PRELIMINARY REPORT OF ECOLOGICAL FACTORS INFLUENCING INCIDENCE AND SEVERITY OF BEECH BARK DISEASE IN THE APPALACHIAN REGION

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Abstract.—Resistance to *Cryptococcus fagisuga,* a primary component of the beech bark disease (BBD) complex, is heritable. Reportedly about 1-2 percent of American beech (*Fagus grandifolia* Ehrh.) are genetically resistant to *C. fagisuga*. This project is designed to identify environmental factors contributing to BBD incidence and severity. Plots were established in stands with endemic BBD and a disease-free beech component. To date 1,479 beech trees have been sampled; 55 percent were scale-free or have trace infestation, and 79 percent were free of *Neonectria* infection. Twenty parameters were evaluated for correlations with infestation/infection. Correlation matrices identified factors possibly contributing to infestation and infection. The strongest correlations with infestation were slope (r= -0.235) and species composition of the canopy (r = -0.187). Beech height and *Neonectria* infection had the strongest correlation (r = 0.420); slope had the strongest negative correlation with infection (r = -0.344). Regression analyses estimated scale infestation was affected only by canopy composition (p = 0.034). Infection was impacted by beech height (p = 0.031), slope (p = 0.033), and ground coarse woody debris (CWD) species (p = 0.0001). Results indicate BBD-free beech appear on the landscape at rates much greater than expected, suggesting that environmental factors may influence disease incidence and severity.

INTRODUCTION

American beech (*Fagus grandifolia* Ehrh.) is the only native species of the genus *Fagus* in the United States, although local races and one variety may be recognized (Rushmore 1961). Considering its relatively low commercial value, American beech often is considered a nuisance species in forest management. However, the wood of beech is hard, strong, and useful for veneer, pulping, railroad ties, flooring, furniture, and food storage (Carpenter 1974). Its value as a fuelwood is nearly equal to white oak (Mielke et al. 1987). Beech is important ecologically as a climax species (Halls 1977) and resource for wildlife (Jakubas et al. 2005, Storer et al. 2005).

Beech bark disease (BBD) is a canker disease affecting bark tissues. It is a complex of interacting causal agents, primarily the beech scale (*Cryptococcus fagisuga* Lindinger) and several species of ascomycetous fungi now classified in the genus *Neonectria*. Both insect and fungus can injure beech individually, but serious damage does not occur without their combination (Shigo 1964). The disease has been known in Europe since the 1700s (Ehrlich 1934). There it is of concern because of its widespread effects on beech plantations, but in forest stands it more often is innocuous with small disease pockets developing around a single infected inoculum source.

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European beech (*Fagus sylvatica* L.) enjoys a substantial level of resistance to BBD that has either evolved as a natural trait in the species or from extended relationships with causal agents (Wainhouse and Howell 1983). The mortality of single or small groups of beech during disease development in Europe contrasts with the death of whole stands in North America. Resistance studies of sibling and clonal European beech reveal genetic control of beech scale resistance. Since the late 1800s, the beech scale has been known in North America, and by the 1920s, its complex with species of *Neonectria* was established in Canada and New England (Houston 2005). Currently the disease is spreading through Ohio, Pennsylvania, Virginia, and West Virginia. Outlying infections in Michigan, North Carolina, and Tennessee also are known (Morin et al. 2005). Beech bark disease has reached less than 30 percent of the range of beech while spreading an estimated 14.9 ± 0.9 km per year (Morin et al. 2007). Spread of the disease in North America is widely considered frontal in nature; accumulating populations of causal agents in an advancing front are followed by a killing front of widespread, heavy mortality and then an aftermath of defective sprout thickets, and occasionally, a few large survivors (Shigo 1972).

