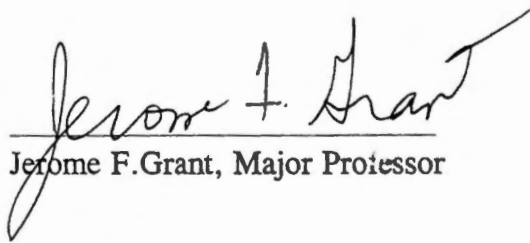
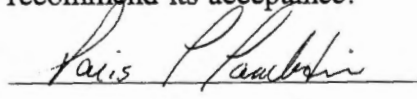
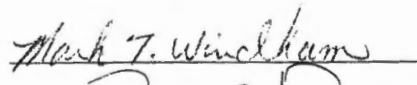


To the Graduate Council:

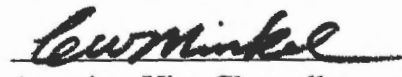
I am submitting herewith a thesis written by Gregory James Wiggins entitled "Temporal incidence, progression, and impact of beech scale, *Cryptococcus fagisuga* Lindinger, and beech bark disease in the Great Smoky Mountains National Park". I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Entomology and Plant Pathology.


Jerome F. Grant, Major Professor

We have read this thesis and
recommend its acceptance:


Accepted for the Council:


Associate Vice Chancellor
and Dean of the Graduate School

**TEMPORAL INCIDENCE, PROGRESSION, AND IMPACT
OF BEECH SCALE, *CRYPTOCOCCUS FAGISUGA*
LINDINGER, AND BEECH BARK DISEASE IN THE
GREAT SMOKY MOUNTAINS NATIONAL PARK**

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Gregory James Wiggins

December 1997

AG-VET-MED.

Thesis
97
.W53

ACKNOWLEDGMENTS

I would like to thank my major professor, Dr. Jerome F. Grant, for his guidance and support throughout this project. I would also like to thank the members of my graduate committee, Dr. Paris Lambdin, Dr. Mark Windham, and Dr. M. L. Pan, for their attention and consideration of my research. In addition, I would like to thank Kristine Johnson and the Vegetation Management personnel at the Great Smoky Mountains National Park for their aid and assistance in collection of data. Special thanks to Glenn Taylor and Michael Kunzi for their eagerness to provide me with selected maps for my thesis and Renee Follum for her assistance with the preparation of graphics for the thesis. I would especially like to thank Dr. Arnold Saxton for his aid with all statistical analyses performed on data used in this thesis. Special thanks to Dr. Calvin Welbourn who was eager and willing to examine and identify mite specimens collected during this project. I would like to thank Rob Klein for his assistance with collection of data for this project. In addition, many thanks to the following people for assisting me in collection of data throughout the project: Tracey Ellis, Jerome Grant, Bryan Hed, Dan Noon, Pete Obenauer, Shawn Servoss, Brent Wiggins, and Mark Windham. I would like to thank my parents, who instilled a love of nature in me early in my life and have always shown a close interest in whatever I have undertaken. Finally, I would like to thank my best friend Tracey Ellis, who assisted me with data collections and aided and supported me throughout this research project and the M.S. program.

ABSTRACT

American beech, *Fagus grandifolia* Ehrhart, is a dominant species in cove hardwood, northern hardwood and hemlock forests. Beech bark disease (BBD), which can cause mortality of American beech, is a complex which includes beech scale, *Cryptococcus fagisuga* Lindinger, and the fungi *Nectria galligena* Bresadola and *N. coccinea* var. *faginata* Lohman, Watson, and Ayers. Beech scale was accidentally introduced into North America from Europe on stocks of European beech, *Fagus sylvatica* Linnaeus, in the 1890s. In 1993, beech scale and *Nectria* spp. were discovered in beech stands in the Great Smoky Mountains National Park (GSMNP). A research project was conducted to: 1) monitor incidence, progression, and impact of beech scale and BBD in the GSMNP (project initiated in spring 1994 by other cooperators), 2) assess the incidence and seasonality of predatory mites in selected plots in the GSMNP, and 3) investigate areas outside of the GSMNP for the presence of beech scale.

Beech scale is currently present in all ten plots evaluated in the GSMNP. At Gregory Bald, the last plot to become infested, percent infestation reached about 25% in spring 1997. The percent of live trees within all plots infested with beech scale increased significantly from 55.6% in spring 1994, to 87.9% in spring 1997. Percent incidence of *Nectria* spp. has fluctuated, peaking at 19.6% in spring 1995 and decreasing to about 10% in spring 1997. The percent mortality of all trees within plots (n=455) has increased significantly from the initial value of 16.0% in spring of 1994 to 26.7% in spring of 1997. Forney Ridge exhibited the highest percent mortality of any single plot, reaching

90.9% of American beech dead in the plot by spring 1997. These data suggest that beech scale can be expected to continue to increase through areas once free from this pest and become increasingly vulnerable to infection by *Nectria* spp. As incidence of infection by *Nectria* spp. increases, beech mortality should also be expected to increase.

A new species of mite, in the genus *Allothrombium*, was observed to feed on scale. Populations of this predatory mite were monitored during the spring and summer of 1996 and 1997. While *Allothrombium* new sp. feeds consistently on beech scale, the presence of beech scale did not significantly effect the presence of mites on beech trees. Factors such as temperature, time of day, and time of year were significant influences on mite presence. The first-instar, of which most species of this genus are parasitic on arthropods, is inactive. The observations during spring and summer of 1997 suggest that the mites overwinter as adults and have one generation each year.

Five areas outside of the GSMNP, four in Tennessee and one in North Carolina, were examined for the presence of beech scale. No beech scale was found outside of the GSMNP in the areas investigated. *Nectria* spp. were found on one tree, but this infection was not suspected to be associated with BBD.

As the infestation of beech scale on beech trees increases, tree mortality is also expected to increase. The high tree mortality at Forney Ridge is an example of the devastation that beech scale and BBD can cause, and may be a prelude to what may happen in other areas of the GSMNP. Although *Allothrombium* sp. has been observed feeding on beech scale, further research needs to be conducted to evaluate its feasibility as a possible biological control agent of beech scale. This predator may help to slow the

dispersal of beech scale and consequently the effects of BBD. While beech scale is presently not found in this area outside the GSMNP, research suggests that it is highly likely for beech scale to eventually spread to these areas. Continued monitoring of beech scale, both within the GSMNP and areas surrounding the GSMNP, is necessary to better understand, and perhaps eventually control, beech scale and BBD.

TABLE OF CONTENTS

CHAPTER	PAGE
I. LITERATURE REVIEW	1
II. INCIDENCE AND DISTRIBUTION OF BEECH SCALE AND BEECH BARK DISEASE IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK	14
Introduction	14
Materials and Methods	16
Results and Discussion	21
Summary	38
III. INCIDENCE OF A PREDATORY MITE OF BEECH SCALE IN SELECTED PLOTS IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK	40
Introduction	40
Materials and Methods	42
Results and Discussion	45
Summary	58
IV. SURVEY FOR BEECH SCALE, <i>CRYPTOCOCCUS FAGISUGA</i> , IN AREAS OUTSIDE OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK	60
Introduction	60
Materials and Methods	61
Results and Discussion	63
Summary	64

V. CONCLUSIONS	66
REFERENCES CITED	71
APPENDIX	76
VITA	88

LIST OF TABLES

TABLE	PAGE
1. Permanent plots established in the Great Smoky Mountains National Park for long-term monitoring of beech scale and beech bark disease.	17
2. Description of rating system used to evaluate the presence of beech scale and <i>Nectria</i> spp. on American beech in the Great Smoky Mountains National Park . . .	19
3. Correlation coefficients and probabilities for <i>Nectria</i> spp. vs. beech scale ratings the previous rating season and beech scale ratings the previous year	29
4. Regression variables that best explained mortality of American beech in the Great Smoky Mountains National Park.	33
5. Correlation coefficients and probabilities of beech scale ratings on the first through the seventh sampling dates vs. elevation, average aspect, and dbh	36
6. Correlation coefficients and probabilities for ratings of <i>Nectria</i> spp. on the first through the seventh sampling dates vs. elevation, average aspect, and dbh . . .	37
7. Dates of sampling for <i>Allothrombium</i> sp. at Sweat Heifer and Indian Gap in the Great Smoky Mountains National Park, 1997.	49
8. Correlation coefficients and probabilities for incidence of <i>Allothrombium</i> sp. vs. the north, south, and overall beech scale ratings for spring 1997 in the Great Smoky Mountains National Park.	56
9. Probabilities of variables that explained 27.48% of the variation of the incidence of <i>Allothrombium</i> sp. at Sweat Heifer and Indian Gap in the Great Smoky Mountains National Park, 1997	57
10. Areas outside the Great Smoky Mountains National Park where American beech were inspected for beech scale, <i>Cryptococcus fagisuga</i>	62

LIST OF FIGURES

FIGURE	PAGE
1. The range of American beech, <i>Fagus grandifolia</i>	2
2. American beech monitoring plots in the Great Smoky Mountains National Park .	18
3. Percent incidence of beech scale on live American beech in all plots over seven rating periods [Bars with the same letters are not significantly different, Duncan's Multiple Range Test (P=0.05)][Data for 1994 and 1995 are from Vance (1995)] . .	22
4. Percent incidence of beech scale on live American beech in each plot from 1994 to 1997 [Plot letters are described in Table 1][Data for 1994 and 1995 are from Vance (1995)]	22
5. Fluctuations of overall ratings of beech scale on American beech in all plots [Bars with the same letters are not significantly different, pairwise contrasts (P=0.05)][Data for 1994 and 1995 are from Vance (1995)]	24
6. Fluctuations in beech scale ratings in each plot from 1994 to 1997 [Plot letters are described in Table 1][Data for 1994 and 1995 are from Vance (1995)]	24
7. Fluctuations in percent incidence of <i>Nectria</i> spp. in all plots [Bars with the same letters are not significantly different, Duncan's Multiple Range Test (P=0.05)][Data for 1994 and 1995 are from Rutherford (1996), and data for 1996 and 1997 are from Klein (1997)]	26
8. Fluctuations of average ratings of <i>Nectria</i> spp. on American beech in each plot from 1994 to 1997 [Plot letters are described in Table 1][Data for 1994 and 1995 are from Rutherford (1996), and data for 1996 and 1997 are from Klein (1997)]	26
9. Percent mortality of American beech in each plot from 1994 to 1997 [Plot letters are described in Table 1][Data for 1994 and 1995 are from Vance (1995)] . .	27
10. Overall mortality of American beech in all plots over seven rating periods [Bars with the same letters are not significantly different, pairwise contrasts (P=0.05)][Data for 1994 and 1995 are from Vance (1995)]	31
11. Percent incidence of <i>Xylococcus betulae</i> on American beech in each selected plot over four years [Plot letters are described in Table 1][Data for 1994 and 1995 are from Vance (1995)]	34

FIGURE	PAGE
12. Enlarged view of nine of the ten American beech monitoring plots in the Great Smoky Mountains National Park, 1996 and 1997	44
13. Percent incidence of <i>Allothrombium</i> sp. on live American beech in spring 1996 [Plot letters are described in Table 1]	47
14. Mean number of <i>Allothrombium</i> sp. on beech at Sweat Heifer and Indian Gap during 1996.	47
15. Mean number of <i>Allothrombium</i> sp. on live American beech on each of thirteen sampling times at Sweat Heifer (A) and Indian Gap (B), 1997 [Bars with the same letters are not significantly different, Duncan's Multiple Range Test ($P=0.05$)] [See Table 7 for actual sampling dates]	50
16. Numbers of adults and immatures of <i>Allothrombium</i> sp. observed throughout sampling dates at Sweat Heifer (A) and Indian Gap (B), 1997.	51
17. Percent of live trees at Sweat Heifer (A) and Indian Gap (B) with <i>Allothrombium</i> sp. present at each sampling date, 1997 [Bars with the same letters are not significantly different, Duncan's Multiple Range Test ($P=0.05$)] [See Table 7 for actual sampling dates]	52
18. Estimated seasonality of life stages of <i>Allothrombium</i> sp. observed in the Great Smoky Mountains National Park, 1996 and 1997	55

CHAPTER I

LITERATURE REVIEW

American beech, *Fagus grandifolia* Ehrhart, is the only native species of beech in forests of eastern North America, where it ranges from Nova Scotia westward to eastern Wisconsin, southward from eastern Texas and Arkansas to northern Florida (Fig. 1) (Carpenter 1974, Hepting 1971). American beech can live as long as 350 to 400 years and can reach heights up to 36 m (Carpenter 1974). Beech, an important ecological component of forests, is found in at least 16 cover types and is a dominant species in cove hardwood, northern hardwood, and hemlock forests (Carpenter 1974, Stupka 1964). Beech is one of the six most shade tolerant tree species in cove hardwood forests in the southern Appalachians and can remain a major component of the canopy by capturing single-tree gaps formed by a fallen tree (Barden 1980).

Three varieties of American beech, white, red, and gray, are known. These are distinguished by the color of their heartwood and their occurrence at different elevations. White beech occurs at the lowest elevations, from sea level to 1060 m, in cove forests and cove forest transitions, being primarily southern in distribution. Red beech occurs between 1060-1700 m in upper cove forests (Russell 1953, Stupka 1964). Gray beech occurs above 1700 m, most often found in areas known as beech gaps. In the Great Smoky Mountains National Park (GSMNP) these beech gaps, or areas predominately composed of beech with boundaries sharply marked from surrounding forest types that

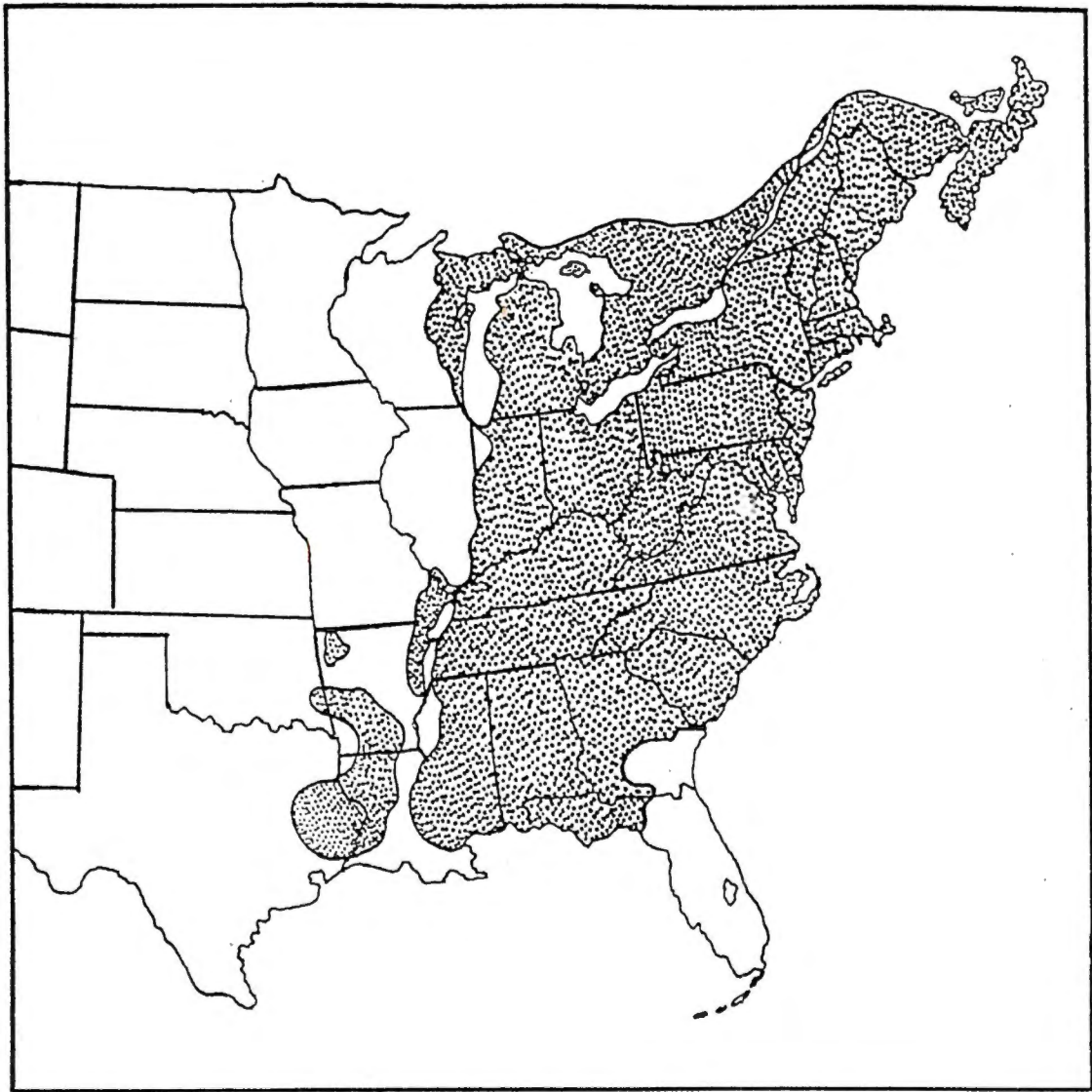


Figure 1. The range of American beech, *Fagus grandifolia*.

usually consist of spruce-fir, *Picea rubens* Sargent-*Abies fraseri* (Pursh) Poirer, or eastern hemlock, *Tsuga canadensis* (Linnaeus) Carriere, occur above 1525 m and can include both red and gray beech (Russell 1953). The production of seedlings via seeds (beechnuts) and root sprouts lends to the high density of beech in beech gaps at higher elevations, especially on south-facing slopes where beech may represent as much as 90% to 98% of the total basal area of a stand (Bratton 1975, Jones and Raynal 1987, Russell 1953). Heavy beechnut production, which can be about 990,000 nuts per hectare in stands with more than 70% beech, occurs roughly one out of every three years in stands greater than 50 years old (Leak and Graber 1993).

Beech is utilized by many animals for both habitat and food. Mixed deciduous-coniferous forests containing beech are distinct habitats for avian assemblages, such as hairy woodpecker, *Picoides villosus* (Linnaeus), brown creeper, *Certhia americana* Bonaparte, and solitary vireo, *Vireo solitarius* (Wilson). Other avian assemblages, such as dark-eyed junco, *Junco hyemalis* (Linnaeus), black-throated blue warbler, *Dendroica caerulescens* (Gmelin), and black-capped chickadee, *Parus atricapillus* (Linnaeus), occur in partially disturbed areas of these mixed deciduous-coniferous forests (Thompson and Capen 1988, Walters 1980). The trunks of beech are microhabitats where insects (such as some homopterans, hymenopterans, lepidopterans, and dipterans) and other arthropods (such as some araneidans and phalangidans) are found and are potential food sources for birds (Peterson et al. 1989). Larvae of the gray-patched prominent, *Dasylophia thyatiroides* Walker, a rare species in Canada, feed primarily, if not exclusively, on beech in the moth's Canadian range (Lindquist 1978). In the northeastern United States

(U.S.) in areas primarily forested with beech, the buds and bark of beech may account for as much as 60% of the winter diet of the Canada porcupine, *Erethizon dorsatum* Linnaeus (Roze 1984). Beechnuts, which are high in crude fat and moderate in crude protein, are a preferred food of ruffed grouse, *Bonasa umbellus* Linnaeus, eastern chipmunk, *Tamias striatus* Linnaeus, wild turkey, *Meleagris gallopavo* Linnaeus, squirrels, *Sciurus* spp., northern bobwhite, *Colinus virginianus* Linnaeus, and black bear, *Ursus americanus* Pallas (Halls 1977). Beechnuts are included in a substantial part of the diet of the black bear in the GSMNP, accounting for about 6% of its fall diet (Beeman and Pelton 1978).

