal area following disease outbreak. Others have also extensively studied replacement patterns of beech and sugar maple (Hane, 2003; Forrester and Runkle, 2000; Poulson and Platt, 1996; Runkle, 1981; Woods, 1979). From these studies, it seems likely that future stand composition may depend at least partially upon climatic conditions of the area. In southern Michigan, self-replacement of beech may be frequent (Forrester and Runkle, 2000; Poulson and Platt, 1996) but in northern Michigan where severe climates are present, reciprocal replacement- in which the presence of overstory beech promotes sugar maple regeneration- may be common (Runkle, 1981; Woods, 1979).

Beech reproduction by seed was by far more common in Michigan as compared to reproduction by sprouting, which differs from findings in the eastern U.S. and Wisconsin (White, 1991; Jones and Raynal, 1986; Held, 1983; Ward, 1961) (Figure 4). When sprouting did occur, this type of reproduction was more common in the Lower Peninsula compared to the Upper Peninsula, again differing with Ward's (1961) Wisconsin study (Figure 4). Held (1983) determined that freeze-thaw injury is a primary cause of beech sprouting. The Lower Peninsula is more vulnerable to late spring freezes and frost throughout the growing season as compared to the Upper Peninsula (Albert et al., 1986); this may explain the high numbers of beech sprouts in the Lower Peninsula relative to the Upper Peninsula.

Regeneration by sprouting was similar in stands with and without BBD (Figure 4). Jones and Raynal (1986), studying stands in NY, also found that BBD did not seem to have a stimulatory effect on sprout production. However, number of beech sprouts was also similar in unthinned and thinned stands in Michigan, in contrast to findings of White (1991), who determined that sprouts of several species, including beech, dominated woody plant biomass after harvesting in Maine (Figure 5).

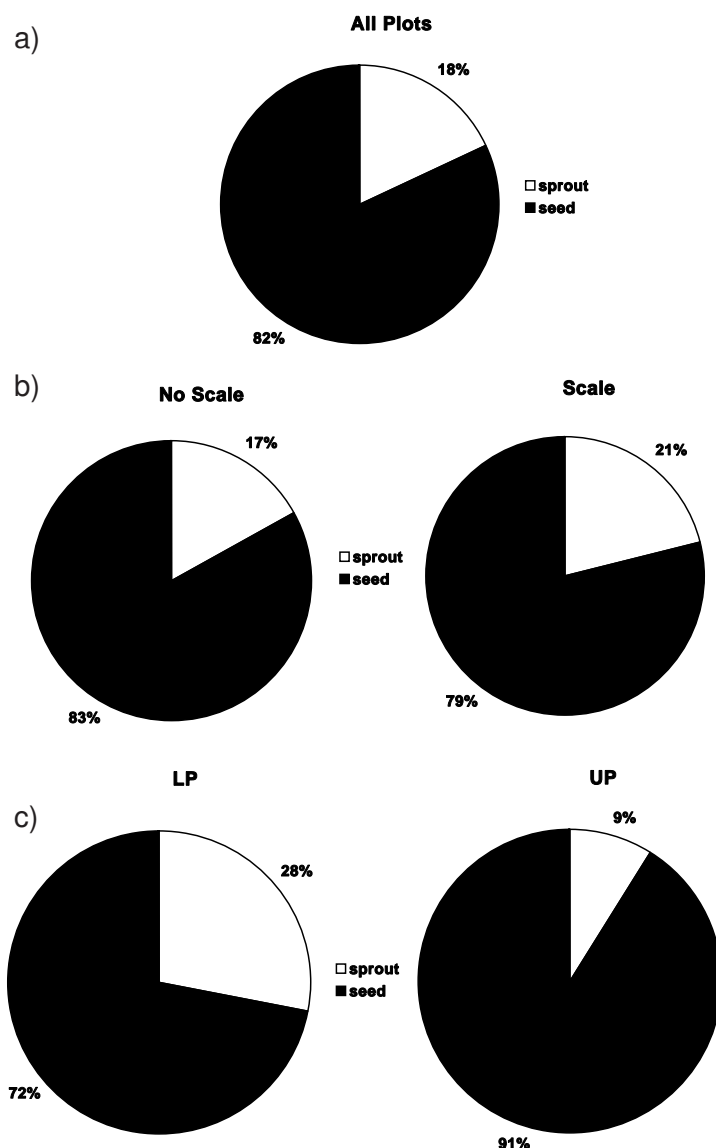


Figure 4.—Percent of beech stems from seed and sprout origins in a) all research stands in Michigan b) stands with and without beech scale and c) the Lower Peninsula (LP) and Upper Peninsula (UP) of Michigan.