Despite an overall frontal nature of spread, BBD does not operate strictly on a frontline. In the last 20 years, 10 cases of isolated pockets of scale infestation ahead of an advancing front have been documented (Morin et al. 2007). Often, BBD progresses as a conglomeration of eruptive centers of disease emanating from randomly distributed inoculation sources. Whatever the case, the establishment of the disease in a stand is dependent on beech scale infestation (Houston 1994). The *Neonectria* fungal component of the BBD complex is an opportunistic weak pathogen capitalizing on the activities of the beech scale whose infection can normally be contained by defenses of healthy hosts (Houston 1980, Manion 1991).

For many years, some beech trees have been observed to escape both signs and symptoms of disease (Ehrlich 1934; Houston 1983; Shigo 1962, 1964; Wainhouse and Howell 1983). Studies of sibling and clonal European beech reveal resistance to beech scale is genetically controlled (Wainhouse and Howell 1983). Beech scale challenge trials confirm a small percentage of American beech (~1-2 percent) is genetically resistant to scale infestation (Koch and Carey 2004, Koch and Carey 2005).

This project is designed to determine whether ecological factors are related to the incidence of disease-free American beech. Specific objectives are to: 1) examine stand features including incidence and severity of BBD, species composition, stand density, canopy features, management activities, and BBD longevity; 2) measure landscape and topographical features including climate, slope, aspect, and elevation; and 3) evaluate other forest components including coarse woody debris (CWD) load, litter layer, soil types, and mycorrhizal associations.

STUDY AREAS

Seven Appalachian hardwood stands with a several-decade history of BBD and a component of disease-free beech have been sampled (Table 1). Data collection was completed at five West Virginia sites and partially completed at Kumbrabow State Forest and Great Smoky Mountains National Park. Sites at the Holden Arboretum in northeast Ohio and the Allegheny National Forest in north central Pennsylvania have been selected for study based on preliminary visits. Upcoming reconnaissance may identify additional sites in Maryland and West Virginia.

Table 1.—Study sites in the Appalachian region

Location	Number of plots
Shaver's Fork Recreation Area, Monongahela National Forest, WV	10
Gaudineer Scenic Area, Monongahela National Forest, WV	10
Middle Mountain, Monongahela National Forest, WV	10
Blackwater Falls State Park , WV (I)	7
Blackwater Falls State Park , WV (II)	6
Kumbrabow State Forest, WV	10
Great Smoky Mountains National Park, TN	6

Table 2.—Detailed descriptions of *Cryptococcus* infestation and *Neonectria* infection categories

Category	*Cryptococcus*	*Neonectria*
0	No beech scale evident	No *Neonectria* evident
1	Trace scale population; tree initially looks scale-free but infestation evident upon close inspection, may need hand lens	Trace *Neonectria*; tree initially looks infection-free but cankers or perithecia evident upon close inspection; may need hand lens
2	Beech scale clearly evident from a short distance; scales singular or uniformly dispersed in clusters; majority of stem scale-free	Cankers/perithecia clearly evident from short distance; few scattered or clusters of cankers; majority of stem infection-free
3	Beech scale clearly evident from a short distance; scales singular or uniformly dispersed AND in small clusters OR many clusters of scales; majority of stem may or may not be scale-free	Cankers/perithecia clearly evident from short distance; cankers litter large portion of stem; majority of stem likely cankered; streaks may appear; bark may be peeling off in small sections
4	Beech scale clearly evident from short distance; large clusters of scales all over stem; majority of stem likely infested	Cankers/perithecia clearly evident from short distance; cankers affect nearly entire stem; multiple streaks; bark may be peeling off in small sections; tree dead?