American beech has moderate economic value. Before the 1960s, beech was not regarded as a valuable source of timber, but the timber industry has since developed ways of using beech profitably (Wainhouse and Gate 1988). Lumber production increased from 166 million board feet in 1952 to 252 million board feet in 1965. Beech was formerly not considered a useful source for paper pulp. Presently, although not classified as high-quality pulp, beech is easily converted into paper pulp by most currently used processes. Due to its durability, beech was widely used as factory flooring (Carpenter 1974). Because of its hardness, beech has been increasingly used for items turned with a lathe. Beech is rated high for nearly all wood-machining processes and, accordingly, is used to make such items as furniture, doors, trim, woodenware, and handles (Carpenter 1974, Record and Hess 1943).

Although it is difficult to quantify its value in recreational areas, beech contributes to the natural beauty of national and state parks throughout the eastern U.S.

The local economies of areas surrounding parks are benefitted by the millions of visitors to these areas every year. The Tennessee Department of Tourist Development estimates that about 29.8 million people visited the 51 Tennessee State Parks in 1996 (Anonymous 1997). It is estimated that about 9.26 million people visited the GSMNP in 1996, adding about 772 million dollars to the economies of towns surrounding the park (Gray 1997). The death of large numbers of beech, especially in beech gaps, would detract from the beauty and health of park forests. Currently, in the eastern U.S. and locally in the GSMNP, the threat of large-scale loss of American beech exists in the form of beech bark disease (BBD) (Ehrlich 1934).

Beech bark disease is a disease complex involving the beech scale, *Cryptococcus fagisuga* Lindinger (Homoptera: Cryptococcidae), and two species of fungi, *Nectria galligena* Bresadola and *Nectria coccinea* var. *faginata* Lohman, Watson, and Ayers (Cotter and Blanchard 1981, Ehrlich 1934, Lohman and Watson 1943). Initially, beech scale infests the bark of the tree and inserts its stylet through the corky layer, cork cambium and phelloderm, and into the cortex and phloem, withdrawing protoplasmic fluids. When individuals in a large colony feed in relatively close proximity to each other, clusters of parenchyma cells die and shrink. The shrinking of the dead cells causes fissures in the phellem and underlying tissues. The *Nectria* spp. then infect these wounds, and, once established, the mycelia spread into and around the phellogen, phelloderm, cortex, phloem, and cambium and eventually kill the bark tissues. Light infestations on healthy trees can be resisted by the activation of traumatic secondary meristem, which forms a callus around the infected area blocking its spread (Ehrlich

1934). Heavy infestations of beech scale, in addition to providing entry courts for *Nectria* spp., lower the tree's resistance to infection by other fungal pathogens (Lonsdale 1980). If the spread of the fungal infection is not stopped by the callusing action of the tree, the regions of infection expand and coalesce, enlarging the dead areas of bark and eventually preventing waterflow by girdling the tree. The combination of dead vascular tissues and decreased photosynthetic activity of the diminishing crown eventually causes the death of the tree (Coulson and Witter 1984, Ehrlich 1934).

Beech scale is one of two apterous North American species in the genus *Cryptococcus* (Kosztarab 1996). *C. fagisuga* is parthenogenic and has one generation per year (Kosztarab 1996, Vance 1995). The only mobile stage, the first instars or crawlers, can crawl along the trunk of the tree, settle in cracks and crevices in the bark to begin feeding, or can disperse and infest other trees (Houston and O'Brien 1983, Shigo 1972). The primary method of dispersal of first instars to other trees is passively via wind currents, the average distance of dispersal at windspeeds less than 1 m/s is 10 m. Eggs of beech scale also may be dispersed by wind, but in insignificant numbers (Wainhouse 1980). Dispersal also may take place possibly by animals, such as migratory birds, and even human activities (Houston 1994). Upon settling on the tree, crawlers may begin to feed (Ehrlich 1934, Shigo 1972). Once feeding has begun, beech scales remain stationary for the remainder of their life. Molting occurs after initiation of feeding, and a waxy coat begins to form over the second instar. The second instar overwinters and molts into an adult in the spring (Houston and O'Brien 1983, Shigo 1972). Eggs are oviposited by the adult underneath the waxy coat from June to September in New

England, from May through November in the GSMNP, and require at least 20 days to hatch (Houston 1994, Kosztarab 1996, Vance 1995).

The immobility of the scale once it begins feeding would seem to make it vulnerable to a range of parasites, parasitoids, and predators. In fact, beech scale has relatively few natural enemies. No parasites or parasitoids of beech scale have been found (Houston 1983b, Vance 1995). However, a few minor predators have been observed to feed on various stages of the scale.

In Europe, the larvae and adults of lady beetle (Coleoptera: Coccinellidae) species in the genera *Exochomus* and *Chilocorus* have been observed to feed on scale. The larvae of *Lestodiplosis* sp. (Diptera: Cecidomyiidae), as well as green (Neuroptera: Chrysopidae) and brown (Neuroptera: Hemerobiidae) lacewings, also have been observed to feed on beech scale. All are generalist predators and feed incidentally on scale (Houston 1983b).

In the U.S., several species of mites prey on scale, including *Anystis* sp. nr. *kochi* Oudemans, *Tydeus* sp., *Abrolophus* sp., *Leptus* sp., and a species believed to be in the genus *Trombidium* (Mayer and Allen 1983, Vance 1995). All of these feed on one or more stages of beech scale. *A. sp. nr. kochi* has been observed to feed on all stages (Mayer and Allen 1983). The *Trombidium* sp. observed by Vance (1995) mostly preyed upon the immobile stages of scale.

The predator most commonly associated with beech scale in the U.S. is the twice-stabbed lady beetle, *Chilocorus stigma* (Say) (Houston 1983b, Mayer and Allen 1983, Shigo 1964). *Chilocorus stigma* commonly aggregate to areas where scale populations

are high. Both adults and larvae are predaceous (Mayer and Allen 1983). Although *C. stigma* may somewhat decrease scale populations, they are limited in effectiveness by three factors: 1) adults disperse after eclosion, 2) *C. stigma* do not feed on all life stages of beech scale, and 3) beech scale has a high rate of reproduction (Houston 1983b). *C. stigma* also may be a vector of *Nectria* spp. due to its mode of search (Shigo 1964).

Some fungi may be useful as biological control agents against *C. fagisuga*.

Cladosporium sp. can degrade the wax secreted by the scale and render it vulnerable to desiccation and/or predation. It is suspected that *Verticillium lecanii* (Zimmermann) Viegas also may inhibit scale population growth, although the mode of action is unclear. *Ascodichaena rugosa* Butin, which is a bark epiphyte, has been shown to be negatively associated with beech scale on the bark of beech (Houston 1983b).

The causative agents of BBD, both in the genus *Nectria*, are members of the family Hypocreaceae. *Nectria* spp. are characterized by bright (often red) superficial perithecia, which contain 8-hyaline one-septate ascospores (Cotter and Blanchard 1981). *N. galligena* and *N. coccinea* var. *faginata* both have smooth perithecia that are taller than wide and *Cylindrocarpon* imperfect states, which produce microconidia that can be dispersed in water films and by wind. One characteristic that differentiates *N. galligena* and *N. coccinea* var. *faginata* is the size of the ascospores, which can be dispersed via wind (Cotter and Blanchard 1981, Houston 1994). The ascospores of *N. galligena* range from 10.0 to 13.0 micrometers, while the ascospores of *N. coccinea* var. *faginata* range from about 14.3 to 18.5 micrometers (Cotter and Blanchard 1981, Lohman and Watson 1943). *N. galligena* is a native pathogen that causes perennial cankers on several

hardwood species. *N. galligena* rarely affected American beech until the introduction of the beech scale (Houston 1994). While its origin is not known, *N. coccinea* var. *faginata* is believed to be an imported pathogen that initially infected trees following attack of *C. fagisuga* until *N. galligena* was isolated as the sole pathogen in an outlying BBD outbreak in West Virginia (Houston 1994, Mielke et al. 1982).

Nematogonum ferrugineum (*Gonatorrhodiella highlei* A.L. Smith), which is a biotrophic contact mycoparasite, parasitizes both *Nectria* spp. that attack beech (Houston 1983b, Shigo 1964). It was first associated with beech in North America and also has parasitized *Nectria* spp. on beech in England (Houston 1983b). Growth of *N. ferrugineum* initiates when specialized hyphae, called hook cells, physically contact *Nectria* spp. *N. ferrugineum* has received little attention as a biological control agent of *Nectria* spp. because it seems to have negligible control effects (Shigo 1964). Although production of conidial and perithecial initials are reduced, growth of *Nectria* spp. is not significantly affected by *N. ferrugineum* (Houston 1983b).

The development of BBD in an area can be arbitrarily classified into three stages: 1) the advancing front--areas recently invaded by beech scale, 2) the killing front--areas characterized by high populations of beech scale, severe infections of *Nectria* spp., and tree mortality, and 3) the aftermath zone--areas where heavy mortality has occurred and regrowth of small trees is present (Houston and O'Brien 1983, Shigo 1972). A second scale, *Xylococcus betulae* (Pergande) (Homoptera: Margarodidae), while it does not usually kill beech, can weaken trees by causing wilted and cracked areas on the bark of

young beech, especially in aftermath zones (Houston 1975, Hubbard and Pergande 1899, Kosztarab 1996).

Resistant American beech occur in low numbers (less than 1% of trees in stands studied in Nova Scotia); thus, BBD can cause both major damage and major changes to beech stands that are attacked (Houston 1983a). A massive infestation by beech scale and infection by *Nectria* spp. can result in more than 80% mortality of trees greater than 25.4 cm in diameter. Such high mortality translates into losses of as much as 300 million board feet of once-merchantable timber in the U.S. (Houston 1994). Using a pricing scale from 1984, such a loss would equal about 70.5 million dollars in beech timber (DeBald and Dale 1991).

The composition of forests attacked by BBD is often changed or altered after mortality of beech. In New England, beech tends to increase in proportion to other dominant species in hardwood forests barring major disturbance (Twery and Patterson 1984). In the aftermath of BBD, few beech mature at normal rates, and other tree species, such as eastern hemlock, become the major component of the forest (Gavin and Peart 1993, Twery and Patterson 1984). Also, species such as yellow birch, *Betula alleghaniensis* Britton, may respond poorly to the sudden opening of the canopy due to beech mortality and gradually diminish in numbers (Twery and Patterson 1984).

Beech scale and BBD were first observed on European beech, *Fagus sylvatica* Linnaeus, in Europe in the mid-1800s. Beech scale and probably the fungal pathogen *N. coccinea* var. *faginata* were accidentally imported on stocks of ornamental European beech (Wainhouse and Gate 1988). The first observation of beech scale in North

America was on European beech in Halifax Public Gardens, Halifax, Nova Scotia, around 1890 (Ehrlich 1934, Houston 1994). The beech scale was first observed in stands of American beech near Bedford, Nova Scotia, around 1911 (Houston 1994). By 1931, infestations of beech scale had been found in Massachusetts and Maine (Ehrlich 1934). Fifty years later, BBD had spread as far south as West Virginia, where beech scale and *N. galligena* were first reported in August 1981 within an approximate 28,328 ha area in the Monongahela National Forest (Mielke et al. 1982). *C. fagisuga* was reported in George Washington National Forest in northwestern Virginia in 1983, and by 1984, the infestation had spread to Holden Arboretum in Ohio (Mielke et al. 1985). In 1993, beech scale and BBD were reported in GSMNP, some 644 km from the nearest known infestation in Monongahela National Forest (Houston 1994).

Researchers from the National Park Service and The University of Tennessee at Knoxville began a two-year cooperative project in 1994 to study the effects of BBD on American beech in the GSMNP. The objectives of this research were to: 1) initiate long-term monitoring of incidence and distribution of beech scale, *Nectria* spp., and BBD in selected plots in the GSMNP, 2) monitor the life history and seasonal incidence of beech scale, and 3) monitor occurrence of natural enemies of beech scale (Vance 1995).

After the completion of the first two-year research project, additional research was initiated and conducted to better understand beech scale and BBD in the GSMNP. The objectives of this research were to: 1) continue the long-term monitoring of incidence, distribution, and spread of beech scale and BBD in the GSMNP, 2) further investigate the incidence and seasonality of natural enemies of beech scale, specifically

the red velvet mite, *Trombidium* sp., and 3) investigate areas outside of the GSMNP for presence of beech scale and/or BBD.

Most research conducted on BBD in North America has been conducted in eastern Canada and in the northeastern U.S. By continuing the long-term monitoring of beech scale and BBD in the GSMNP, data from several years may be compiled and used to analyze the effects of BBD in the southeastern U.S. These data may enable future researchers to develop and implement management techniques which can be used in efforts to control the spread of BBD.

Although research has been conducted on natural enemies of beech scale, few predators and no parasitoids have been found, and none of these are considered to be effective enough to be developed as biological control agents of beech scale. The concerns of potential ineffectiveness of *C. stigma* as a predator of beech scale have been listed previously. The predaceous red mite found in the GSMNP may be a more effective predator than *C. stigma* because it has less likelihood of dispersal upon eclosion and it may feed on all stages of beech scale. This study examines its presence and association with beech scale.

Although beech scale and BBD may spread slowly through an area, it has been shown that the disease can appear in an area almost spontaneously. It is important, therefore, to investigate areas outside of the GSMNP to detect the presence of BBD in an area early so that proper management techniques, which may slow its spread or eliminate it from an area, may be implemented. Four Tennessee State Parks and areas of

the Cherokee National Forest were investigated for the presence of beech scale and BBD in this study.

CHAPTER II

INCIDENCE AND DISTRIBUTION OF BEECH SCALE AND BEECH BARK DISEASE IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

I. Introduction

American beech, *Fagus grandifolia* Ehrhart, is an important ecological component of forests in the Great Smoky Mountains National Park (GSMNP) (Carpenter 1974, Russell 1953, Stupka 1964). Beech is a dominant species in cove hardwood, northern hardwood and hemlock forests and is one of the six most shade tolerant tree species in cove hardwood forests (Barden 1980, Stupka 1964). In the GSMNP, beech often occur in gaps, or areas of high numbers of beech in relation to other tree species (Russell 1953). In some beech gaps, beech may account for as much as 90% to 98% of the total basal area of the stand (Bratton 1975). Beech also is an important habitat and source of food for many animals in the forest (Beeman and Pelton 1978, Halls 1977, Peterson et al. 1989, Thompson and Capen 1988).

A disease complex, known as beech bark disease (BBD), currently threatens American beech in the GSMNP (Ehrlich 1934, Houston 1994, Vance 1995). BBD is a disease complex involving beech scale, *Cryptococcus fagisuga* Lindinger, and two species of pathogenic fungi, *Nectria galligena* Bresadola and *Nectria coccinea* var.

faginata Lohman, Watson and Ayers (Ehrlich 1934, Houston 1983a, Lohman and Watson 1943). Beech scale feeds on the vascular fluid of the tree by inserting its stylet through the bark tissue and into the cortex and phloem (Ehrlich 1934). The fungi infect trees weakened by the feeding of beech scale through wounds made in the bark by the scale, eventually killing the bark tissues (Ehrlich 1934, Lonsdale 1980). Large areas of bark tissue mortality on a tree can cause the death of the tree (Ehrlich 1934). BBD can result in mortality higher than 80% in beech stands consisting of trees greater than 25.4 cm in diameter and, accordingly has the potential to drastically impact beech and beech gaps in the GSMNP (Houston 1994).

Long-term monitoring of beech scale and BBD in the GSMNP is essential to understanding the effects of the disease on forests in the southeastern U.S., because much of the research on BBD in the U.S. has been conducted in New England. Long-term monitoring also may provide clues to possibly finding a means of control of one or more of the organisms involved in BBD. A monitoring project was implemented by The University of Tennessee and the National Park Service in the GSMNP in 1994 to investigate the effects of beech scale and BBD on beech in the GSMNP (Vance 1995).

As a continuation of the initial two-year monitoring project, additional research was conducted, beginning in 1996, to further assess the relationship of beech scale and BBD in the GSMNP. The objectives of this research were to: monitor the incidence of beech scale and *Nectria* spp., monitor progression of beech scale through established plots, and monitor impact of beech scale and BBD on American beech in selected plots in the GSMNP.

ii. Materials and Methods

Ten permanent plots were established at various locations in the GSMNP (Table 1 and Fig. 2). Each plot measured 20 m x 20 m after correction for slope, and contained at least 20 trees 3.5 cm diameter at breast height (dbh). Nine of the permanent plots were established in spring and summer of 1994. The one remaining plot was established during previous research involving American beech (Vance 1995). Methods of establishment of plots and initial plot conditions are described in Vance (1995).

For consistency with the previous two-year research project and to ensure meaningful comparisons, methodologies established by Vance (1995) were used to monitor *C. fagisuga* and the effects of BBD on beech. A rating scale was used to evaluate the presence of *C. fagisuga* on the bark surface of beech trees in the plots. The rating scale, in efforts to account for both the level of *C. fagisuga* present and the distribution of *C. fagisuga* on the surface of the bark, was as follows: 0 - no beech scale present, 1 - low level and scattered distribution, 2 - low level and uniform distribution, 3 - moderate level and scattered distribution, 4 - moderate level and uniform distribution, 5 - high level and scattered distribution, and 6 - high level and uniform distribution (Table 2). The area of bark surface that was rated was determined by using a rating square measuring approximately 33 cm x 33 cm centered at 122 cm above the ground. Ratings for beech scale and *Nectria* spp. were taken on both the north and south sides of trees using the rating square and, an overall rating was taken on each tree from ground level to about 2 m up the trunk. The rating scale and the rating square were used to evaluate the presence of both *C. fagisuga* and *Nectria* spp. Ratings were taken at every plot twice

Table 1. Permanent plots established in the Great Smoky Mountains National Park for long-term monitoring of beech scale and beech bark disease.

Plot	Location	n ^a	n ^b	Elevation	Avg. Aspect ^c
A	Gregory Bald	45	44	1420 m (4660 ft)	358
B	Jenkins Knob	54	51	1341 m (4400 ft)	10
C	Forney Ridge	77	10	1670 m (5480 ft)	258.5
D	Trillium Gap	55	47	1451 m (4760 ft)	277
E	Deep Creek	31	31	1378 m (4520 ft)	178
F	Indian Gap	55	53	1596 m (5235 ft)	193
G	Chimney Tops	20	17	1109 m (3638 ft)	315.5
H	Sweat Heifer	34	29	1778 m (5834 ft)	133
I	Fork Ridge	35	31	1451 m (4760 ft)	171
J	Newfound Gap	49	47	1596 m (5240 ft)	187

^a Total number of American beech in plot in spring 1994.

^b Number of live American beech in plot during spring 1996.

^c Average aspect values in degrees.

Table 2. Description of rating system used to evaluate the presence of beech scale and *Nectria* spp. on American beech in the Great Smoky Mountains National Park.

Rating	Description of rating
0	No beech scale or perithecia of <i>Nectria</i> spp. present.
1	Beech scale/perithecia present and sporadic or in clusters less than 50 mm in diameter and individuals within clusters at distances greater than 10 mm apart.
2	Beech scale/perithecia evenly dispersed (no distinct clusters) and individuals at distances greater than 10 mm apart.
3	Beech scale/perithecia in clusters of greater than 50 mm in diameter and individuals within clusters between 5 mm and 10 mm apart.
4	Beech scale/perithecia evenly dispersed (no distinct clusters) and individuals at distances greater than 5 mm but less than 10 mm apart.
5	Beech scale/perithecia in clusters of greater than 50 mm in diameter and individuals within clusters less than 5 mm apart.
6	Beech scale/perithecia evenly dispersed (no distinct clusters) and individuals within clusters at distances less than 5 mm apart.

a year during 1996 and 1997, once in spring/summer and once in fall/winter. All beech scale data used from spring 1994 through spring 1995 were collected by Vance (1995). All data used for *Nectria* spp. from spring 1994 through fall 1995 were collected by Rutherford (1996). *Nectria* spp. data shown from spring 1996 through spring 1997 were collected by Klein (1997).