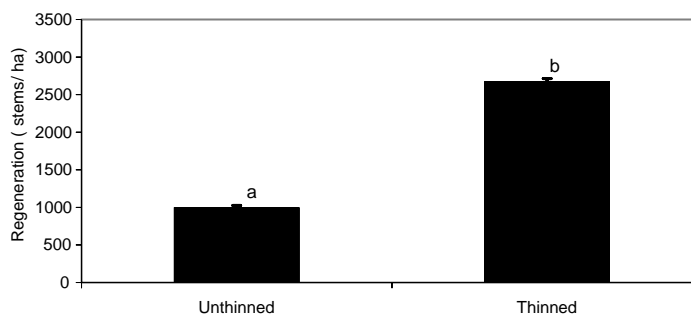


Figure 5.—Mean amounts of beech regeneration in unthinned and thinned stands in Michigan. Bars indicate standard errors. Different letters indicate mean values that are significantly different.

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## Knowledge Gaps and Research Priorities

### *Knowledge Gaps (aftermath forests)*

- How do we identify resistance and encourage it?
- What are the appropriate stand densities to reduce regeneration of susceptible beech?
- What is the best equipment system to use and appropriate silvicultural techniques?
- Factors that control sprouting.
- Understand more about season of harvest.
- What site factors influence resistance?
  - o Nitrogen fertilization?
  - o Moisture availability?
  - o Role of other nutrients?
- Is biological control an option?
- How to increase mast production.

### *Knowledge Gaps (killing front)*

- Interaction with BBD and beetles (exotic species).
- How do we identify resistance and susceptibility?
- What are the factors that control sprouting?
- Harvesting strategies:
  - o Should we harvest?
  - o How much harvest?
  - o When should we harvest?
  - o Post harvest treatment?

### *Knowledge Gaps (advancing front)*

- How to identify a resistant tree?
- Develop a challenging technique to test trees.
- Identify appropriate silvicultural practices.

### *Knowledge Gaps (scale-free zone)*

- Manage to increase species diversity.
- Manage to increase growth.
- Identify site quality.
- Identify stand vulnerability.
- Choose appropriate management techniques.
- Human role in transporting the scale.

### *Research Priorities*

Addressing specific management needs.

Site suitability and nutritional requirements.

Identifying sites that disease severity should be low.

Locate funding sources.

Effect of the disease on forest productivity.

Identifying markets.

Interactions between deer densities and BBD.

Propagation of seedlings.

Web site development for BBD awareness.

## Summary and Conclusions

Celia A. Evans, Jennifer A. Lucas, Mark J. Twery, and Daniel B. Twardus

This symposium was a first step in a necessary direction, to assess what we know, determine promising areas of research and management opportunities, and develop a strategic plan to focus our efforts in a more concerted manner. For the past 20 or more years, BBD research has been sporadic, dependent upon individual efforts and interests, and without a unified direction that builds upon collective efforts. We hope this symposium was only the first step in pulling together international expertise, talent, and interest not only to identify a strategic approach to BBD research and management, but also to help secure the necessary governmental backing and support to see that strategic approach implemented.

Research on BBD has received only a small amount of government funding probably for some of the following reasons: 1) historically, beech has not been considered to be economically important; 2) rather than declining in abundance, beech appears to be regenerating, often prolifically; and 3) other tree species that have received funding to combat invasive species have higher ornamental value (e.g., hemlock). It is clearer than ever to scientists and managers who have been working with infected beech stands that there is a strong need for funding of new research. Increased funding will likely come only when both the general public (landowners) and granting agencies are convinced of the significance (current and future) of the impacts of the disease over large parts of North America. During symposium discussions it became evident that there was effectively no current public education about beech bark disease. Participants agree that education about the ecological and economic importance of beech must be directed at the general public and decision makers, not only academics or those involved in managing and protecting forests. Venues such as the world-wide web may be useful in developing awareness of BBD among the general public. This education must emphasize the non-timber, wildlife, and aesthetic values of beech as well as the economic and ecological importance of the species.

International collaboration between Canada and United States, among scientists, managers, and industry are examples of collaborations that would improve our understanding of the disease impacts under all disease scenarios. The establishment of national and regional working groups, data bases, and an information clearing house would improve the dissemination of information as data continue to become available. Potentially fundable collaborative research topics may be those that link BBD to larger issues such as carbon cycling, climate change, ecosystem effects and services, and wildlife habitat loss. Perhaps comparing the disease to other invasive species that have, unlike BBD, received a good amount of funding (Hemlock Woolly Adelgid) would also be fruitful.