METHODS

Field Sampling

At each study site circular 0.04 ha plots were established in a northeast-southwest direction about 80-100 m apart. Variations of this design where employed as necessary to include beech in study plots. Plot centers was marked with pin flags and boundaries were marked in the cardinal directions. The slope, aspect, and elevation of each plot were recorded. Canopy density was estimated at several points in a plot using a concave spherical densiometer (Forest Densiometers, Bartlesville, OK). Basal area (BA) was estimated from the plot center using a basal area factor (BAF) 10 (~1 m^2/acre BA). A TruPulse 360° laser rangefinder (Laser Tecnology Inc., Centennial, CO) was used to establish distances from plot centers. Total height, canopy class, and diameter at breast height (d.b.h.) were recorded for all beech > 5 cm d.b.h. and non-beech >10 cm d.b.h. Scale infestation and *Neonectria* infection were rated separately on four sides of each beech using a qualitative five-category rating system of no infestation/infection (0), trace infestation/infection (1), light infestation/infection (2), moderate infestation/infection (3), or heavy infestation/infection (4). Detailed descriptions of categories are displayed in Table 2. Mean infestation/infection ratings were calculated for each tree from ratings on four sides and calculated for plots from mean ratings of all beech in each plot. Bark samples with *Neonectria* perithecia were collected for laboratory examination and processing. Samples were collected with a 1.3 cm diameter leather punch from three beech trees within each plot or nearby if necessary. Severely cracked, blocky, or blistered bark was sampled using the same methodology.

Table 3.—Parameters related to beech, non-beech trees species, overall tree species composition, and site features used as independent variables in regression analyses

Beech	Non-beech species	Overall species	Site features
Beech per ha	Non-beech stems per ha	Trees per ha	Volume CWD
Beech basal area per ha	Non-beech species basal area per ha	Basal area per ha	Volume standing CWD
Mean beech d.b.h.	Mean non-beech species d.b.h	Mean overall d.b.h.	Aspect
Mean beech height	Mean non-beech species height	Percent intermediate crown class species	Slope
Percent beech	Percent dominant/codominant non-beech		Canopy density
	Most abundant non-beech species (percent)		

Coordinates of beech stems were recorded with a Mobilemapper™ CE (Magellan Corp., Deerfield, IL) for digital mapping. Coarse woody debris (CWD) was measured on 13 m transects from plot center to the north and east boundaries. Diameter, species (if known), and decay level were recorded for debris crossing transects and greater than 1 cm diameter. All standing dead stems and stumps > 10 cm were counted as standing CWD and their height, species (if known), diameter measured at breast height or the stump's highest point, and decay level were recorded. Debris decay was recorded at four levels: sound wood with or without bark (1); sapwood decayed (2); sapwood and some heartwood decayed (3); or decayed throughout (4).

Laboratory Procedures

Neonectria samples recovered from bark plugs were identified to species using ascospore morphology as described by Castlebury et al. (2006). Perithecia were slide mounted in water under a Leica EZ 4 stereoscope (Leica Microsystems Inc., Buffalo Grove, IL) and ascospores viewed at 400x-1000x magnification with a Nikon Eclipse E600 light microscope (Nikon Instruments Inc., Melville, NY). Perithecia and bark tissues, sampled from plugs with a bone biopsy tool were surface sterilized in 10 percent bleach for 5-10 minutes and placed on Difco™ potato dextrose agar to isolate *Neonectria* species and other fungi. The confirmation of *Neonectria* samples will be by molecular analysis.

Statistical Analyses

An Excel 2010 (Microsoft®, Redmond, WA) database compiled from field sampling describing stand features including species composition and density, canopy, topography, forest floor, and bark organisms was analyzed for significant relationships with scale infestation and *Neonectria* infection. Proportions of beech with a given infestation or infection rating, or both, were calculated in Excel as a percent of total beech sampled. Mean ratings of infestation and infection for individual beech were rounded to the nearest whole number to fit each beech into a category. All other statistical analyses were performed in JMP 9.0® (SAS Institute Inc., Cary, NC). Twenty parameters (Table 3) were evaluated for correlation with mean beech scale and *Neonectria* ratings using plots as the sampling units. Scatterplot matrices and correlation coefficients generated in JMP identified those parameters that may have a relationship with scale infestation or *Neonectria* infection. Forward stepwise regression with minimum BIC stoppage and combine rules for control settings analyzed the individual and additive effects of parameters on infestation and infection rates. Regression analyses were performed on continuous and categorical data separately.