On each sampling date, trees also were examined for the presence of another scale insect, *Xylococcus betulae* (Pergande) (Homoptera: Margarodidae), which can weaken the tree, possibly making it more susceptible to the effects of BBD (Houston 1975, Vance 1995). *X. betulae* was not rated, but rather, noted as being present or absent on trees. *X. betulae* can be distinguished from *C. fagisuga* by a distinctive, long, waxy filament produced by *X. betulae* (Kosztarab 1996). High numbers of *X. betulae* on trees can give the tree a “hairy” appearance, due to these long waxy filaments.

The mean incidence of beech scale and *Nectria* spp. in plots were evaluated for statistical differences over time using Duncan’s Multiple Range Test ($P = 0.05$). Differences in percent mortality and mean ratings of beech scale and *Nectria* spp. over time were evaluated using pairwise contrasts ($P = 0.05$) (SAS Institute Incorporated 1989). Data also were analyzed to evaluate associations among beech scale and *Nectria* spp. by correlating ratings of *Nectria* spp. with beech scale ratings from both the previous season and year. Other factors, such as elevation, average aspect, and dbh, also were correlated with beech scale and ratings of *Nectria* spp. on each sampling date. Stepwise regression was used to identify variables, such as ratings of beech scale and *Nectria* spp., presence or absence of *X. betulae*, dbh, etc., that could best explain

mortality of American beech. Statistical analyses, including logistic regression, analysis of variance, and correlation, were performed using SAS (SAS Institute Incorporated 1989).

iii. Results and Discussion

For comparative purposes, beech scale data collected by Vance (1995) and data for *Nectria* spp. collected by Rutherford (1996) and Klein (1997) are used in conjunction with recently collected beech scale data throughout the following discussion of BBD in the GSMNP. The overall incidence of beech scale on live beech in all plots has increased significantly from 55.6% in spring 1994 to 87.9% in spring 1997 (Fig. 3). Although overall incidence peaked at 95.9% in spring 1996, Gregory Bald (A) was not rated that season due to difficulties in getting to the plot (Fig. 4). Accounting for the live trees within the plot that were most likely not infested with scale and the plot's low tree mortality, the actual percentage of overall infestation for spring 1996 should be between 80-86%. While still high, this percent incidence is lower than the uncorrected percentage and coincides with the steady increases of incidence that were observed the previous and following seasons. During the current two-year study, incidence of beech scale has maintained levels above 80%.

Beech scale is now present at Gregory Bald (A), Trillium Gap (D), and Deep Creek (E), which were initially free from *C. fagisuga* (Fig. 4). Through spring 1995, scale was absent at Gregory Bald and present at low levels in Trillium Gap (2.17%), while Deep Creek exhibited infestation levels near 26%. By spring 1997 incidence of all

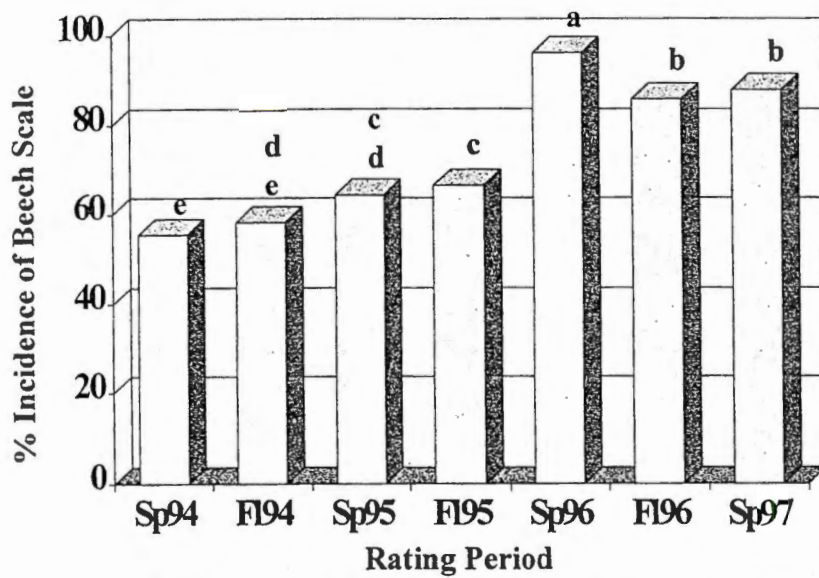


Figure 3. Percent incidence of beech scale on live American beech in all plots over seven rating periods [Bars with the same letters are not significantly different, Duncan's Multiple Range Test ($P=0.05$)] [Data for 1994 and 1995 are from Vance (1995)].

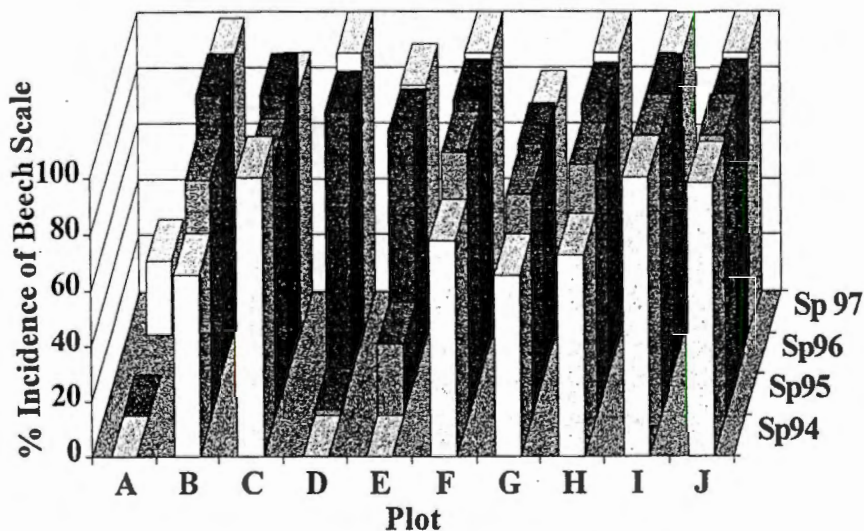


Figure 4. Percent incidence of beech scale on live American beech in each plot from 1994 to 1997 [Plot letters are described in Table 1] [Data for 1994 and 1995 are from Vance (1995)].

three initially scale-free plots had increased substantially, with Gregory Bald reaching 25.5%, Deep Creek reaching 88.5%, and Trillium Gap reaching 100% incidence of beech scale on live trees (Fig. 4). These data illustrate how rapidly beech scale can infest and spread through a beech stand. In general, by spring 1997 all plots, with the exception of Gregory Bald, exhibited at least 78.5% incidence of beech scale on live trees. Infestation of beech trees by beech scale is normally followed by infection by *Nectria* spp., culminating in BBD. It is difficult to predict how long these high levels of incidence of beech scale will be maintained in each plot before trees become infected with *Nectria* spp. and succumb to the effects of BBD.

Gregory Bald (A) was the last plot to become infested with beech scale. Its location, relatively isolated from the other beech plots, heavy vehicle traffic, and lessened hiking traffic, has probably contributed to the delay of beech scale infestation within the plot (Fig. 2). In addition, environmental stress may be lower due to the reduction of the other factors mentioned. Because genetic resistance of trees to beech scale at Gregory Bald is probably not a strong factor related to the plot's low incidence of beech scale, percent incidence of scale and *Nectria* spp. and tree mortality should be expected to increase over time.

Since spring 1996, the average overall rating of beech scale for all plots has increased significantly from 1.28 to 1.71 in spring 1997 (Fig. 5). Compared with the initial ratings, the average overall rating of beech scale for all plots has increased significantly from 1.10 in spring 1994 to 1.71 in spring 1997 (Fig. 5). Beech scale ratings have increased in all plots except Forney Ridge (C) and Fork Ridge (I) (Fig. 6).

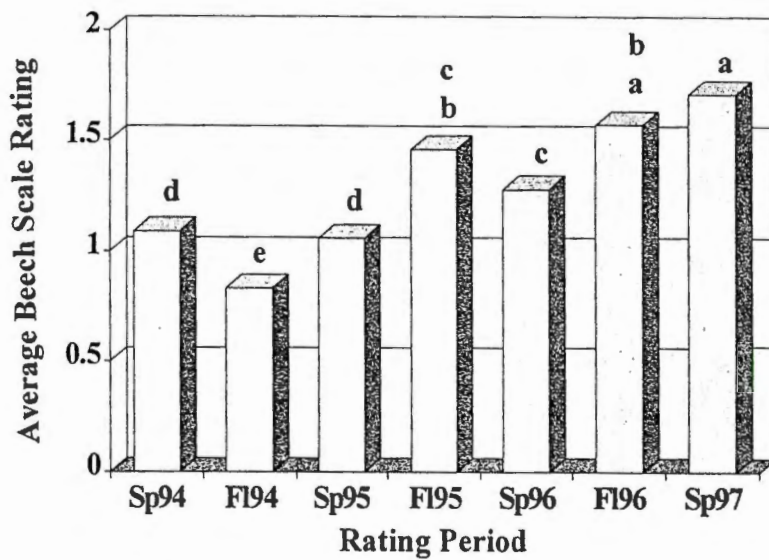


Figure 5. Fluctuations of overall ratings of beech scale on American beech in all plots [Bars with the same letters are not significantly different, pairwise contrasts ($P=0.05$)] [Data for 1994 and 1995 are from Vance (1995)].

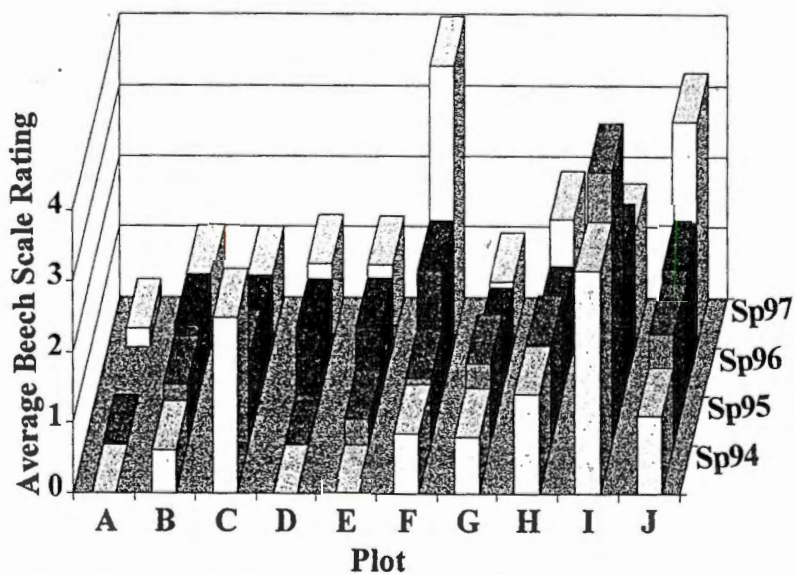


Figure 6. Fluctuations in beech scale ratings in each plot from 1994 to 1997 [Plot letters are described in Table 1] [Data for 1994 and 1995 are from Vance (1995)].

Beech scale ratings have decreased in these three plots. Percent incidence has slightly decreased at Forney Ridge, from 100% in spring 1994 to 85.7% in spring 1997, which could partially explain decreases in the average overall rating (Fig. 4). However, percent incidence has remained at 100% at Fork Ridge since the study began, while the average overall rating has decreased from its peak in spring 1995 of 3.86 to 1.63 in spring 1997. As scale infestation and feeding increase, the tree becomes weaker. As the tree weakens, or becomes infected with *Nectria* spp., it becomes less capable of supporting scale feeding, and consequently scale becomes less able to feed on the tree (Vance 1995). So, while scale can be present on trees in the plot (i.e., 100% incidence), less scales are surviving and feeding on those trees, thereby lessening scale ratings.

Incidence of *Nectria* spp. has fluctuated throughout the study, reaching a high of 19.6% in spring 1995 (Fig. 7). Levels of *Nectria* spp. were not significantly different between spring 1997 and initial levels of *Nectria* spp. in spring 1994 (Fig. 7). The peak season of percent incidence of *Nectria* spp., spring 1995, also was the peak season for the average rating of *Nectria* spp. (1.57) and the season of greatest increase in tree mortality (12.9%) at Forney Ridge (C) (Figs. 8 and 9). The peak in overall percent incidence of *Nectria* spp. in spring 1995 was probably influenced by the peak in ratings of *Nectria* spp. at Forney Ridge that same year, due to the high number ($n = 77$) of American beech at Forney Ridge. When more trees began to die, the inability of *Nectria* spp. to effectively compete with saprophytes, which specialize in the infection and decay of dead, woody tissues, caused both incidence and ratings to decrease at Forney Ridge.

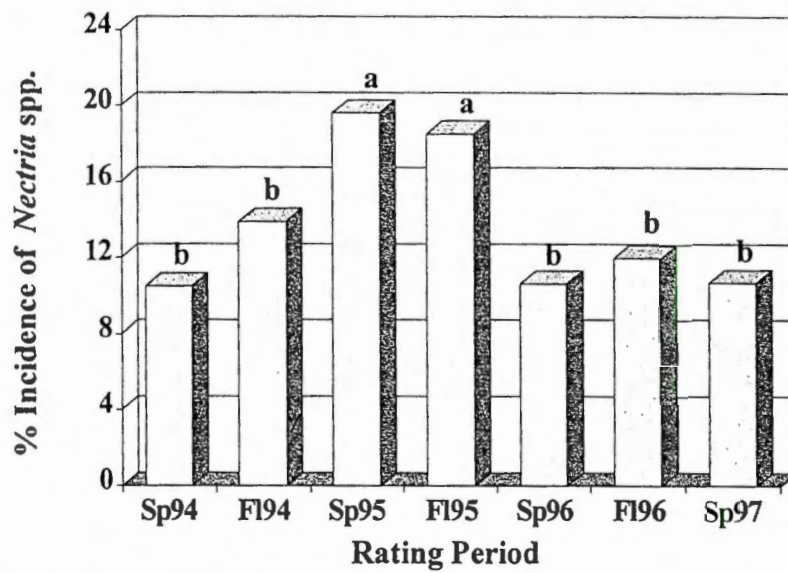


Figure 7. Fluctuations in percent incidence of *Nectria* spp. in all plots [Bars with the same letters are not significantly different, Duncan's Multiple Range Test ($P=0.05$)] [Data for 1994 and 1995 are from Rutherford (1996), and data for 1996 and 1997 are from Klein (1997)].

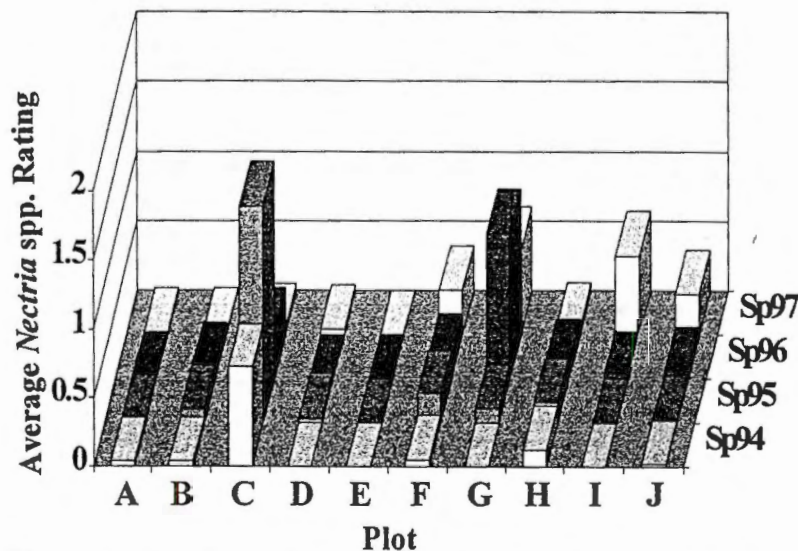


Figure 8. Fluctuations of average ratings of *Nectria* spp. on American beech in each plot from 1994 to 1997 [Plot letters are described in Table 1] [Data for 1994 and 1995 are from Rutherford (1996), and data for 1996 and 1997 are from Klein (1997)].

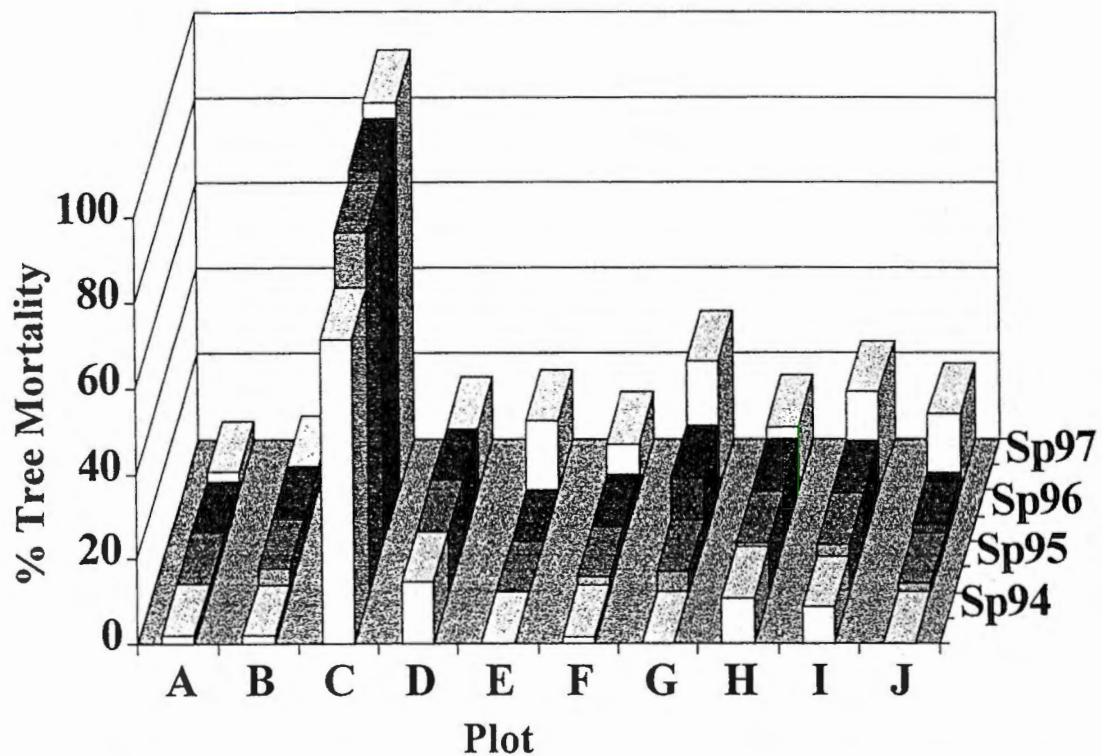


Figure 9. Percent mortality of American beech in each plot from 1994 to 1997 [Plot letters are described in Table 1] [Data for 1994 and 1995 are from Vance (1995)].

This decrease of the incidence and ratings at Forney Ridge seemed to influence fluctuations of overall percent incidence of *Nectria* spp. in all plots the following years.

The average rating of *Nectria* spp. increased to 1.05 at Chimney Tops (G) plot in spring 1996, the second highest average rating observed thus far (Fig. 8). This increase followed the highest average rating of beech scale in that plot, 1.15, in spring 1995 (Fig. 6). The overall rating for beech scale in spring 1995 was weakly but significantly correlated ($P < 0.01$) to the overall rating for *Nectria* spp. in spring 1996, showing some relationship between the two (Table 3). Mortality doubled from 15% in spring 1996 to 30% in spring 1997 (Figs. 9). The increase in mortality at Chimney Tops follows the typical scenario of beech scale infestation, infection by *Nectria* spp., and finally, tree mortality, associated with BBD (Figs. 4, 8, and 9, respectively) (Ehrlich 1934).