There is a pressing need for research that examines patterns and mechanisms at all temporal and spatial scales and that demonstrates the economic and ecological importance of beech. Useful research tools that may provide access to data over large spatial scales and long temporal scales are FIA plot data, remote sensing using hyperspectral information, and data from aerial surveys. Just as Houston (these proceedings) summarized the research and history of the disease, it would be valuable to managers to have a summary of the existing management options. In their struggle with diseased beech and beech mortality in northeastern forests, managers have attempted various silvicultural solutions with more or less success. The two papers in these proceedings by Heyd and Ostrofsky begin to document approaches that have been tried, but generalized guidelines applicable over a wide range of conditions are not yet established. This information will not only inform managers, but will provide insights into future testable hypotheses. We must maintain the long term data bases that already exist for beech, and reestablish those that have been abandoned, because the best data on long term effects of the disease will come from those plots.

Dr. David Houston has provided an excellent historical and research summary paper for these proceedings that will serve as a much needed, inclusive review of the literature to date. The findings of studies included in these proceedings (and other recent papers published elsewhere and referenced here) demonstrate an overdue resurgence of interest in the science and management of beech bark disease. These papers begin to fill some knowledge gaps and illuminate others that when filled will allow us to better understand the response of different forests to the disease complex. These studies also reinforce the recognition that stands differ in response to the disease depending on geographic location (which may be driven by climatic variables), land use history, and species composition. If structure affects the beech nut crop (as it may have done already) then there is potential for impacts to large and small wildlife species. While we explore the use of models to develop testable hypotheses regarding characteristics that predispose certain forests to major state changes in structure as a result of the disease, we must also continue to explore the nature and mechanism of resistance and to identify techniques that facilitate the propagation of these resistant beech in infected forests.

Considering the importance of American beech and the devastating impact this introduced disease complex has had it is appropriate that this symposium has helped identify some of the gaps in our knowledge that if solved, may help both in protecting un-infested beech and restoring already impacted areas. We know, for example, that resistance to beech scale exists but we know little about the nature of that resistance and the genetic mode of inheritance of resistance. More research involving resistance including the identification of genetic markers of resistance may prove extremely useful in capitalizing upon the resistance within the gene pool that empirical observations tell us is there. This coupled with advances in our technological abilities in the area of gene research make opportunities for conserving a resistant gene pool possible. This is particularly important as we attempt to refine silvicultural approaches, developing protocols to introduce and establish resistant genotypes, and managing for resistance in the long term. From an ecological standpoint, it is apparent that we still have much to learn in the areas of scale dispersal, the predisposition of beech to scale infestation, and the role of parasites and predators in limiting scale infestation.

During the course of the symposium we asked participants to join in outlining research needs and priorities for each section of discussion. This important aspect of the symposium was intended to provide research and management the opportunity to discuss what we know, focus upon what we need to know, and offer suggestions about promising avenues to pursue. While the presentations of information formed the basis of the symposium, these 'research agenda' discussion groups may well form the basis of where we go from here.

## Appendix

### Beech Bark Disease Symposium Working Group Participants

These individuals participated in the discussion sessions that generated the lists of knowledge gaps and research priorities identified in this proceedings.

Robert Acciavatti	Jason Klink
Matt Ayres	Jennifer Koch
Russ Barrett	Marek Krasowski
Brian Beachy	Erika Latty
Dale Bergdahl	Matt Leonard
E. Michael Blumenthal	Andrew Liebhold
Michael Birmingham	Shane Lishawa
Chris Buddle	Robert Long
Barbara Burns	Judy Loo
Charlie Butler	Martin MacKenzie
Charlie Canham	David McCann
David Carey	Stacy McNulty
John Castello	Tania Motchula
Charlie Cogbill	William Ostrofsky
Chuck Davis	Michael Papaik
Joseph DeMatties	Holly Petrillo
Don Eggen	Robert Rabaglia
Mike Francis	Nela Ramirez
Geoff Gardner	Brad Regester
Jacob Griffin	George Robinson
Thomas Hall	Scott Roche
Elizabeth Hane	Jason Rodrigue
Frank Hennion	Justin Rosemier
Bob Heyd	Lincoln Rowlinson
Andrea Hille	Dan Ruddell
Richard Hoppe	Allen Saberniak
Steve Horsley	Daniel Twardus
Dave Houston	Shahla Werner
Christina Idziak	Bob White
Wayne Ingram	Joe Wiley
William Jones	John Witter
Douglas Kane	Jeffrey Williams
Amy Kearney	Rodney Wilson
Ron Kelley	

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

**Key Words:** Beech Bark Disease, forest structure, wildlife, silviculture and management, genetics, Northeastern forests, research agenda, *Cryptococcus fagisuga*, *Nectria coccinea* var. *faginata*, *Fagus grandifolia*





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**Parsons, West Virginia**

**Princeton, West Virginia**

**Syracuse, New York, in cooperation with the State University of New York, College of Environmental Sciences and Forestry at Syracuse University**

**Warren, Pennsylvania**

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