Table 4.—Categories of non-numerical parameters

Category	Dominant/ codominant non-beech	Intermediate/ suppressed non-beech	Most abundant non-beech	Ground CWD species	Standing CWD species	Aspect
1	Maples	Maples	Red/sugar maples	Beech	Beech	N
2	Maples/ hardwoods	Hardwoods	Other maples	Unknown	Unknown	NE
3	Yellow birch	Hardwood mix	Yellow birch	Beech/ unknown	Beech/ unknown	E
4	Hardwoods	Hardwood/conifer mix	Hardwoods	Hardwood	Hardwood	SE
5	Conifers	Conifers	Conifers	Hardwood/ conifer	Hardwood/ conifer	S
6	--	--	--	Conifer	Conifer	SW
7	--	--	--	--		W
8	--	--	--	--	--	NW

With the exception of aspect, all non-numerical data were grouped and analyzed in categories representing individual species or roughly defined forest cover types (Table 4). For example, dominant/codominant species compositions were grouped in five categories; maples (*Acer* spp.), maples/other hardwoods, yellow birch (*Betula alleghaniensis* Britton), miscellaneous hardwoods, and conifers. Aspect was analyzed in eight categories representing compass headings. Volumes of CWD were calculated as cubic meters per hectare for each plot with a line intersect sampling formula ($V = (\pi^2 10000/80000L)(\sum d^2)$) where L = length of sample line in meters and d = diameter in centimeters of woody debris intersecting the sample line. Standing CWD volumes were calculated as volumes of a cylinder ($V = r^2HT$) in cubic meters, summed, and converted to cubic meters per hectare for each plot.

RESULTS

Infestation and Infection Rates

Table 5.—Percent of beech at all study sites (N = 1,479) exhibiting an individual *Cryptococcus* or *Neonectria* rating

Rating	*Cryptococcus*	*Neonectria*
0	14	79
1	41	7
2	41	6
3	3	4
4	1	2

To date, 1,479 beech have been sampled. Considering only scale infestation, 14 percent of beech were scale-free, 41 percent had trace infestation, and another 41 percent had light infestation (Table 5). Individual assessment of *Neonectria* infection indicates 79 percent of beech had no infection, 7 percent had trace infection, and 6 percent had light infection (Table 5). When evaluating disease as a combination of infestation and infection, 13 percent of the beech trees were free of both scale infestation and *Neonectria* infection, 37 percent had trace infestation and no infection, and 29 percent were lightly infested but not infected (Table 6). Overall, disease-free to lightly infested/ infected beech appear in the highest proportions, but heavily diseased trees do persist, some with both heavy infestations and infections.

Table 6.—Percent of beech at all study sites (N = 1,479) exhibiting combined ratings of *Cryptococcus* infestation and *Neonectria* infection

	Cryptococcus rating				
Neonectria rating	0	1	2	3	4
0	13	37	29	2	<1
1	<1	2	3	<1	0
2	<1	1	4	<1	<1
3	<1	1	4	<1	<1
4	<1	<1	1	0	<1

All *Neonectria* samples from Gaudineer Scenic Area and Shaver's Fork Recreation Area have been identified as *Neonectria faginata* (M.L. Lohman, A.M.J. Watson & Ayers) Castl. & Rossman based on ascospore morphology. Although light disease levels predominated, there were heavily infested/infected beech, and there was evidence of past beech mortality in CWD. American beech accounted for 65 percent of dead stems; another 11 percent of dead stems were unknown species. Furthermore, beech dominated ground CWD on 29 percent of the plots, and species of CWD were unknown on 47 percent of the plots.