Average ratings of *Nectria* spp. remained virtually the same in all other plots, with the exception of Indian Gap (F), Fork Ridge (I), and Newfound Gap (J), which all had peak average ratings, 0.33, 0.57, and 0.29, respectively, in spring 1997 (Fig. 8). While not excessively high, these average ratings do reflect a trend of increasing abundance of *Nectria* spp. relative to the previous years. Trees in these three plots should be particularly vulnerable to BBD in the future. Beech at Newfound Gap are vulnerable due to the increased presence of *Nectria* spp. in the plot in conjunction with the weakened condition of beech as a result of both increasingly higher average beech scale ratings (3.18 in spring 1997) and storm damage that occurred in the winter of 1995. Beech at Indian Gap also are susceptible due to increased incidence (100% in spring 1997) and increased average ratings (3.98 in spring 1997) of beech scale (Figs. 4 and 6).

Table 3. Correlation coefficients and probabilities for *Nectria* spp. vs. beech scale ratings the previous rating season and beech scale ratings the previous year^a.

Correlation Analysis						
Scale Ratings/Time ^b	<i>Nectria</i> North 5		<i>Nectria</i> South 5		<i>Nectria</i> Overall 5	
	Cor. Cof. ^c	Prob. ^d	Cor. Cof.	Prob.	Cor. Cof.	Prob.
Scale North 3	0.0102	0.8471	0.0143	0.7863	0.0502	0.3399
Scale North 4	0.0082	0.9045	-0.0082	0.9046	0.0577	0.3985
Scale South 3	0.0188	0.7208	0.0244	0.6437	0.0779	0.1380
Scale South 4	0.0323	0.6372	0.0036	0.9586	0.0459	0.5023
Scale Overall 3	0.0556	0.2910	0.0745	0.1569	0.1352	0.0099
Scale Overall 4	-0.0299	0.6614	-0.0354	0.6048	-0.0051	0.9412
	<i>Nectria</i> North 6		<i>Nectria</i> South 6		<i>Nectria</i> Overall 6	
Scale North 4	0.1544	0.0232	0.0176	0.7965	0.1652	0.0150
Scale North 5	0.1837	0.0010	0.1274	0.0235	0.1438	0.0105
Scale South 4	0.1121	0.1005	0.0415	0.5444	0.1418	0.0374
Scale South 5	0.0502	0.3729	0.0797	0.1571	0.1148	0.0410
Scale Overall 4	0.0616	0.3677	-0.0135	0.8434	0.0935	0.1711
Scale Overall 5	0.0911	0.1056	0.0778	0.1669	0.1161	0.0388
	<i>Nectria</i> North 7		<i>Nectria</i> South 7		<i>Nectria</i> Overall 7	
Scale North 5	0.1589	0.0048	0.0446	0.4312	0.2576	0.0001
Scale North 6	0.0792	0.1405	0.1165	0.0297	0.1146	0.0325
Scale South 5	0.0632	0.2638	-0.0075	0.8944	0.1848	0.0010
Scale South 6	0.1176	0.0283	0.1541	0.0040	0.1823	0.0006
Scale Overall 5	0.0747	0.1863	-0.00843	0.8816	0.1999	0.0004
Scale Overall 6	0.0729	0.1739	0.1087	0.0424	0.1894	0.0004

^a For complete correlation table see Appendix.

^b Time 3 = spring 1995, time 4 = fall 1995, time 5 = spring 1996, time 6 = fall 1996, and time 7 = spring 1997 [Beech scale ratings for 1994 and 1995 are from Vance (1995), and ratings for *Nectria* spp. are from Rutherford (1996) and Klein (1997)].

^c Correlation coefficient.

^d Probability.

Finally, beech at Fork Ridge, due to the constant, high incidence (100%) of beech scale since spring 1994, also are vulnerable to be effected by BBD in the near future (Fig. 4).

The ultimate result of BBD is mortality of beech. Overall mortality of American beech in all plots has increased significantly from 16.0% in the spring of 1994 to 26.8% in spring of 1997 (Fig. 10). While most mortality occurred in six of the ten plots [Forney Ridge (C), Deep Creek (E), Indian Gap (F), Chimney Tops (G), Fork Ridge (I), and Newfound Gap (J)], mortality remained relatively low (below 20%) in 7 of the 10 plots (Fig. 9). Even though most plots exhibit relatively mild mortality, with the increases in percent incidence and average rating of beech scale in most plots, mortality can be expected to eventually increase in all plots with beech scale. Increased mortality was expected in Fork Ridge (22.9%) and Forney Ridge (90.9%) due to their initial "high" classification of beech scale in the plots at the beginning of the study (Vance 1995). Mortality at Chimney Tops has previously been discussed. Most of the mortality that occurred at the remaining plots, Deep Creek, Indian Gap, and Newfound Gap, which substantially contributed to overall mortality was a result of windsnap which probably occurred during a winter storm. In these plots, some trees may have been weakened by the feeding of beech scale and become more susceptible to storm damage. So, while mortality in these plots probably should not be attributed to BBD, since *Nectria* spp. was present in low numbers (Indian Gap and Newfound Gap) or not present at all (Deep Creek), the feeding of beech scale may have sufficiently weakened trees and increased their vulnerability (Fig. 8).

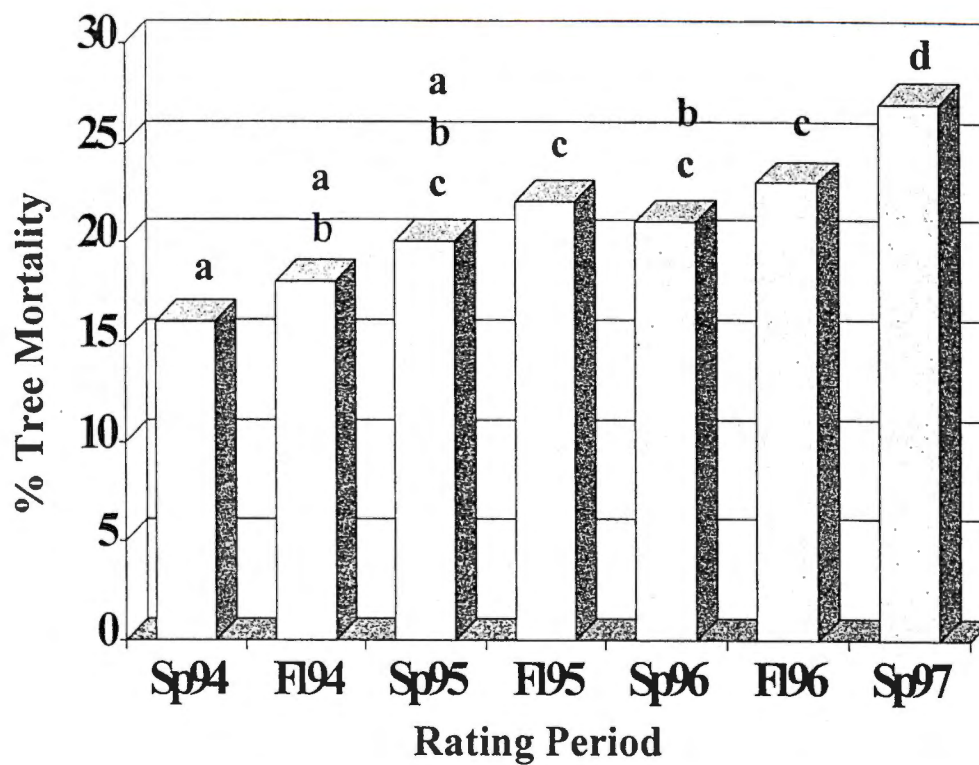


Figure 10. Overall mortality of American beech in all plots over seven rating periods [Bars with the same letters are not significantly different, pairwise contrasts ($P=0.05$)] [Data for 1994 and 1995 are from Vance (1995)].

To test for variables that showed a significant relationship to tree mortality, stepwise regression was used as the variable selection technique within logistic regression on all data collected from spring 1994 to spring 1997. A model was selected that included the following variables for all individual trees: average overall beech scale ratings ($P=0.0001$), the sum of overall beech scale ratings ($P=0.0001$), average overall ratings of *Nectria* spp. ($P=0.0041$), and presence of *X. betulae* ($P=0.0022$). This model explained 67.0% of beech mortality in all plots. Also, predicted probabilities of beech mortality from the model were 94.7% concordant (or 94.7% likely to increase or decrease in a corresponding direction) with the observed data (Table 4).

The strong positive relationship of the average overall beech scale ratings and ratings of *Nectria* spp. is somewhat expected, considering that the effects of BBD on American beech in the northeastern U.S. have been well documented. The sum of overall beech scale ratings reflects the cumulative impact beech scale can have on a tree over time and suggests that as mortality increases the sum of overall beech scale ratings decreases. The strong negative relationship of presence of *X. betulae* to beech mortality would suggest that as tree mortality increases the presence of *X. betulae* decreases. The presence of *X. betulae* is a variable that reflects plot conditions, not individual trees. In short, as trees die in a plot, incidence of *X. betulae* can decrease (Fig. 11). This trend can be seen at Deep Creek (E), Indian Gap (F), Sweat Heifer (H) and Fork Ridge (I) (Figs. 9 and 11). Following increases in mortality in these plots, the incidence of *X. betulae* decreased.

Table 4. Regression variables that best explained mortality of American beech in the Great Smoky Mountains National Park.

Variable added	Slope	Overall max-rescaled R^2	Probability
Average Overall Beech Scale Ratings	15.17	0.6136	0.0001
Sum of Beech Scale Ratings	-2.62	0.6136	0.0001
Average Overall <i>Nectria</i> spp. Rating	1.76	0.6513	0.0041
Presence of <i>Xylococculus betulae</i>	-2.27	0.6781	0.0022

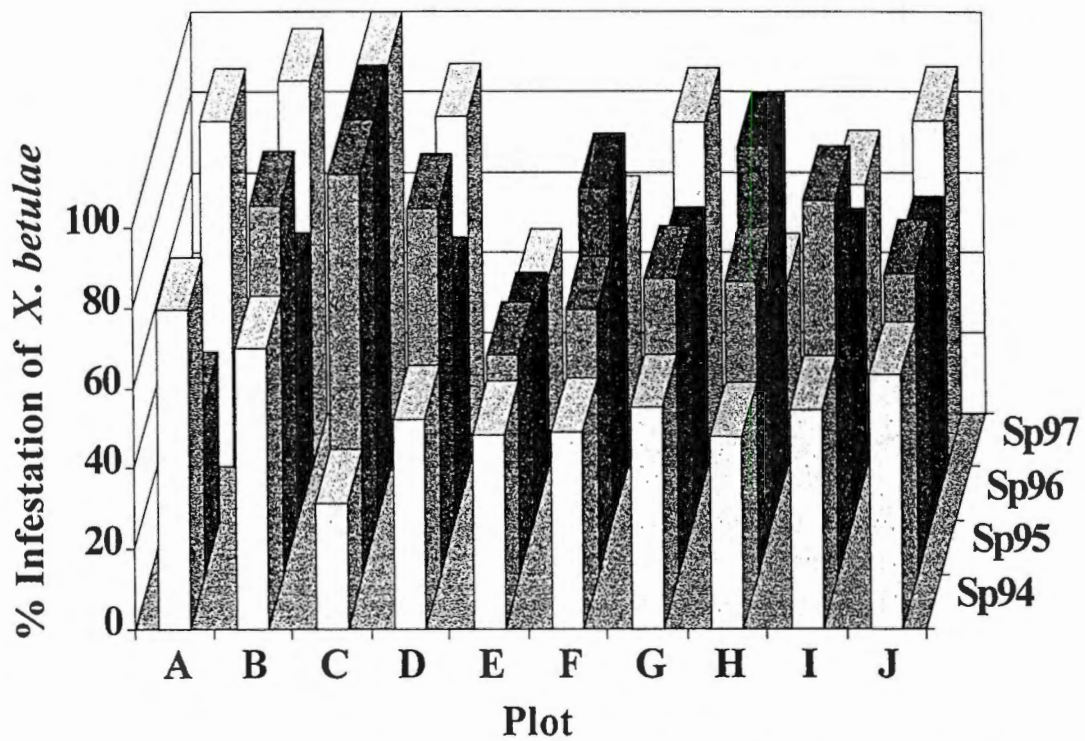


Figure 11. Percent incidence of *Xylococcus betulae* on American beech in each selected plot over four years [Plot letters are described in Table 1][Data for 1994 and 1995 are from Vance (1995)].

Correlation analysis was performed between beech scale ratings and ratings of *Nectria* spp. in all plots at each sampling time with plot elevation, average aspect, and dbh to examine possible associations. Moderate correlations (coefficients between 0.300 and 0.600) for beech scale with elevation on north, south, and overall ratings on the sixth (fall 1996) and seventh (spring 1997) sampling dates were documented (Table 5). These moderate correlations may reflect the increased incidence of beech scale in most plots over time rather than a relationship with elevation. *Nectria* spp. were weakly correlated (coefficients between 0.100 and 0.290) among elevation with north, south, and overall ratings on the first three sampling dates (spring 1994, fall 1994, and spring 1995) (Table 6). Again, decreased incidence of *Nectria* spp. over time may have effected these data (Fig. 7). Similar results were found for both scale and *Nectria* spp. when correlated with average aspect and dbh (Tables 5 and 6). While several significant correlations were found, few coefficients were even moderate in strength (coefficients >0.33). Therefore, while both beech scale and *Nectria* spp. may be effected by these factors, the effect is probably not biologically significant.

Correlation analysis also was performed among all average beech scale ratings and ratings of *Nectria* spp. for all seven sampling times (Appendix). Particular pairs of interest were the last three sampling times for all ratings of *Nectria* spp. with all beech scale ratings from the previous season and year (Table 6). By attempting to correlate these pairs it is possible to examine the relationship between beech scale ratings at a given season and ratings of *Nectria* spp. the next season and the next year. Weak associations (coefficients between 0.100 and 0.290) were found with all pairs that

Table 5. Correlation coefficients and probabilities of beech scale ratings on the first through the seventh sampling dates^a vs. elevation, average aspect, and dbh^b.

Correlation Analysis						
Rating and Time	Elevation		Average Aspect		DBH	
	Cor. Cof. ^c	Prob. ^d	Cor. Cof.	Prob.	Cor. Cof.	Prob.
Scale North 1	0.3134	0.0001	-0.0489	0.3449	-0.0706	0.1726
Scale North 2	0.3015	0.0001	-0.2166	0.0001	-0.06695	0.1975
Scale North 3	0.31299	0.0001	-0.2081	0.0001	-0.1255	0.0167
Scale North 4	0.3368	0.0001	-0.5677	0.0001	-0.0596	0.3842
Scale North 5	0.1970	0.0004	-0.0497	0.3792	-0.0374	0.5085
Scale North 6	0.4041	0.0001	-0.1485	0.0055	0.0433	0.4272
Scale North 7	0.4132	0.0001	-0.1374	0.0130	0.0148	0.7900
Scale South 1	0.1556	0.0025	-0.1112	0.0314	0.0234	0.6523
Scale South 2	0.1788	0.0005	-0.1706	0.0010	0.0584	0.2613
Scale South 3	0.1522	0.0037	-0.1507	0.0040	0.0482	0.3602
Scale South 4	0.1523	0.0256	-0.5337	0.0001	0.11397	0.0956
Scale South 5	0.0626	0.2674	-0.1936	0.0005	0.1833	0.0011
Scale South 6	0.3547	0.0001	-0.2295	0.0001	0.1952	0.0002
Scale South 7	0.3968	0.0001	-0.1734	0.0017	0.2073	0.0002
Scale Overall 1	0.2538	0.0001	-0.1537	0.0028	0.0663	0.2001
Scale Overall 2	0.1831	0.0004	-0.2264	0.0001	0.1321	0.0108
Scale Overall 3	0.1513	0.0039	-0.2536	0.0001	0.1127	0.0318
Scale Overall 4	0.2397	0.0006	-0.5967	0.0001	0.1218	0.0748
Scale Overall 5	0.2152	0.0001	0.0128	0.8214	0.0708	0.2097
Scale Overall 6	0.3787	0.0001	-0.1633	0.0022	0.1364	0.0106
Scale Overall 7	0.4297	0.0001	-0.1150	0.0368	0.1593	0.0037

^a Time 1 = spring 1994, time 2 = fall 1994, time 3 = spring 1995, time 4 = fall 1995, time 5 = spring 1996, time 6 = fall 1996, and time 7 = spring 1997 [Ratings for 1994 and 1995 are from Vance (1995)].

^b Diameter at breast height.

^c Correlation coefficient.

^d Probability.

Table 6. Correlation coefficients and probabilities for ratings of *Nectria* spp. on the first through the seventh sampling dates^a vs. elevation, average aspect, and dbh^b.

Correlation Analysis						
Rating and Time	Elevation		Average Aspect		DBH	
	Cor. Cof. ^c	Prob. ^d	Cor. Cof.	Prob.	Cor. Cof.	Prob.
<i>Nectria</i> North 1	0.2479	0.0001	0.1252	0.0079	-0.1475	0.0017
<i>Nectria</i> North 2	0.2413	0.0001	0.0967	0.0392	-0.1429	0.0022
<i>Nectria</i> North 3	0.3202	0.0001	0.1532	0.0010	-0.1732	0.0002
<i>Nectria</i> North 4	0.1710	0.0013	0.0787	0.1407	-0.0321	0.5483
<i>Nectria</i> North 5	0.0104	0.8254	0.0730	0.1211	0.0273	0.5628
<i>Nectria</i> North 6	0.0446	0.3437	0.0223	0.6368	0.0522	0.2678
<i>Nectria</i> North 7	-0.0358	0.4483	0.0232	0.6240	0.1020	0.0305
<i>Nectria</i> South 1	0.2365	0.0001	0.0997	0.0348	-0.1281	0.0066
<i>Nectria</i> South 2	0.2404	0.0001	0.09194	0.0500	-0.1262	0.0070
<i>Nectria</i> South 3	0.2802	0.0001	0.1322	0.0047	-0.1561	0.0008
<i>Nectria</i> South 4	0.1023	0.0552	0.0639	0.2315	-0.0522	0.3287
<i>Nectria</i> South 5	-0.1441	0.0021	0.0683	0.1473	0.0505	0.2840
<i>Nectria</i> South 6	-0.0907	0.0539	0.0459	0.3302	0.1463	0.0018
<i>Nectria</i> South 7	-0.0346	0.4637	0.0174	0.7133	0.0927	0.0493
<i>Nectria</i> Overall 1	0.2716	0.0001	0.1108	0.0189	-0.1599	0.0007
<i>Nectria</i> Overall 2	0.2627	0.0001	0.11398	0.0150	-0.1125	0.0163
<i>Nectria</i> Overall 3	0.3352	0.0001	0.1456	0.0018	-0.1857	0.0001
<i>Nectria</i> Overall 4	0.1985	0.0002	0.0408	0.4451	-0.0820	0.1245
<i>Nectria</i> Overall 5	-0.0764	0.1050	0.0933	0.0475	0.0505	0.2840
<i>Nectria</i> Overall 6	-0.0135	0.7752	0.0145	0.7590	0.1206	0.0103
<i>Nectria</i> Overall 7	-0.0568	0.2292	0.0108	0.8186	0.2022	0.0001

^a Time 1 = spring 1994, time 2 = fall 1994, time 3 = spring 1995, time 4 = fall 1995, time 5 = spring 1996, time 6 = fall 1996, and time 7 = spring 1997 [Ratings of *Nectria* spp. are from Rutherford (1996) and Klein (1997)].

^b Diameter at breast height.

^c Correlation coefficient.