Correlation Analysis

Correlation matrices and coefficients of twenty parameters identified those that most likely influenced *Cryptococcus* infestation and *Neonectria* infection. Larger absolute values for correlation coefficients indicate stronger relationships, and negative correlations indicate inverse relationships. Taller beech may incur more scale infestation (r = 0.1603) and *Neonectria* infection (r = 0.420) and a larger mean beech d.b.h. may correlate with increased *Neonectria* (r = 0.357) (Fig. 1). Considering all tree related factors, higher canopy density (r = 0.387) and larger overall mean d.b.h. (r = 0.278) may correlate with increased infection (Fig. 2). Scale infestation (r = -0.235) and infection (r = -0.344) may increase as slope decreases (Fig. 2). Increases in standing CWD volume may contribute to increased infection (r = 0.384), and as non-beech species density increases, infection may decrease (r = -0.259) (Fig. 3). *Neonectria* infection may be negatively affected by ground CWD species (r = -0.308), and scale infestation by canopy composition (r = -0.187) (Fig. 4). Some of these factors may significantly contribute to BBD severity individually or when combined with other parameters.

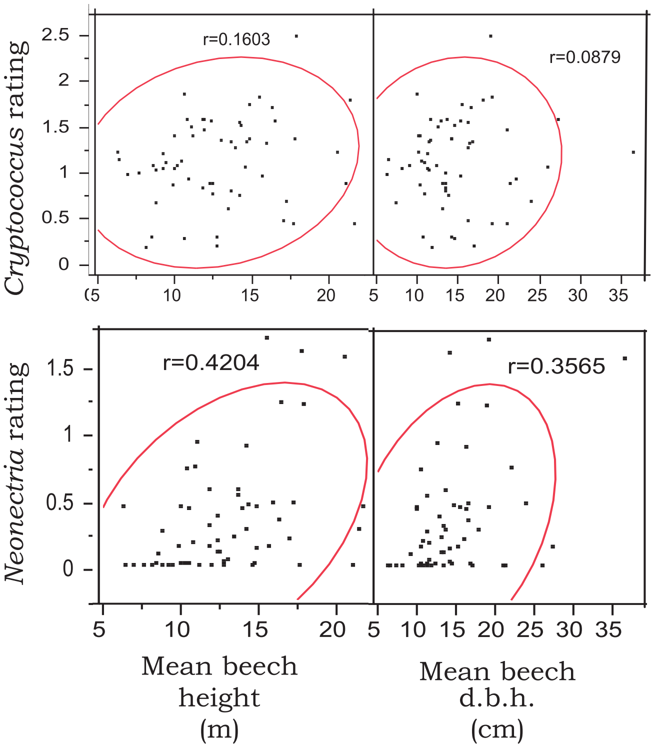

Figure 1.—Correlation matrices and coefficients of mean beech height and d.b.h. with *Cryptococcus* and *Neonectria* ratings, narrower ellipses indicate stronger correlation.

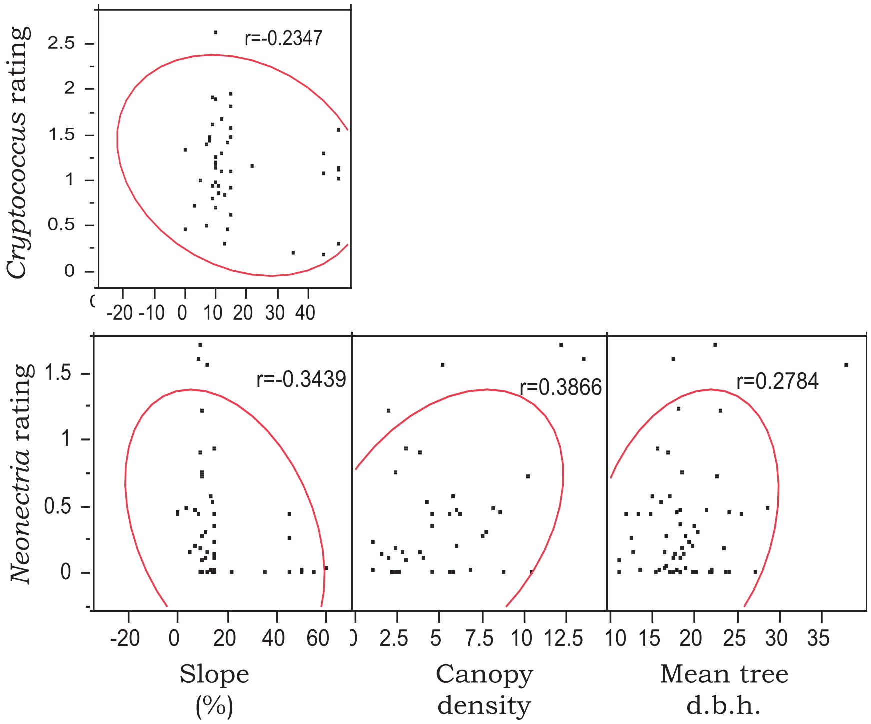

Figure 2.—Correlation matrices and coefficients of slope with *Cryptococcus* ratings and slope, canopy density, and mean tree d.b.h. with *Neonectria* ratings, narrower ellipses indicate stronger correlation.

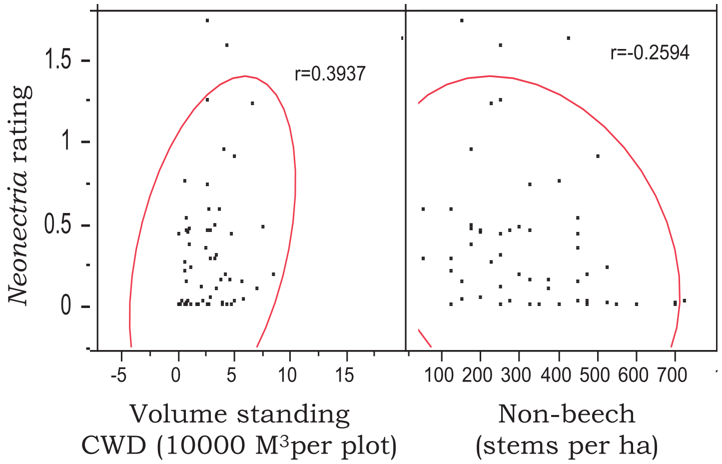

Figure 3.—Correlation matrices and coefficients of non-beech per hectare and volume of standing coarse woody debris with *Neonectria* ratings, narrower ellipses indicate stronger correlation.