^d Probability.

exhibited significance. All but two of the significant pairs occurred when the overall ratings of *Nectria* spp. were paired with scale ratings. Beech scale ratings from both the previous season and the previous year showed significant associations with most overall ratings of *Nectria* spp. from fall 1996 and spring 1997 (Table 3). These weak associations could be due to environmental factors exerting unknown pressures on the variables or the subjectiveness of the rating system used to evaluate scale and *Nectria* spp., which qualifies the presence of beech scale and *Nectria* spp. on the bark rather than quantifying it.

iv. Summary

Overall incidence of beech scale in all plots has increased from 55.6% to 87.9% in only four years. Incidence has increased to 100% at Trillium Gap (D), Indian Gap (F), Sweat Heifer (H), Fork Ridge (I), and Newfound Gap (J) since spring 1996. The average overall rating of beech scale has increased significantly, from 1.10 in spring 1994 to 1.81 in spring 1997. Ratings of *Nectria* spp. have peaked at Forney Ridge (C) and Chimney Tops (G). Mortality at Forney Ridge has reached 90.9%, while mortality at Chimney Tops has reached 30.0%. Overall mortality of beech in all plots has increased significantly from 16.0% in spring 1994 to 26.8% in spring 1997. In all plots mortality can be expected to increase, following increased scale incidence and presence of *Nectria* spp.

Currently, methods to slow or stop the spread of scale and/or *Nectria* spp. are limited to removal of trees affected by BBD. However, removal of infected trees is not a

control option in the GSMNP. The most desirable option for controlling the spread of beech scale, and consequently BBD, would be to find an indigenous organism that hinders or kills beech scale in some way and develop a means in which it could be used as a biological control agent against beech scale. Preliminary monitoring for potential biological control organisms has been conducted in the GSMNP and has revealed a potential arthropod predator of beech scale (Vance 1995). Further research conducted on this predator will be discussed in Chapter III.

CHAPTER III

INCIDENCE OF A PREDATORY MITE OF BEECH SCALE IN SELECTED PLOTS IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

I. Introduction

The beech scale, *Cryptococcus fagisuga* Lindinger, is an insect that is a major component of a disease complex, known as beech bark disease (BBD), which impacts American beech, *Fagus grandifolia* Ehrhart (Ehrlich 1934, Houston and O'Brien 1983). The bark of beech is damaged when the scale initiates feeding by inserting its stylet through the outer bark into the vascular tissue of the tree (Ehrlich 1934). Wounds caused by feeding of the scale weaken the tree and provide entry ways for two pathogenic fungi, *Nectria galligena* Bresadola and *Nectria coccinea* var. *faginata* Lohman, Watson and Ayers, to infect the tree (Ehrlich 1934, Lonsdale 1980). The spread of the mycelia of *Nectria* spp. through the bark tissues can eventually result in the death of the tree (Ehrlich 1934). Large outbreaks of BBD can result in more than 80% mortality of beech in a stand (Houston 1994). Because *C. fagisuga* has such a vital role in the development of BBD, effective biological control of beech scale could possibly slow the spread of BBD considerably, provided a proper control organism was discovered.

Presently, few natural arthropod enemies of beech scale are known. While no parasitoids of beech scale have been found, few minor predators have been observed to prey on beech scale (Houston 1983b, Vance 1995).

The twice-stabbed lady beetle, *Chilocorus stigma* (Say) (Coleoptera: Coccinellidae), was one of the first predators associated with beech scale by Ehrlich (1934), who identified it as *C. bivulnerus* Muls. (Mayer and Allen 1983). All instars of *C. stigma* have been observed to feed on the eggs, second instar, and adults of beech scale. Unfortunately, adults of *C. stigma* also can vector *Nectria* spp. from tree to tree in their search for prey (Mayer and Allen 1983, Shigo 1964). Another species of coccinellid, *Calvia quatuordecimguttata* var. *similis* Randall, which closely resembles *C. stigma*, has been reported to feed on beech scale in New York and Pennsylvania but has not been observed often (Mayer and Allen 1983). The voracity of coccinellid larvae is offset by the frequent dispersal of newly-emerged adults which can limit the value of *C. stigma* as a biological control organism (Houston 1983b).

Several mite species, in such genera as *Anystis*, *Tydeus*, *Abrolophus*, and *Leptus*, have been observed to feed on beech scale in the New England area (Mayer and Allen 1983). Mites in the genus *Anystis* were observed feeding on all stages of beech scale, especially the eggs and crawlers. As with lady beetles and other predators, these species of mites appear to be generalists and, at natural population levels, may not consistently feed on beech scale (Mayer and Allen 1983).

In 1994, a research project was begun to study, in part, the parasitoids and predators of beech scale that may occur in the Great Smoky Mountains National Park

(GSMNP). While no parasitoids were found, a predaceous red mite, believed to be *Trombidium* sp. (Acari: Trombidiidae), was often observed to feed mostly on the immobile stages of beech scale. During the spring of 1995 the mites were found on about 18.8% of beech trees monitored (n=452) (Vance 1995). Although both the twice-stabbed lady beetle and the *Trombidium* mite are generalist predators, the mite may be more advantageous to attempt to evaluate as a biological control organism because it is apterous and does not have the potential to disperse like lady beetles. By staying on the tree for longer periods of time, it is more likely that the *Trombidium* mite will feed on beech scale because it has increased contact with the scale life stages. Also, because the mite is less likely to disperse to other trees, it is less likely to vector fungal pathogens, such as *Nectria* spp.

Previous research identified the *Trombidium* mite as a predator of beech scale in the GSMNP (Vance 1995). However, little research has been conducted on environmental factors, such as temperature, time of day, time of year, etc., that may contribute to numbers of mites on trees. Also, little is known of the life cycle and behavior of this mite. Thus, a two-year research study was conducted in 1996 and 1997 to further evaluate the incidence, seasonality, and biology of this *Trombidium* mite and to evaluate possible environmental influences on *Trombidium* predation on beech scale.

ii. Materials and Methods

During spring 1996, each tree in each of the ten plots (previously discussed in Chapter II) was examined for mites when scale ratings were taken. The presence or

absence of mites on each tree was recorded. Mites were monitored in four selected plots, Deep Creek (E), Indian Gap (F), Chimney Tops (G), and Sweat Heifer (H), during the summer (Figs. 2 and 12). These plots were selected because mites were observed consistently at these locations when ratings of beech scale and *Nectria* spp. were taken (Vance 1995). Mites were counted on the surface of the bark of each beech tree in the plot from ground level to about 2 m up the tree. Three to five observations were made at each selected plot throughout summer 1996.

In spring 1997, more detailed observations were conducted to try to determine what factors may influence incidence of mites on individual trees within selected plots. Monitoring of mites was conducted at Indian Gap (F) and Sweat Heifer (H) during 1997 due to the absence of mites from Deep Creek (E) and Chimney Tops (G) the previous year. Plots were visited approximately every two weeks. Each live beech tree >3.5 cm diameter at breast height (dbh) within selected plots was monitored, noting such variables as the number of mites present, moss density on bark surface, time of day, the sampling date (time of year), and temperature. The ratings for beech scale and *Nectria* spp. for that season also were recorded for each tree. Temperatures for each sampling date were obtained from the Newfound Gap weather station by contacting the GSMNP Public Relations Office (Anonymous 1997). The life stage of each mite observed was distinguished by size and noted as adult or immature.

Analysis of the mite data was performed using SAS. A general linear model was used to test for significance of sample variables on mite incidence, and correlation analysis was performed to test for associations among mite and beech scale data.

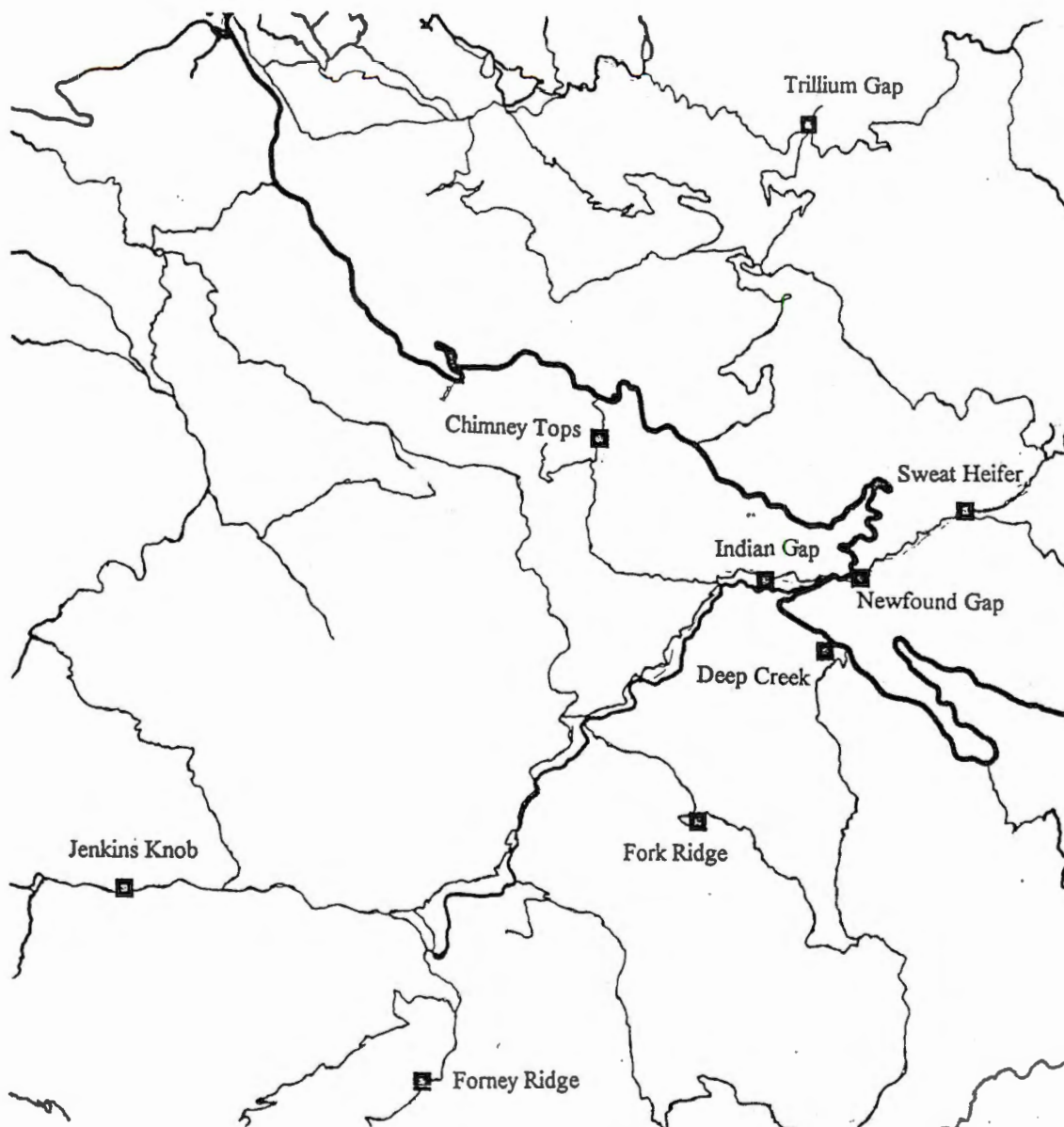


Figure 12. Enlarged view of nine of the ten American beech monitoring plots in the Great Smoky Mountains National Park, 1996 and 1997.

Duncan's Multiple Range test was used to test significant differences among the mean number of mites within sampling dates (SAS Institute Incorporated 1989).

First-instar larvae of the mites are necessary to obtain the most accurate species identification (Welbourn, personal communication). To obtain the appropriate life stage, adults were collected from the field and reared in the laboratory. On June 2, 1997, seven adult mites were collected from the vicinity of both Sweat Heifer and Indian Gap. Each adult mite was placed in a 2.5 dram glass vial with a moistened 2 cm² section of paper towel placed at the bottom of the vial to prevent desiccation. Vials were observed daily for presence of egg masses. Upon observation of an egg mass, the adult mite was removed and preserved in 70% denatured ethyl alcohol for comparison with larvae. All egg masses (n=7) were observed daily for changes in shape and structure. Several (ca. 25) first-instar larvae from three egg masses and corresponding adults were sent for identification to Dr. W. Calvin Welbourn at the Florida Department of Agriculture, Division of Plant Industry, Gainesville, Florida.

iii. Results and Discussion

Previous research dealing with predators of beech scale in the GSMNP tentatively identified the red mite predaceous on beech scale as *Trombidium* sp. (Vance 1995). However, no mites collected during 1997 were identified in this genus. All of the first-instar larvae submitted for identification and examined were identified as *Allothrombium* new species (Acari: Trombidiidae) (Welbourn, personal communication). A similar species in the same genus, *Allothrombium mitchelli* Davis, was described in 1961 as a

predator of balsam wooly adelgid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), on Mt. Mitchell, North Carolina (Davis 1961). A somewhat unique feature of the new species of *Allothrombium* is that the first-instar larva is quiescent. Eggs are laid in the soil by adults, and the only mobile immature stage is the deutonymph (Welbourn, personal communication). Also, from the data collected during 1997, it appears that the new species of *Allothrombium* has one generation per year and may overwinter as adults or eggs or both. These data will be discussed later in this section.

Percent incidence of mites on live beech in all plots during spring and summer of 1996 ranged from 0% at Gregory Bald (A), Trillium Gap (D), and Deep Creek (E) to 85% at Sweat Heifer (H) (Figs. 2 and 13). Mites were found in seven of the ten plots monitored (Fig. 13). All plots were monitored once to obtain a general idea of the occurrence of the mites throughout the study area, and, with only one observation, much variation was expected. The purpose of selecting four plots to monitor *Allothrombium* sp. throughout spring and summer of 1996 was to increase the number of specific observations on the mites.

During 1996, the observed mean number of mites per tree at Sweat Heifer varied from 0.20 in June to 3.73 in September, and between 0.06 in June to 2.32 in August at Indian Gap (Fig. 14). No mites were found on any trees in Deep Creek throughout the season, and only one mite was found on a single sampling date at Chimney Tops (Fig. 12). Densities of mites at Sweat Heifer and Indian Gap varied widely among trees and on the same tree, with the highest density on single trees at Sweat Heifer reaching 45 on September 1, and at Indian Gap reaching 22 on August 20.

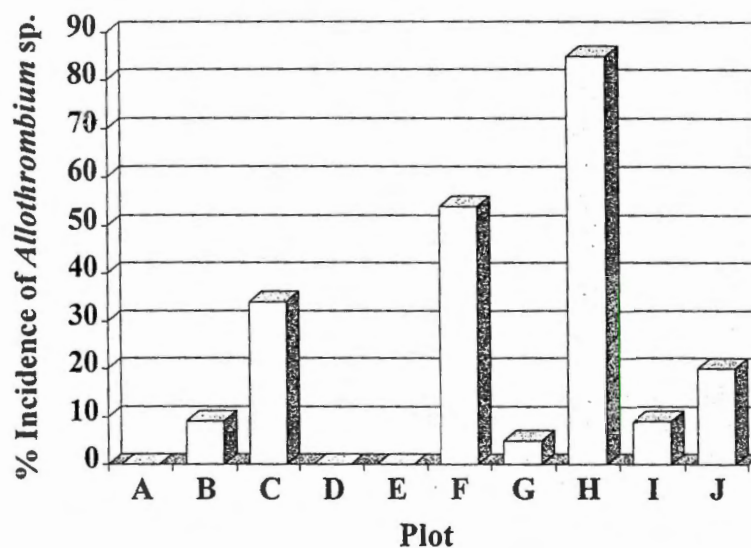


Figure 13. Percent incidence of *Allothrombium* sp. on live American beech in spring 1996 [Plot letters are described in Table 1].

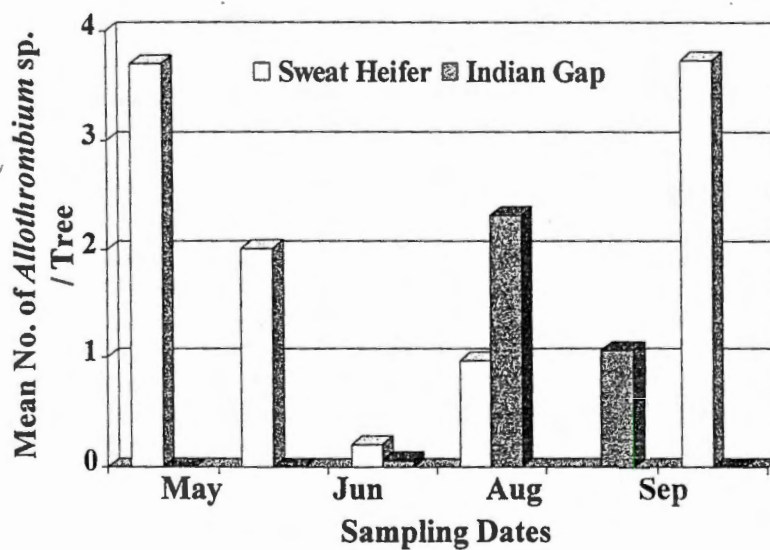


Figure 14. Mean number of *Allothrombium* sp. on beech at Sweat Heifer and Indian Gap during 1996.

However, only five samples at Sweat Heifer, four samples at Chimney Tops, and three samples at both Deep Creek and Indian Gap were taken during spring and summer 1996. More samples were needed to more accurately assess mite occurrence and factors which may effect mite incidence.

During the spring and summer of 1997, Sweat Heifer and Indian Gap were sampled thirteen times, from March 24 to September 12 (Table 7). The mean number of mites per tree on each sampling date ranged from 0 on July 9 (sample 6) to 2.79 on August 28 (sample 11) at Sweat Heifer and from 0.02 on April 8, May 23, and July 11 (samples 1, 3, and 7, respectively) to 1.02 on July 25 (sample 9) at Indian Gap (Figs. 15a and b). The mean numbers of mites on trees at Sweat Heifer from August 8 (sample 9) to September 5 (sample 12) were significantly different ($P<0.05$) from the means observed on other sampling dates (Fig. 15a). The high numbers of deutonymphs observed during August ($n=216$) and September ($n=65$) show that *Allothrombium* sp. are most active during late summer (Fig. 16a). The mean number of mites per tree at Indian Gap on July 25 (sample 9) was significantly different ($P<0.05$) from all other sampling dates (Fig. 15b). Again, high total numbers of adult and immature mites observed during July ($n=63$) reflect the time of year the mites are most active (Fig. 16b).

Percent incidence of mites on trees for each respective plot followed a trend extremely similar to the mean number of mites. Percent incidence at Sweat Heifer was greatest on August 28 (sample 11) at 78.6% and at Indian Gap on July 25 (sample 9) at 34.7% (Figs. 17a and b). The similarity in trends between mite incidence and mean number of mites per tree for both Sweat Heifer and Indian Gap may show that large

Table 7. Dates of sampling for *Allothrombium* sp. at Sweat Heifer and Indian Gap in the Great Smoky Mountains National Park, 1997.