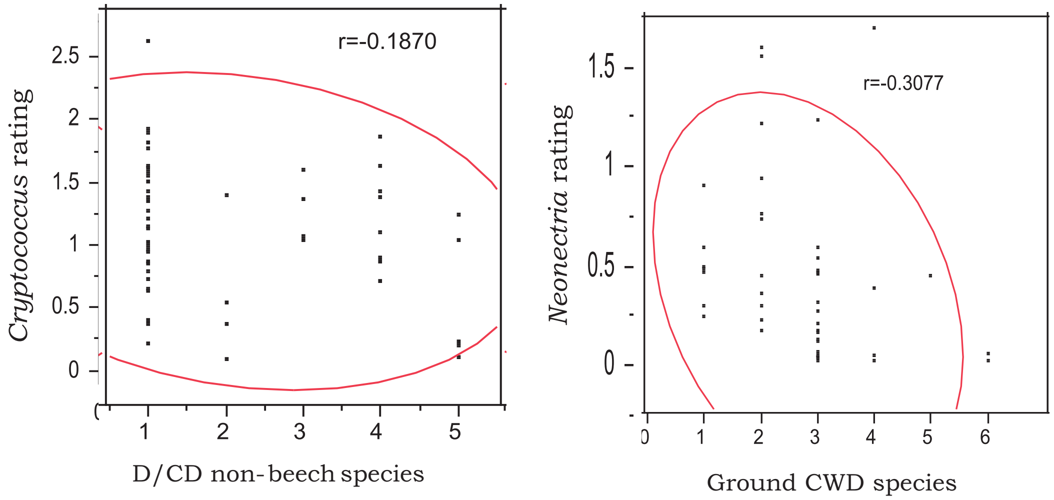

Figure 4.—Correlation matrices and coefficients of dominant and codominant non-beech species composition with *Cryptococcus* ratings and species of ground coarse woody debris with *Neonectria* ratings, narrower ellipses indicate stronger correlation.

Stepwise Regression Analyses

Regression analyses estimated none of the continuous variables analyzed had an effect on scale infestation and only beech height ($p = 0.031$) and slope ($p = 0.033$) were indicated as important to *Neonectria* infection. When these variables were crossed, there was no effect from the interaction ($p = 0.453$). The amount of variability explained by the whole model is small ($r^2 = 0.0633$), but beech height and slope account for essentially all explained variability (combined $r^2 = 0.0633$). Categorical parameters that correlated with scale infestation included species composition of the dominant/codominant canopy strata ($p = 0.034$) and species of ground CWD ($p = 0.008$). These two variables accounted for 70 percent of the variability (combined $r^2 = 0.047$) explained by the model, but again, only a small portion of the variability is explained by the model ($r^2 = 0.067$). Species of ground CWD was the only categorical parameter relevant to *Neonectria* infection ($p < 0.0001$, $r^2 = 0.092$) but only accounted for 11 percent of the variability explained by the model. Precisely which if any categories of these non-numerical parameters (see Table 4) actually influence infestation or infection will be determined in future analysis. When results were validated with additional regression analyses using alternate control settings, canopy species and ground CWD species remained the only correlated variables impacting infestation. Likewise, in analyses to validate results for *Neonectria,* only beech height, slope, and species of ground CWD were consistently estimated as important for infection.

DISCUSSION

About 1-2 percent of American beech are estimated to be genetically resistant to BBD (Koch and Carey 2004). However, 13 percent of beech sampled in this study were free of both scale and *Neonectria* and an overwhelming majority were lightly infested/infected. Predominance of *Neonectria faginata* indicates an extended period of BBD activity (Houston 1994). Also, past mortality with some heavy infection is indicative of an aftermath zone with a long history of BBD (Shigo 1972). The low levels of disease and several decade history of BBD evidenced by CWD and the predominance of *N. faginata* indicated the selected sites were ideal for this study.

This project endeavored to discover ecological factors influencing BBD. Inherited resistance is expressed as gene products or physical attributes of a host that enable it to deter or tolerate pests. Ecological resistance is another mechanism not related to gene expression that defends plants from deleterious effects from insects. It is a noninherited pseudoresistance derived from the effects of environmental conditions more than genetics. Ecological resistance is a temporary condition appearing randomly with little or no relation to coevolution of host and pest and could occur in three ways: host evasion, host escape, and induced resistance (Pedigo and Rice 2006).

Hosts can evade infestation with a reduced exposure time to potential inoculum. Early planting and crop rotations evade damaging insect life cycles. Host escapes seemingly occur by pure chance when susceptible hosts in an affected population remain unaffected. Houston and Valentine (1988) describe severe winter temperatures that negatively affect scale populations and BBD; this may be considered an escape due to climate. Escapes are poorly understood. Induced resistance occurs when the environment or plant ecology exclude insect infestation (Pedigo and Rice 2006). Transient environmental factors such as interspecific competition, changes in nutrient cycles (i.e. fertilization), or plant production of unpalatable substances may temporarily induce resistance (Painter 1951).