Sample number	Sampling dates for Sweat Heifer	Sampling dates for Indian Gap
1	March 24	April 8
2	April 8	May 16
3	June 2	May 23
4	June 10	June 2
5	June 20	June 10
6	July 9	June 20
7	July 18	July 11
8	July 25	July 18
9	August 8	July 25
10	August 15	August 8
11	August 28	August 15
12	September 5	September 5
13	September 12	September 12

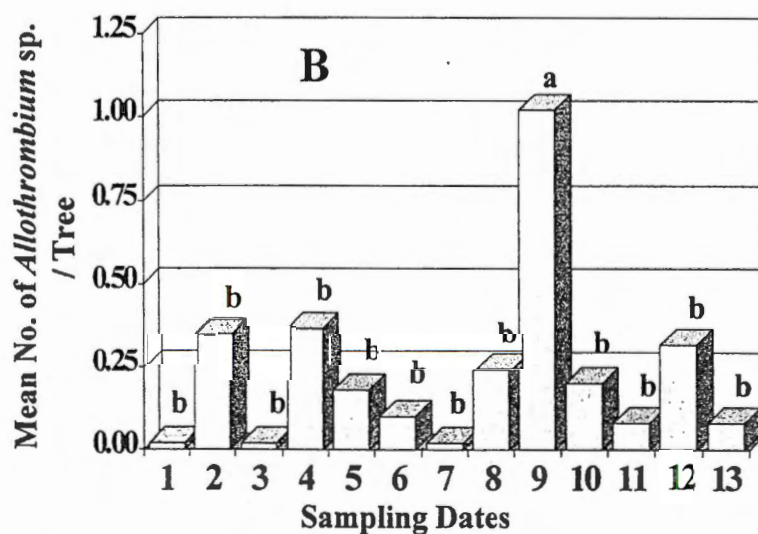
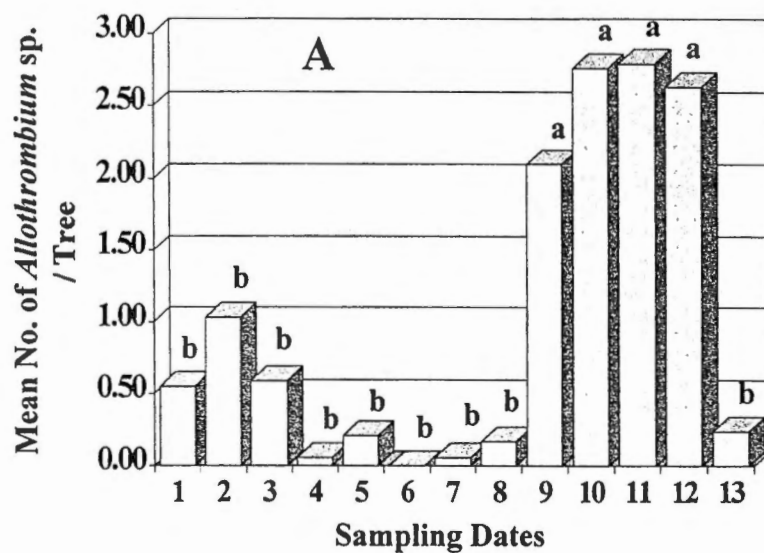


Figure 15. Mean number of *Allothrombium* sp. on live American beech on each of thirteen sampling times at Sweat Heifer (A) and Indian Gap (B), 1997 [Bars with the same letters are not significantly different, Duncan's Multiple Range Test ($P=0.05$)][See Table 7 for actual sampling dates].

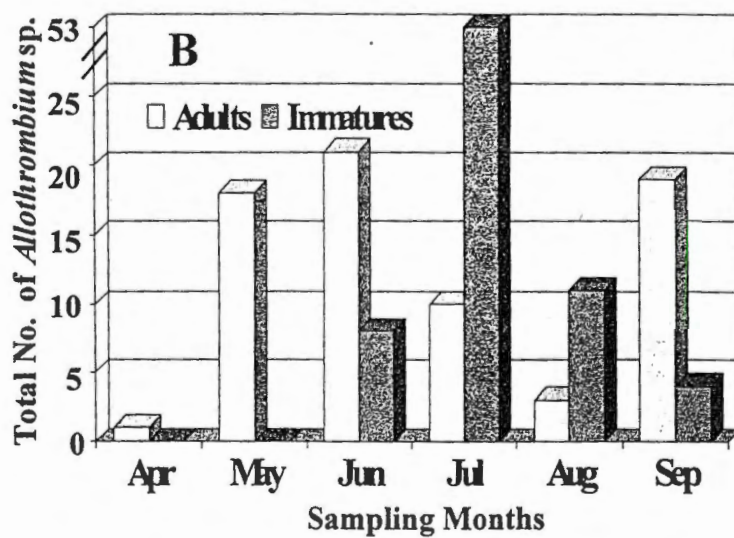
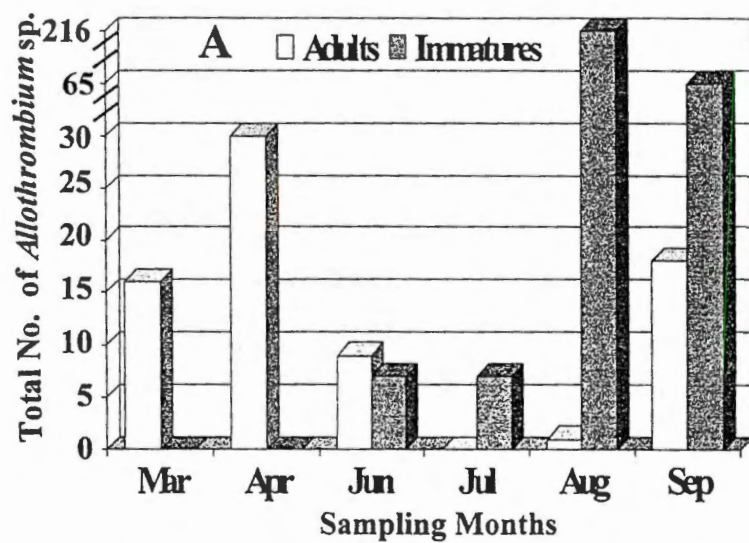


Figure 16. Numbers of adults and immatures of *Allothrombium* sp. observed throughout sampling dates at Sweat Heifer (A) and Indian Gap (B), 1997.

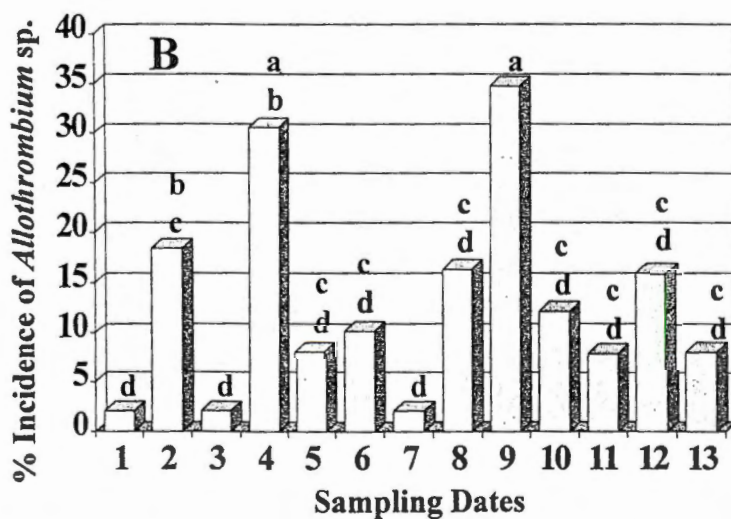
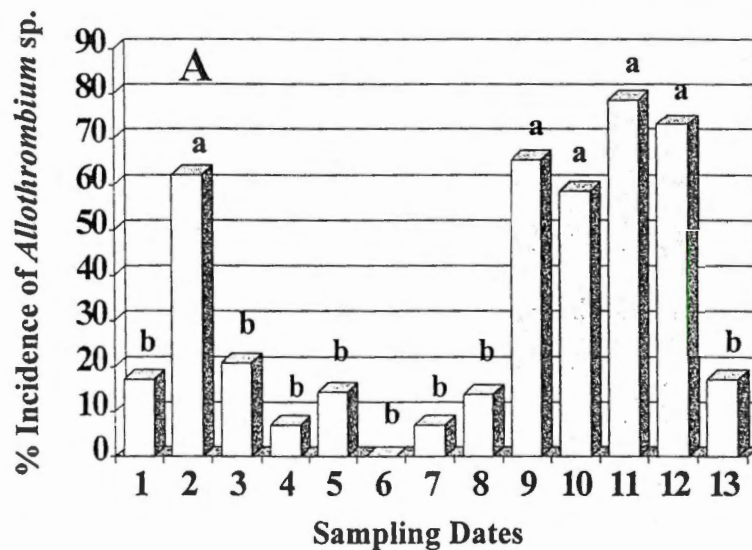


Figure 17. Percent of live trees at Sweat Heifer (A) and Indian Gap (B) with *Allothrombium* sp. present at each sampling date, 1997 [Bars with the same letters are not significantly different, Duncan's Multiple Range Test ($P=0.05$)] [See Table 7 for actual sampling dates].

numbers of mites are observed on individual trees rather than being more evenly distributed on trees throughout the plots (Figs.15a, b, 17a, and b) . Both the mean number of mites per tree and percent incidence of *Allothrombium* sp. on live trees were lower at Indian Gap than at Sweat Heifer except on sample numbers 4, 6, and 8 (Figs.15a, b, 17a, and b, and Table 7). Some storm damage occurred at Indian Gap during the winter of 1996 and may partially account for the lower numbers of mites observed at Indian Gap. Also, the canopy at Sweat Heifer is more dense than at Indian Gap. The area below the canopy at Sweat Heifer should be more sheltered, and, perhaps, the mites prefer a more sheltered environment.

During observations, adult *Allothrombium* sp. were distinguished from third-instar nymphs, or deutonymphs, by size, adults ranging from approximately 3-4 mm in length and deutonymphs ranging from about 1-2 mm in length. All mobile stages of *Allothrombium* sp. were observed feeding on beech scale. Adult *Allothrombium* sp. were observed at Sweat Heifer early in the year from March 24 to June 20 and again later in the summer from August 8 to September 12 (Fig.16a). Adults were observed from April 8 through September 12 at Indian Gap (Fig.16b). Deutonymphs were first observed on trees at both locations in June and were found through September 12 (Figs.16a and b). It appears that adults overwinter, because they were observed in early spring and late fall of the same year but rarely observed during summer months. It is not probable that *Allothrombium* sp. overwinters as eggs, because most species in the family Trombidiidae do not exhibit this behavior (Welbourn, personal communication). Also, the author has

made casual observations of adults of possibly the same species on beech along the Appalachian Trail in winter months.

Based on data collected during 1996 and 1997, the seasonality of life stages of *Allothrombium* sp. was estimated (Fig. 18). Adults may lay eggs from late April through mid August. Egg masses observed in the laboratory required from 20-22 days to hatch. Thus, eggs in the field may hatch from late May through mid August. Deutonymphs were not observed earlier than June possibly because the first-instar larvae are quiescent, and therefore, a lag time exists between hatching and mobility of the deutonymphs (Fig. 18) (Welbourn, personal communication).

Adults and deutonymphs of *Allothrombium* sp. have been observed to feed on beech scale numerous times in the GSMNP. Correlation analysis was performed to test for a relationship between scale presence on beech and mite incidence. Significant correlations between north and overall scale ratings ($P=0.0001$) and mite incidence were documented (Table 8). Most mites were found on trees with overall scale ratings less than 3, a moderate and scattered distribution of scale on the bark surface. As average beech scale ratings increased above 3, fewer mites were observed on these trees. However, the impact of beech scale on mite incidence was not statistically significant when beech scale ratings were entered into a general linear model which also contained environmental variables (Table 9). While the density of moss on the surface of the bark had no significant effect on the number of mites present, increased temperatures had a significant influence on numbers of *Allothrombium* sp. on trees. Time of day also had a significant influence on mite numbers, the peak time for mite activity falling between

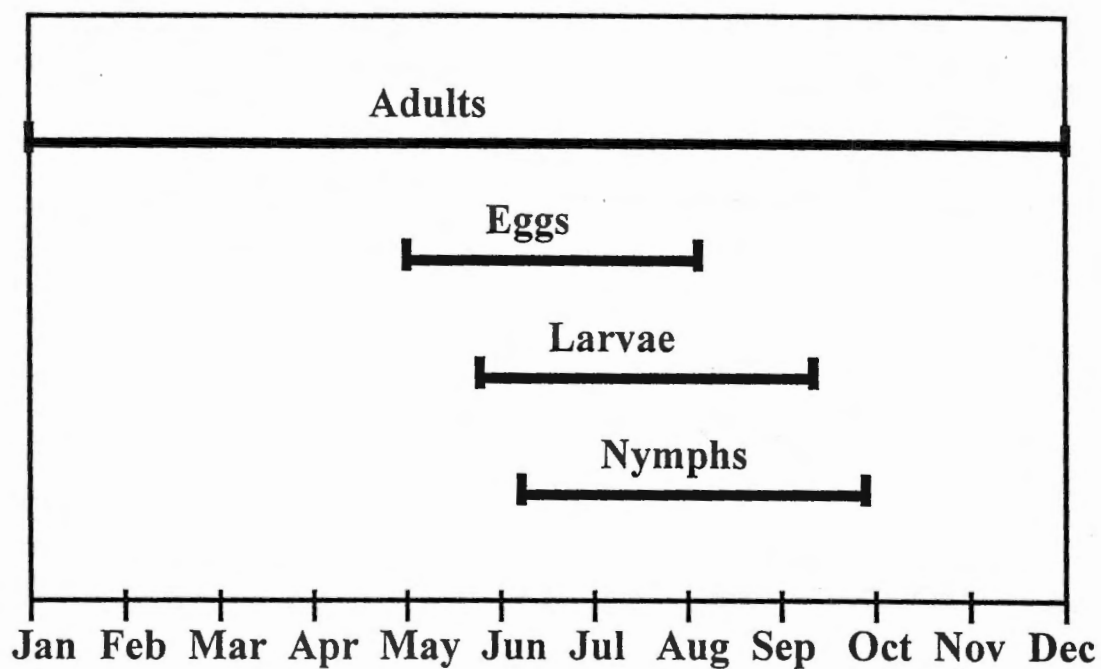


Figure 18. Estimated seasonality of life stages of *Allothrombium* sp. observed in the Great Smoky Mountains National Park, 1996 and 1997.

Table 8. Correlation coefficients and probabilities for incidence of *Allothrombium* sp. vs. the north, south, and overall beech scale ratings for spring 1997 in the Great Smoky Mountains National Park.

Correlation Analysis					
Scale North		Scale South		Scale Overall	
Corr. Coef. ^a	Prob. ^b	Corr. Coef.	Prob.	Corr. Coef.	Prob.
-0.1442	0.0001	-0.0529	0.0944	-0.1341	0.0001

^a Correlation coefficient.

^b Probability.

Table 9. Probabilities of variables that explained 27.48% of the variation of incidence of *Allothrombium* sp. at Sweat Heifer and Indian Gap in the Great Smoky Mountains National Park, 1997.

	Scale North	Scale South	Scale Overall	Temp. ^a	Hour	Date	DBH ^b
Prob. ^c	0.6906	0.5685	0.5835	0.0001	0.0001	0.0001	0.0100
R-Square=0.2748, (P=0.0001)							

^a Temperature.

^b Diameter at breast height.

^c Probability.

11:00 am and 2:00 pm on the days observed. Mite activity increased at both Indian Gap and Sweat Heifer as the summer progressed, and accordingly, the time of year showed a significant relationship to number of *Allothrombium* sp. present. The model also showed that as tree size (dbh) increased, the number of mites present also increased. These variables were more influential on presence of mites on trees and made the effects of beech scale become negligible (Table 9).

The development of *Allothrombium* sp. as a biological control organism against beech scale would be difficult because of the strong influence of environment on mite incidence. Even though *Allothrombium* sp. has been consistently observed to feed on beech scale, it is difficult to determine from these data if artificially elevated populations of the mite would significantly reduce or hinder scale populations in a given area.

iv. Summary

In summary, a new species of *Allothrombium* was observed feeding on beech scale in selected plots in the GSMNP. *Allothrombium* sp. appears to have one generation per year with peaks of incidence of adults in the late spring and peaks of adults and deutonymphs in early fall within the areas studied. All mobile instars of the mite are predaceous on beech scale and adults appear to be active to varying degrees throughout the year. While presence and concentration of beech scale on the bark surface of American beech influence the presence of mites on trees, environmental factors are more influential.

Natural populations of *Allothrombium* sp. were studied and most observations were made in the field. In a forest setting many unknown variables may have an impact on mite activity and incidence. Presently, *Allothrombium* sp., while it does feed on beech scale, does not appear to be an optimum candidate for development as a biological control agent against beech scale. However, to better assess the relationship between *Allothrombium* sp. and beech scale, research should be conducted within the laboratory where many of the unknown factors can be eliminated or greatly reduced. Perhaps the elimination of unknown variables would allow a better opportunity to study beech scale-*Allothrombium* sp. interactions. Potential research on *Allothrombium* sp. could involve, for example, consumption and dispersal studies. Nonetheless, more research on the interactions of beech scale and *Allothrombium* sp. must be conducted before this new species of *Allothrombium* could be considered for development as a biological control agent against beech scale.

CHAPTER IV

SURVEY FOR BEECH SCALE, *CRYPTOCOCCUS FAGISUGA*, IN AREAS OUTSIDE OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK

i. Introduction

The beech scale, *Cryptococcus fagisuga* Lindinger, is one of two apterous species in the family Cryptococcidae found in North America (Kosztarab 1996). Primary means of dispersal of first-instar larvae or crawlers of beech scale, the only mobile stage, is by wind. Eggs of beech scale also may be dispersed by wind, but with limited success. At windspeeds less than 1 m/s, the average distance of dispersal is about 10 m (Wainhouse 1980). Beech scale possibly may be phoretic on animals, such as migratory birds, and even humans (Houston 1994). Beech scale is a major component of a disease complex, known as beech bark disease (BBD), which affects American beech, *Fagus grandifolia* Ehrhart (Ehrlich 1934, Houston and O'Brien 1983). Feeding of beech scale on the vascular fluid of the tree is initiated by the scale inserting its stylet through the bark tissue into the cortex and phloem (Ehrlich 1934). High numbers of scale feeding weaken the tree and also provide entry courts through which two pathogenic fungi, *Nectria galligena* Bresadola and *Nectria coccinea* var. *faginata* Lohman, Watson and Ayers, may infect the tree (Ehrlich 1934, Lonsdale 1980). The combination of high scale numbers and infection by *Nectria* spp. can eventually result in the death of the tree.

Large outbreaks of BBD can result in more than 80% mortality of beech in a stand (Houston 1994).

In 1993, beech scale was found in the Great Smoky Mountains National Park (GSMNP), some 644 km from the nearest known infestation in Monongohela National Forest, West Virginia. Phoresis on other animals may explain the ability of beech scale to disperse such a large distance with no major infestation between the two areas (Houston 1994). In 1994, a research project was begun to study infestation and spread of beech scale and BBD in selected plots in the GSMNP. Because beech scale has the potential of sporadic dispersal, research was initiated in 1996 to investigate, in part, areas outside of the GSMNP for the presence of beech scale. These data could provide limited information on the occurrence of beech scale and possibly *Nectria* spp. in areas surrounding the GSMNP. Also, if beech scale and/or BBD were detected in stands outside of the GSMNP, management decisions concerning those stands could be made more quickly and effectively.

ii. Materials and Methods

During 1996, areas in Frozen Head State Natural Area, Norris Dam State Park, and the Cherokee National Forest were examined for the presence of beech scale (Table 10). An area along the Blue Ridge Parkway also was examined for the presence of beech scale as well as *Nectria* spp. (Table 10). Naturalists and rangers stationed at the state park, state natural areas, and the Cherokee National Forest were contacted and asked about prominent stands of American beech in their respective land areas. Unfortunately,

Table 10. Areas outside the Great Smoky Mountains National Park where American beech were inspected for beech scale, *Cryptococcus fagisuga*.

Search Area	County, State	n ^a	n ^b
Frozen Head State Natural Area	Morgan, Tennessee	15	0
Norris Dam State Park	Anderson, Tennessee	20	0
Hiwassee State Scenic River	Polk, Tennessee	10	0
Cherokee National Forest	Monroe, Tennessee	≤15	0
Blue Ridge Parkway ^c	Haywood, North Carolina	20	0

^a number of trees inspected.

^b number of trees on which beech scale were present.

^c *Nectria* sp. was found on one tree in this area.

all were unsure of the locations, if any, of beech stands on their land. Therefore, 15 beech trees along Flat Fork Trail at Frozen Head State Natural Area and 20 beech trees along Tall Timber Trail at Norris Dam State Park were randomly chosen and examined for presence of beech scale. Ten trees were randomly chosen and examined at Quinn Springs Campground along the Hiwassee State Scenic River, which lies within Cherokee National Forest south of the GSMNP. Also, approximately 15 beech were examined at various locations along Forest Roads 217 and 61 in Cherokee National Forest. In fall of 1996, there was a reported siting of beech scale at Beech Gap, a scenic area at the junction of state road 215 and the Blue Ridge Parkway, southwest of Asheville, North Carolina (S. Oaks, personal communication). Approximately 20 beech trees at Beech Gap were examined for the presence of beech scale and perithecia of *Nectria* spp. The boles of beech trees at all locations were examined visually from about 2.5 m to the ground surface. Two bark samples approximately 2.5 cm^2 were taken from Beech Gap to the laboratory to confirm presence or absence of beech scale.

iii. Results and Discussion

No beech scale were observed on any of the trees at any of the areas examined outside of the GSMNP (Table 10). White, fluffy bodies similar in appearance to, but larger in size than beech scale were observed on two trees at Beech Gap on the Blue Ridge Parkway. No scale adults, immatures, or eggs were found within the samples upon examination in the laboratory. Perithecia of *Nectria* spp. were observed on one tree

at Beech Gap. However, the tree appeared to be damaged and in general decline, and, therefore, the infection by *Nectria* spp. probably was not associated with BBD.

iv. Summary

While no beech scale was found outside of the GSMNP in the areas examined, the survey of these areas was most rudimentary. Lack of knowledge of where stands of beech may have occurred in these areas made it difficult to effectively sample them. Only at Beech Gap on the Blue Ridge Parkway did beech occur in stands similar to what is found in many areas of the GSMNP. Even at the higher elevations (about 1160 m) in Cherokee National Forest along Forest Road 61 no beech gaps were observed.

A more effective means of identifying where stands of beech occur, and consequently where they may be sampled for beech scale and BBD, would be aerial surveillance. This means of surveying could be especially useful on large tracts of land, such as the Cherokee National Forest or along the Blue Ridge Parkway. One drawback of aerial surveillance is the difficulty of identifying single or moderately dispersed beech within a stand from the air. The main drawback of aerial surveillance is high expense. Because beech is of little comparative economic importance, many do not feel justified in expenditures towards its monitoring. However, American beech is an ecologically important tree species in the southern Appalachians. Whittaker (1956) stated that above 1370 m beech is the most important tree of mesic deciduous forests. Beech scale and BBD have the potential to destroy most areas of American beech as they exist today.

Attempts to preserve this most important tree species should include expanded monitoring outside of the GSMNP. By increasing the number of areas monitored and the number of trees within each area, the status of beech scale can be more effectively assessed and, possibly, managed. Perhaps in the future proper attention will be given to the importance of BBD and the detrimental impact it can have on forests containing American beech.

CHAPTER V

CONCLUSIONS

American beech is an ecologically important tree species in forests of eastern North America. Beech is found in at least 16 cover types and is the most important deciduous tree species above 1370 m in the southern Appalachians (Carpenter 1974, Whittaker 1956). The nuts, leaves, bark, and roots are an important food source for many species of wildlife (Halls 1977, Lindquist 1978, Roze 1984). American beech is currently threatened by a disease complex known as beech bark disease (BBD) (Ehrlich 1934, Houston 1994).

Beech bark disease is a complex involving the beech scale, *Cryptococcus fagisuga* Lindinger, which is an insect that feeds on beech, and two pathogenic fungi of the genus *Nectria* Fries, which infect trees weakened and wounded by the feeding of the beech scale (Ehrlich 1934, Lonsdale 1980). The disease complex was first observed in North America in 1911 (Ehrlich 1934). In 1993, beech scale and BBD were discovered in the Great Smoky Mountains National Park (GSMNP) (Houston 1994).

As a continuation of research initiated in 1994 by the National Park Service and The University of Tennessee, a two-year research project was begun in 1996 to monitor, in part, progress of beech scale through selected plots and to assess impact of BBD on beech in those plots. Another objective of this research was to study incidence and biology of a predatory mite observed to feed on beech scale (Vance 1995). A third

aspect of the study was to investigate areas outside of the GSMNP for presence of beech scale and/or BBD.

By 1997, beech scale was present in all ten permanent plots, and percent incidence of beech scale on live trees in all plots had increased to 87.9%. Percent incidence increased from zero to 25.5% at Gregory Bald, 88.5% at Deep Creek, and 100% at Trillium Gap in four years. Percent incidence of beech scale on American beech at all plots except Gregory Bald is at least 78.5%.

Average beech scale ratings also have increased from 1.34 in spring 1996 to 1.81 in spring 1997. Scale ratings have increased in all plots except Forney Ridge and Fork Ridge. Increases in beech scale ratings reflect an increase in beech scale numbers. Higher numbers of beech scale feeding on trees may cause progressive weakening of the trees and, therefore, cause beech to become more susceptible to infection by *Nectria* spp. The decreases in scale ratings observed at Forney Ridge and Fork Ridge reflect weakened trees and increasing tree mortality (Forney Ridge), or increased percent incidence of *Nectria* spp. (Fork Ridge).

Overall incidence of *Nectria* spp. has decreased from its peak of 19.6% in spring 1995 to about 10% in spring 1997. The highest average ratings of *Nectria* spp. at Forney Ridge were in spring 1995, which, due to the high number of trees (n=77) in the plot, may reflect the high overall percent incidence that season. Subsequent decreases in ratings of *Nectria* spp. at Forney Ridge may have influenced the decrease in overall percent incidence of *Nectria* spp. for all plots.

Average ratings of *Nectria* spp. decreased at Forney Ridge, from 1.57 in spring 1995 to 0.05 in spring 1997, and at Chimney Tops from 1.05 in spring 1996 to 0.60 in spring 1997. Average ratings of *Nectria* spp. increased to 0.29 at Newfound Gap, 0.33 at Indian Gap, and 0.57 at Fork Ridge in by spring 1997. Ratings of *Nectria* spp. remained virtually the same at the remaining plots. While decreases in average ratings of *Nectria* spp. at Forney Ridge and Chimney Tops are a result of decreased tree health and increased tree mortality, increases in ratings of *Nectria* spp. at Newfound Gap, Indian Gap, and Fork Ridge suggest trees in these plots will become increasingly vulnerable to mortality in the near future.

Correlation analysis showed weak but significant associations between the overall ratings for *Nectria* spp. taken in fall 1996 and spring 1997 and beech scale ratings the respective previous season and year. These data show a definite association between the presence of beech scale and the presence of *Nectria* spp. Significant correlations also were found among both beech scale and *Nectria* spp. when correlated against elevation, average aspect, and diameter at breast height (dbh).

Overall mortality has increased about 5% since spring 1996 to 26.8% in spring 1997. Mortality has exceeded 90% at Forney Ridge. Mortality at Chimney Tops reached 30% in spring 1997, and appeared to be a direct result of BBD. Some mortality occurring at Deep Creek, Indian Gap, and Newfound Gap was a result of windsnap probably caused by a winter storm. Increasing levels of beech scale in these plots could have contributed to trees being weakened and, therefore, more susceptible to windsnap.

A model was found, when stepwise selection was performed using SAS, that explained about 67% percent ($P=0.0022$) of tree mortality in the selected plots. Variables of the model included average overall beech scale ratings, the sum of all beech scale ratings, the average overall ratings of *Nectria* spp., and the presence of another scale insect, *Xylococcus betulae* (Pergande).

A predaceous red mite, identified as a new species in the genus *Allothrombium*, was monitored during the spring and summer in 1996 and 1997. This new species is unusual because the first-instar larva is quiescent instead of parasitic on arthropods. It is estimated that the mite has one generation per year and overwinters as adults. All mobile stages were observed feeding on beech scale. While the mite was consistently observed to feed on scale, it is still uncertain whether or not it could be developed into a suitable biological control agent against beech scale.

No beech scale were observed at any of the five areas surveyed outside of the GSMNP during 1996. Perithecia of one or more species of *Nectria* were observed on one tree examined in North Carolina, but the infection appeared to be natural and not related to BBD. Established monitoring for beech scale and BBD outside of the GSMNP is necessary to quickly detect outbreaks of BBD. Early detection of beech scale and/or BBD will better enable landowners and land managers to make important decisions regarding American beech on their respective lands.

Beech scale and BBD are currently at various stages of progression in the ten permanent plots established in the GSMNP. In one plot BBD has spread throughout and left it virtually stripped of live mature American beech. In other plots, mortality due to

BBD is just beginning to occur. In all plots beech scale and BBD are present at various levels. It can be deduced, therefore, that, through the eventual spread of beech scale and BBD to areas of beech outside of the GSMNP, the future of American beech in the southern Appalachians is uncertain. More attention needs to be given to BBD and more research needs to be conducted, especially on predators that may be somehow manipulated to at least slow the spread of beech scale. If the problem of BBD is not taken seriously, beech in the southeastern U.S. will suffer the same fate as it has suffered in Canada and the northeastern U.S.

The mass decline of American beech in beech gaps and other forest types would drastically effect the ecology of the immediate and surrounding forests. Also, the many species of wildlife that utilize beech for food and shelter would be negatively impacted. Finally, while it is not among the more economically valuable trees in the forest, American beech would be missed by some who, by carving their initials in the silver smoothness of the bark, entrusted a bit of their fond memories to the beech for safe keeping. Perhaps measures can be taken in the future so that American beech will not itself become only a fond memory.

REFERENCES CITED

- Anonymous. 1997. 1996 State park visitation trends. Tennessee Department of Tourist Development, Nashville, TN. July 21, personal communication.
- Barden, L.S. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* 35:16-19.
- Beeman, L.E. and M.R. Pelton. 1978. Seasonal foods and feeding ecology of black bears in the Smoky Mountains, pp.141-147. *IN* C.J. Martinka and K.L. McArthur (ed), Bears--their biology and management. The Bear Biology Association, Kalispell, Montana.
- Bratton, S.P. 1975. The effect of the European wild boar, *Sus scrofa*, on gray beech forests in the Great Smoky Mountains. *Ecology* 56:1356-1366.
- Carpenter, R.D. 1974. American beech. American woods. U.S. Department of Agriculture Forest Service. FS-220:8.
- Cotter, H.V.T. and R.O. Blanchard. 1981. Identification of the two *Nectria* taxa causing bole cankers on American beech. *Plant Disease* 65:332-334.
- Coulson, R.N. and J.A. Witter. 1984. Forest entomology: Ecology and management. John Wiley & Sons, New York, 669 pp.
- Davis, R. 1961. A mite, *Allothrombium mitchelli*, new to science, predator of balsam wooly aphid (Acarina: Trombidiidae). *Proceedings of the Entomological Society of Washington* 63: 269-272.
- DeBald, P.S. and M.E. Dale. 1991. Tree value conversion standards revisited. U.S. Department of Agriculture Forest Service General Technical Report. NE-645:1-28.
- Ehrlich, J. 1934. The beech bark disease: A *Nectria* disease of *Fagus*, following *Cryptococcus fagi* (Baer.). *Canadian Journal of Research* 10:593-701.
- Gavin, D.G. and D.R. Peart. 1993. Effects of beech bark disease on growth of American beech (*Fagus grandifolia*). *Canadian Journal of Research* 23:1566-1575.
- Gray, N. 1997. Personal communication. Public Affairs Office, Great Smoky Mountains National Park, TN. July 21.
- Halls, L.K. 1977. American beech/ *Fagus grandifolia* Ehrhart. Southern fruit-producing woody plants used by wildlife. U.S. Department of Agriculture Forest Service General Technical Report. SO-16:147-148.

- Hepting, G.H. 1971. Diseases of forest and shade trees of the United States. U.S. Department of Agriculture Forest Service. Handbook no. 386:162-167.
- Houston, D.R. 1975. Beech bark disease: the aftermath forests are structured for a new outbreak. *Journal of Forestry* 73:660-663.
- Houston, D.R. 1983a. American beech resistance to *Cryptococcus fagisuga*, pp. 38-42. *IN* D. Houston and D. Wainhouse (ed.), *Proceeding of the I.U.F.R.O. Beech Bark Disease Working Party Conference*. U.S.D.A. Forest Service General Report. WO-37.
- Houston, D.R. 1983b. Developments in biological control of beech bark disease, pp. 1035-1041. *IN* *Proceedings of the 10th International Congress of Plant Protection 1983: Plant protection for human welfare*, Brighton, England, 20-25 November 1983.
- Houston, D.R. 1994. Major new tree disease epidemics: Beech bark disease. *Annual Review of Phytopathology* 32:75-87.
- Houston, D.R. and J.T. O'Brien. 1983. Beech bark disease. U.S. Department of Agriculture Forest Service. NE-75:1-8.
- Hubbard, H.G. and T. Pergande. 1899. A new coccid on birch. Reprint from Bulletin 18, New Series, Division of Entomology, U.S. Department of Agriculture. pp. 13-26.
- Jones, R.H. and D.J. Raynal. 1987. Root sprouting in American beech: Production, survival, and the effect of parent tree vigor. *Canadian Journal of Forest Research* 17:539-544.
- Klein, R. 1997. Influence of biotic and abiotic factors on the epidemiology of beech bark disease in the Great Smoky Mountains National Park. M.S. Thesis, University of Tennessee, Knoxville, 96 pp.
- Kosztarab, M. 1996. Scale insects of northeastern North America: Identification, biology, and distribution, special publication no. 3. Virginia Museum of Natural History, Martinsville, 650 pp.
- Leak, W.B. and R.E. Graber. 1993. Six-year beechnut production in New Hampshire. U.S. Department of Agriculture Forest Service General Technical Report. NE-677:1-7.
- Lindquist, O.H. 1978. Notes on a rare insect, *Dasylophia thyatiroides* (Lepidoptera: Notodontidae), on beech. *The Canadian Entomologist* 110:107-108.

- Lohman, M.L. and A.J. Watson. 1943. Identity and host relations of *Nectria* species associated with diseases of hardwoods in the eastern states. *Lloydia* 6:77-108.
- Lonsdale, D. 1980. *Nectria* infection of beech bark in relation to infestation by *Cryptococcus fagisuga* Lindiger. *European Journal of Forest Pathology* 10:161-168.
- Mayer, M. and D.C. Allen. 1983. *Chilocorus stigma* (Coleoptera: Coccinellidae) and other predators of beech scale in central New York, pp. 89-98. *IN* D. Houston and D. Wainhouse (eds.), *Proceeding of the I.U.F.R.O. Beech Bark Disease Working Party Conference*. U.S.D.A. Forest Service General Report. WO-37.
- Mielke, M.E., C. Haynes, and W.L. MacDonald. 1982. Beech scale and *Nectria galligena* on beech in the Monongahela National Forest, West Virginia. *Plant Disease* 66:851-852.
- Mielke, M.E., D.B. Houston, and D.R. Houston. 1985. First report of *Cryptococcus fagisuga*, initiator of beech bark disease, in Virginia and Ohio. *Plant Disease* 69:905.
- Peterson, A.T., D.R. Osborne, and D.H. Taylor. 1989. Tree trunk arthropod faunas as food resources for birds. *Ohio Journal of Science* 89:23-25.
- Record, S.J. and R.W. Hess. 1943. *Timbers of the New World*. Yale University Press, New Haven, 166 pp.
- Roze, U. 1984. Winter foraging by individual porcupines. *Canadian Journal of Zoology* 62: 2425-2428.
- Russell, N.H. 1953. The beech gaps of the Great Smoky Mountains. *Ecology* 34:366-374.
- Rutherford, B. 1996. Identification, life cycle, and presence of *Nectria* species associated with beech bark disease in the Great Smoky Mountains National Park and the effectiveness of *Nematogonum ferrigineum* as a biocontrol. M.S. Thesis, University of Tennessee, Knoxville, 44 pp.
- SAS Institute Incorporated. 1989. *SAS/STAT user's guide, version 6, vls. 1 & 2*, Cary, North Carolina, 1789 pp.
- Shigo, A.L. 1964. Organism interactions in the beech bark disease. *Phytopathology* 54:263-269.

- Shigo, A.L. 1972. The beech bark disease today in the northeastern U.S. *Journal of Forestry* 70:286-289.
- Stupka, A. 1964. Trees, shrubs, and woody vines of Great Smoky Mountains National Park. The University of Tennessee Press, Knoxville, pp. 43-44.
- Thompson, F.R. and D.E. Capen. 1988. Avian assemblages in seral stages of a Vermont forest. *Journal of Wildlife Management* 52:771-777.
- Twery, M.J. and W.A. Patterson III. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. *Canadian Journal of Forestry Research* 14:565-574.
- Vance, R.A. 1995. Incidence and life history of beech scale, initiator of beech bark disease, in the Great Smoky Mountains National Park. M.S. Thesis, University of Tennessee, Knoxville, 72 pp.
- Wainhouse, D. 1980. Dispersal of first instar larvae of the felted beech scale, *Cryptococcus fagisuga*. *Journal of Applied Ecology* 17:523-532.
- Wainhouse, D. and I. Gate. 1988. The beech scale, pp. 67-85. *IN* A.A. Berryman (ed.), *Dynamics of forest insect populations*, Plenum, New York.
- Walters, M. 1980. *The complete birds of the world*. David and Charles, North Pomfret, 340 pp.
- Whittaker, R. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26:1-80.

APPENDIX

Correlation coefficients and probabilities for all beech scale ratings vs. ratings of *Nectria* spp. over all sampling times.