For example, bark beetle attacks on pine elicit an ecological (induced) resistance when phenols and terpenes accumulate as a general response to stress induced by the beetles. Beech bark is normally smooth through old age, but severe beech scale attacks can produce necrotic areas that roughen outer bark and inhibit scale establishment (Lonsdale 1983). This could be considered a form of induced resistance.

Most of the environmental characteristics influencing beech scale infestation can be considered factors for induced resistance, but they also can lead to chance escapes. Furthermore, ecological factors may influence *Neonectria* infection much the same way. Correlation matrices (Figs. 1-4) indicated which of the factors sampled in this study may have an effect on BBD causal agents. Regression analysis estimated that dominant/codominant canopy species composition is important to scale infestation. Canopy species composition had the highest correlation with infestation, and the relationship is negative overall, with infestation decreasing under specific canopies. The nature of this relationship is unclear and needs further study. Tree species vary in their efficacy for intercepting or deterring dispersing beech scales. Twery and Patterson (1983) found stands dominated by hemlock contained more diseased beech which contrasts with less infestation in conifer-dominated stands found in this study. However, red spruce (*Picea rubens* Sarg.), not hemlock (*Tsuga* spp.), was the predominant conifer species in study sites. Leak (2006) found that BBD incidence decreased in a stand where yellow birch and paper birch (*Betula papyrifera* Marsh.) were removed as part of a 50-year thinning regime, which corroborates the results reported here. Future analyses will determine which species compositions in the canopy affect scale infestation.

Ground CWD had a very low positive correlation with scale infestation, and regression analysis estimated it to be a relevant factor, but currently it is not clear which categories (Table 4) are important. Scale infestation is affected by nutrient availability in beech bark (Latty et al. 2003, Mize and Lea 1979). Different species of debris decompose and release nutrients at varying rates, and species of CWD would affect recycling of nutrients and possibly nutrient availability in beech bark.

Beech height had the strongest correlation with *Neonectria* infection, and regression analysis indicated it had an impact on infection with taller beech incurring more infection. Beech scale is expected to infest larger diameter beech (Ehrlich 1934, Wainhouse and Deeble 1980). Since scale infestation is a required condition for copious infection, it is logical that larger, taller beech are more susceptible to infection because of their size. Furthermore, taller beech in the canopy are more likely to intercept *Neonectria* inoculum dispersed long distances in upper level wind currents. Correlation matrices indicate *Neonectria* infection decreased as slope increased, a relationship that was supported by regression analysis. Scale and fungal inoculum may be blown over steep slopes by wind currents above the canopy. However, this data contradicts Ehrlich (1934) who reported BBD is more extensive on steep slopes than broad ridge tops, and Houston et al. (1979) reported that scale infestation (and thus perhaps *Neonectria* infection) is generally lesser on gentle slopes.

Ground CWD was the only categorical factor in regression analyses that was important for *Neonectria* infection and it was negatively correlated. Future analyses may clarify which categories of CWD, if any, are most influential. Any effects CWD has on nutrient cycling may influence *Neonectria* as well as scale, thus nutrient availability in beech bark for *Neonectria* fungi may be affected by CWD and its decomposition. This is unlikely, but considering the complex nature of disease, no factor should be completely ruled out as a potential influence on BBD. Other data gathered including advanced regeneration, herbaceous, shrub, and litter layers, and soils will be part of future analyses as will a spatial analysis of disease distribution. Some factors such as bark chemistry are beyond the scope of this study, but would be of interest in future studies.

Given the dynamic nature of BBD, stand characteristics affecting beech scale infestation and *Neonectria* infection interact in a complex way and influence each other as well. American beech has yet to be removed from the landscape in North America, and a full understanding of the beech bark disease complex would help improve management of the disease and avoid the loss of this important ecosystem component. The results reported from this study support the hypothesis that factors other than genetics are influencing disease incidence and severity, but a more thorough investigation over a wider geographic range is needed to definitively identify those ecological factors most influencing the progression of BBD.

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