Correlation coefficients / Probabilities / Number of observations (Trees)

	SCLN ^a 1 ^b	SCLN2	SCLN3	SCLN4	SCLN5	SCLN6	SCLN7
SCLN1	1.00000 0.00000 375	0.79090 0.0001 366	0.66421 0.0001 357	0.46802 0.0001 209	0.25140 0.0001 308	0.24091 0.0001 342	0.23916 0.0001 319
SCLN2	0.79090 0.0001 366	1.00000 0.00000 373	0.69009 0.0001 364	0.61593 0.0001 215	0.36212 0.0001 315	0.37426 0.0001 348	0.39665 0.0001 325
SCLN3	0.66421 0.0001 357	0.69009 0.0001 364	1.00000 0.00000 364	0.65899 0.0001 215	0.43422 0.0001 314	0.44177 0.0001 348	0.46911 0.0001 325
SCLN4	0.46802 0.0001 209	0.61593 0.0001 215	0.65899 0.0001 215	1.00000 0.00000 216	0.63788 0.0001 171	0.61221 0.0001 210	0.61961 0.0001 201
SCLN5	0.25140 0.0001 308	0.36212 0.0001 315	0.43422 0.0001 314	0.63788 0.0001 171	1.00000 0.00000 316	0.55754 0.0001 305	0.56246 0.0001 283
SCLN6	0.24091 0.0001 342	0.37426 0.0001 348	0.44177 0.0001 348	0.61221 0.0001 210	0.55754 0.0001 305	1.00000 0.00000 350	0.85988 0.0001 326
SCLN7	0.23916 0.0001 319	0.39665 0.0001 325	0.46911 0.0001 325	0.61961 0.0001 201	0.56246 0.0001 283	0.85988 0.0001 326	1.00000 0.00000 327
SCLS1	0.71293 0.0001 375	0.57525 0.0001 366	0.54503 0.0001 357	0.40042 0.0001 209	0.12955 0.0230 308	0.05978 0.2703 342	0.08682 0.1218 319
SCLS2	0.66122 0.0001 366	0.68392 0.0001 373	0.55651 0.0001 364	0.44351 0.0001 215	0.24933 0.0001 315	0.16492 0.0020 348	0.21617 0.0001 325
SCLS3	0.63017 0.0001 357	0.61205 0.0001 364	0.70100 0.0001 364	0.51283 0.0001 215	0.31833 0.0001 314	0.18988 0.0004 348	0.23812 0.0001 325
SCLS4	0.51959 0.0001 209	0.54786 0.0001 215	0.64308 0.0001 215	0.62803 0.0001 216	0.42161 0.0001 171	0.36795 0.0001 210	0.43308 0.0001 201

	SCLN1	SCLN2	SCLN3	SCLN4	SCLN5	SCLN6	SCLN7
SCLS5	0.22023 0.0001 309	0.29385 0.0001 316	0.32801 0.0001 315	0.33314 0.0001 171	0.38972 0.0001 316	0.17999 0.0016 306	0.22300 0.0002 284
SCLS6	0.25325 0.0001 342	0.36599 0.0001 348	0.42056 0.0001 348	0.45772 0.0001 210	0.45595 0.0001 305	0.74816 0.0001 350	0.70441 0.0001 326
SCLS7	0.23818 0.0001 319	0.37460 0.0001 325	0.44375 0.0001 325	0.44872 0.0001 201	0.42699 0.0001 283	0.66040 0.0001 326	0.74534 0.0001 327
SCLO1	0.75463 0.0001 375	0.59619 0.0001 366	0.60117 0.0001 357	0.49745 0.0001 209	0.24075 0.0001 308	0.17728 0.0010 342	0.19492 0.0005 319
SCLO2	0.62254 0.0001 366	0.69722 0.0001 373	0.59408 0.0001 364	0.51055 0.0001 215	0.26245 0.0001 315	0.20773 0.0001 348	0.25207 0.0001 325
SCLO3	0.63510 0.0001 357	0.64570 0.0001 364	0.70869 0.0001 364	0.52434 0.0001 215	0.32533 0.0001 314	0.16674 0.0018 348	0.21508 0.0001 325
SCLO4	0.46159 0.0001 209	0.55732 0.0001 215	0.57856 0.0001 215	0.76693 0.0001 216	0.52926 0.0001 171	0.50646 0.0001 210	0.51317 0.0001 201
SCLO5	0.26601 0.0001 309	0.33178 0.0001 316	0.45398 0.0001 315	0.45738 0.0001 171	0.65573 0.0001 316	0.40409 0.0001 306	0.44197 0.0001 284
SCLO6	0.26299 0.0001 343	0.38237 0.0001 349	0.47740 0.0001 349	0.60292 0.0001 211	0.54140 0.0001 306	0.89003 0.0001 350	0.82488 0.0001 326
SCLO7	0.24475 0.0001 323	0.38901 0.0001 329	0.43781 0.0001 329	0.57542 0.0001 202	0.52879 0.0001 286	0.81508 0.0001 328	0.89492 0.0001 327
NECN1	0.24637 0.0001 375	0.05103 0.3289 368	0.02602 0.6231 359	-0.00696 0.9200 211	-0.01467 0.7967 311	-0.02429 0.6530 345	-0.02957 0.5970 322
NECN2	0.27417 0.0001 375	0.03594 0.4889 373	-0.00782 0.8818 364	-0.02187 0.7492 216	-0.01939 0.7313 316	0.05467 0.3077 350	0.03211 0.5629 327

	SCLN1	SCLN2	SCLN3	SCLN4	SCLN5	SCLN6	SCLN7
NECN3	0.40814	0.11513	-0.00243	-0.05234	-0.07838	-0.01774	-0.05129
	0.0001	0.0262	0.9632	0.4441	0.1646	0.7409	0.3552
	375	373	364	216	316	350	327
NECN4	0.42438	0.16541	0.10731	0.03878	-0.01849	0.00957	-0.01894
	0.0001	0.0063	0.0812	0.5709	0.7851	0.8787	0.7703
	274	272	265	216	220	257	240
NECN5	0.18143	0.09372	0.01015	0.00821	-0.02048	0.05683	0.04145
	0.0004	0.0710	0.8471	0.9045	0.7169	0.2890	0.4550
	374	372	363	216	316	350	327
NECN6	0.20457	0.20536	0.22276	0.15442	0.18368	0.09766	-0.00584
	0.0001	0.0001	0.0001	0.0232	0.0010	0.0680	0.9162
	374	372	363	216	316	350	327
NECN7	0.15307	0.17268	0.19802	0.24181	0.15887	0.07917	0.00332
	0.0030	0.0008	0.0001	0.0003	0.0048	0.1405	0.9523
	373	371	362	216	314	348	327
NECS1	0.20379	0.05863	0.09611	0.05119	-0.02129	0.02322	0.00618
	0.0001	0.2619	0.0689	0.4595	0.7084	0.6674	0.9120
	375	368	359	211	311	345	322
NECS2	0.26071	0.04144	0.04261	0.05596	-0.01939	0.10649	0.10281
	0.0001	0.4249	0.4177	0.4132	0.7313	0.0465	0.0633
	375	373	364	216	316	350	327
NECS3	0.37187	0.14472	0.02176	-0.00280	-0.05615	0.00101	-0.03005
	0.0001	0.0051	0.6791	0.9673	0.3197	0.9850	0.5882
	375	373	364	216	316	350	327
NECS4	0.34862	0.15453	0.05203	0.02484	-0.06824	0.00213	-0.02023
	0.0001	0.0107	0.3989	0.7166	0.3136	0.9729	0.7552
	274	272	265	216	220	257	240
NECS5	0.08618	0.05709	0.01428	-0.00820	0.02351	0.11592	0.12066
	0.0961	0.2721	0.7863	0.9046	0.6772	0.0301	0.0291
	374	372	363	216	316	350	327
NECS6	0.11089	0.13532	0.14293	0.01764	0.12742	0.12042	0.06824
	0.0320	0.0090	0.0064	0.7965	0.0235	0.0243	0.2184
	374	372	363	216	316	350	327
NECS7	0.04398	0.03808	0.06176	-0.01731	0.04458	0.11654	0.10470
	0.3970	0.4646	0.2411	0.8003	0.4312	0.0297	0.0586
	373	371	362	216	314	348	327

	SCLN1	SCLN2	SCLN3	SCLN4	SCLN5	SCLN6	SCLN7
NECO1	0.23018	0.05199	0.08955	0.03945	-0.02942	0.04118	0.00082
	0.0001	0.3199	0.0902	0.5688	0.6053	0.4458	0.9884
	375	368	359	211	311	345	322
NECO2	0.32039	0.09698	0.03325	0.04785	0.04771	0.14649	0.14827
	0.0001	0.0613	0.5272	0.4842	0.3979	0.0060	0.0072
	375	373	364	216	316	350	327
NECO3	0.37492	0.14696	0.00365	0.00006	-0.03913	0.02583	-0.00331
	0.0001	0.0045	0.9447	0.9993	0.4883	0.6301	0.9525
	375	373	364	216	316	350	327
NECO4	0.40267	0.20089	0.13987	0.05513	-0.03955	0.04093	0.02002
	0.0001	0.0009	0.0228	0.4202	0.5596	0.5136	0.7577
	274	272	265	216	220	257	240
NECO5	0.25444	0.14709	0.05024	0.05773	-0.00341	0.07830	0.05533
	0.0001	0.0045	0.3399	0.3985	0.9519	0.1438	0.3185
	374	372	363	216	316	350	327
NECO6	0.23375	0.24018	0.26065	0.16528	0.14380	0.17477	0.05471
	0.0001	0.0001	0.0001	0.0150	0.0105	0.0010	0.3240
	374	372	363	216	316	350	327
NECO7	0.21413	0.25255	0.32340	0.34440	0.25758	0.11464	0.10942
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0325	0.0480
	373	371	362	216	314	348	327
SCLN1	0.71293	0.66122	0.63017	0.51959	0.22023	0.25325	0.23818
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	375	366	357	209	309	342	319
SCLN2	0.57525	0.68392	0.61205	0.54786	0.29385	0.36599	0.37460
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	366	373	364	215	316	348	325
SCLN3	0.54503	0.55651	0.70100	0.64308	0.32801	0.42056	0.44375
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	357	364	364	215	315	348	325
SCLN4	0.40042	0.44351	0.51283	0.62803	0.33314	0.45772	0.44872
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	209	215	215	216	171	210	201
SCLN5	0.12955	0.24933	0.31833	0.42161	0.38972	0.45595	0.42699
	0.0230	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	308	315	314	171	316	305	283

	SCLS1	SCLS2	SCLS3	SCLS4	SCLS5	SCLS6	SCLS7
SCLN6	0.05978 0.2703 342	0.16492 0.0020 348	0.18988 0.0004 348	0.36795 0.0001 210	0.17999 0.0016 306	0.74816 0.0001 350	0.66040 0.0001 326
SCLN7	0.08682 0.1218 319	0.21617 0.0001 325	0.23812 0.0001 325	0.43308 0.0001 201	0.22300 0.0002 284	0.70441 0.0001 326	0.74534 0.0001 327
SCLS1	1.00000 0.0 375	0.81856 0.0001 366	0.79559 0.0001 357	0.61207 0.0001 209	0.35353 0.0001 309	0.16591 0.0021 342	0.16366 0.0034 319
SCLS2	0.81856 0.0001 366	1.00000 0.0 373	0.80913 0.0001 364	0.69746 0.0001 215	0.45096 0.0001 316	0.30355 0.0001 348	0.30197 0.0001 325
SCLS3	0.79559 0.0001 357	0.80913 0.0001 364	1.00000 0.00000 364	0.74747 0.0001 215	0.49048 0.0001 315	0.33167 0.0001 348	0.30435 0.0001 325
SCLS4	0.61207 0.0001 209	0.69746 0.0001 215	0.74747 0.0001 215	1.00000 0.00000 216	0.68166 0.0001 171	0.52097 0.0001 210	0.50893 0.0001 201
SCLS5	0.35353 0.0001 309	0.45096 0.0001 316	0.49048 0.0001 315	0.68166 0.0001 171	1.00000 0.00000 317	0.46677 0.0001 306	0.30713 0.0001 284
SCLS6	0.16591 0.0021 342	0.30355 0.0001 348	0.33167 0.0001 348	0.52097 0.0001 210	0.46677 0.0001 306	1.00000 0.00000 350	0.76615 0.0001 326
SCLS7	0.16366 0.0034 319	0.30197 0.0001 325	0.30435 0.0001 325	0.50893 0.0001 201	0.30713 0.0001 284	0.76615 0.0001 326	1.00000 0.00000 327
SCLO1	0.86063 0.0001 375	0.74242 0.0001 366	0.76152 0.0001 357	0.60951 0.0001 209	0.31753 0.0001 309	0.26330 0.0001 342	0.27321 0.0001 319
SCLO2	0.74584 0.0001 366	0.83934 0.0001 373	0.80260 0.0001 364	0.70712 0.0001 215	0.43181 0.0001 316	0.31982 0.0001 348	0.34762 0.0001 325
SCLO3	0.74758 0.0001 357	0.78573 0.0001 364	0.88847 0.0001 364	0.75757 0.0001 215	0.50414 0.0001 315	0.31832 0.0001 348	0.30763 0.0001 325

	SCLS1	SCLS2	SCLS3	SCLS4	SCLS5	SCLS6	SCLS7
SCLO4	0.48849	0.58309	0.63827	0.75559	0.52504	0.55449	0.53946
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	209	215	215	216	171	210	201
SCLO5	0.28693	0.41762	0.50194	0.61484	0.57821	0.54629	0.44581
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	309	316	315	171	317	306	284
SCLO6	0.15973	0.29725	0.34285	0.51101	0.33390	0.85442	0.72857
	0.0030	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	343	349	349	211	307	350	326
SCLO7	0.11131	0.24503	0.26201	0.41199	0.19588	0.71109	0.81807
	0.0456	0.0001	0.0001	0.0001	0.0008	0.0001	0.0001
	323	329	329	202	287	328	327
NECN1	0.15626	0.02645	0.01830	0.00355	0.00402	-0.02092	0.01217
	0.0024	0.6130	0.7296	0.9591	0.9436	0.6986	0.8278
	375	368	359	211	312	345	322
NECN2	0.16040	0.01976	0.02174	0.00418	0.00431	0.01822	-0.00855
	0.0018	0.7037	0.6794	0.9512	0.9391	0.7341	0.8775
	375	373	364	216	317	350	327
NECN3	0.22632	0.07982	0.01065	-0.00405	-0.00791	-0.03332	-0.04235
	0.0001	0.1238	0.8396	0.9528	0.8884	0.5344	0.4454
	375	373	364	216	317	350	327
NECN4	0.27920	0.09518	0.07292	0.06650	0.00340	-0.01483	-0.03122
	0.0001	0.1173	0.2368	0.3307	0.9600	0.8130	0.6303
	274	272	265	216	220	257	240
NECN5	0.09550	0.06981	0.01882	0.03227	0.00614	0.06771	0.01857
	0.0650	0.1791	0.7208	0.6372	0.9133	0.2063	0.7380
	374	372	363	216	317	350	327
NECN6	0.12499	0.14409	0.16829	0.11206	0.05021	0.11785	0.06533
	0.0156	0.0054	0.0013	0.1005	0.3729	0.0275	0.2388
	374	372	363	216	317	350	327
NECN7	0.16296	0.15282	0.20756	0.20355	0.06315	0.11759	0.08907
	0.0016	0.0032	0.0001	0.0026	0.2638	0.0283	0.1079
	373	371	362	216	315	348	327
NECS1	0.18588	0.03462	0.04826	0.05088	0.00584	-0.00836	-0.01962
	0.0003	0.5079	0.3619	0.4622	0.9182	0.8771	0.7258
	375	368	359	211	312	345	322

	SCLS1	SCLS2	SCLS3	SCLS4	SCLS5	SCLS6	SCLS7
NECS2	0.14291	-0.02298	0.01915	0.00368	0.00431	0.04100	0.01476
	0.0056	0.6583	0.7158	0.9571	0.9391	0.4445	0.7904
	375	373	364	216	317	350	327
NECS3	0.24976	0.08934	0.00802	0.00501	0.00617	-0.01468	-0.02804
	0.0001	0.0849	0.8789	0.9416	0.9129	0.7844	0.6134
	375	373	364	216	317	350	327
NECS4	0.18809	0.10204	0.03699	0.01897	-0.02318	-0.02243	-0.02640
	0.0018	0.0930	0.5489	0.7816	0.7324	0.7205	0.6841
	274	272	265	216	220	257	240
NECS5	0.02204	0.07015	0.02436	0.00355	-0.00584	0.12761	0.06907
	0.6709	0.1770	0.6437	0.9586	0.9175	0.0169	0.2129
	374	372	363	216	317	350	327
NECS6	0.12170	0.13409	0.20165	0.04147	0.07966	0.16434	0.05992
	0.0186	0.0096	0.0001	0.5444	0.1571	0.0020	0.2800
	374	372	363	216	317	350	327
NECS7	0.03597	0.03995	0.04639	0.01387	-0.00751	0.15410	0.09177
	0.4885	0.4429	0.3788	0.8393	0.8944	0.0040	0.0976
	373	371	362	216	315	348	327
NECO1	0.16893	0.01003	0.02523	0.01995	-0.00953	0.00254	-0.02876
	0.0010	0.8479	0.6337	0.7733	0.8668	0.9626	0.6072
	375	368	359	211	312	345	322
NECO2	0.14249	0.02658	-0.01181	0.00859	-0.04473	0.04625	0.10562
	0.0057	0.6088	0.8224	0.9001	0.4274	0.3884	0.0564
	375	373	364	216	317	350	327
NECO3	0.20614	0.08418	-0.00640	-0.01216	-0.02595	-0.00100	0.00695
	0.0001	0.1046	0.9031	0.8590	0.6453	0.9851	0.9004
	375	373	364	216	317	350	327
NECO4	0.21508	0.13281	0.11135	0.04387	-0.04932	0.00768	0.01824
	0.0003	0.0285	0.0703	0.5213	0.4667	0.9024	0.7786
	274	272	265	216	220	257	240
NECO5	0.14279	0.11805	0.07799	0.04589	-0.01963	0.07598	0.03910
	0.0057	0.0228	0.1380	0.5023	0.7278	0.1561	0.4810
	374	372	363	216	317	350	327
NECO6	0.17849	0.19012	0.23480	0.14176	0.11483	0.20779	0.08498
	0.0005	0.0002	0.0001	0.0374	0.0410	0.0001	0.1251
	374	372	363	216	317	350	327

	SCLS1	SCLS2	SCLS3	SCLS4	SCLS5	SCLS6	SCLS7
NECO7	0.24603 0.0001 373	0.26607 0.0001 371	0.37486 0.0001 362	0.36560 0.0001 216	0.18479 0.0010 315	0.18232 0.0006 348	0.13873 0.0120 327
SCLN1	0.75463 0.0001 375	0.62254 0.0001 366	0.63510 0.0001 357	0.46159 0.0001 209	0.26601 0.0001 309	0.26299 0.0001 343	0.24475 0.0001 323
SCLN2	0.59619 0.0001 366	0.69722 0.0001 373	0.64570 0.0001 364	0.55732 0.0001 215	0.33178 0.0001 316	0.38237 0.0001 349	0.38901 0.0001 329
SCLN3	0.60117 0.0001 357	0.59408 0.0001 364	0.70869 0.0001 364	0.57856 0.0001 215	0.45398 0.0001 315	0.47740 0.0001 349	0.43781 0.0001 329
SCLN4	0.49745 0.0001 209	0.51055 0.0001 215	0.52434 0.0001 215	0.76693 0.0001 216	0.45738 0.0001 171	0.60292 0.0001 211	0.57542 0.0001 202
SCLN5	0.24075 0.0001 308	0.26245 0.0001 315	0.32533 0.0001 314	0.52926 0.0001 171	0.65573 0.0001 316	0.54140 0.0001 306	0.52879 0.0001 286
SCLN6	0.17728 0.0010 342	0.20773 0.0001 348	0.16674 0.0018 348	0.50646 0.0001 210	0.40409 0.0001 306	0.89003 0.0001 350	0.81508 0.0001 328
SCLN7	0.19492 0.0005 319	0.25207 0.0001 325	0.21508 0.0001 325	0.51317 0.0001 201	0.44197 0.0001 284	0.82488 0.0001 326	0.89492 0.0001 327
SCLS1	0.86063 0.0001 375	0.74584 0.0001 366	0.74758 0.0001 357	0.48849 0.0001 209	0.28693 0.0001 309	0.15973 0.0030 343	0.11131 0.0456 323
SCLS2	0.74242 0.0001 366	0.83934 0.0001 373	0.78573 0.0001 364	0.58309 0.0001 215	0.41762 0.0001 316	0.29725 0.0001 349	0.24503 0.0001 329
SCLS3	0.76152 0.0001 357	0.80260 0.0001 364	0.88847 0.0001 364	0.63827 0.0001 215	0.50194 0.0001 315	0.34285 0.0001 349	0.26201 0.0001 329
SCLS4	0.60951 0.0001 209	0.70712 0.0001 215	0.75757 0.0001 215	0.75559 0.0001 216	0.61484 0.0001 171	0.51101 0.0001 211	0.41199 0.0001 202

	SCLO1	SCLO2	SCLO3	SCLO4	SCLO5	SCLO6	SCLO7
SCLS5	0.31753 0.0001 309	0.43181 0.0001 316	0.50414 0.0001 315	0.52504 0.0001 171	0.57821 0.0001 317	0.33390 0.0001 307	0.19588 0.0008 287
SCLS6	0.26330 0.0001 342	0.31982 0.0001 348	0.31832 0.0001 348	0.55449 0.0001 210	0.54629 0.0001 306	0.85442 0.0001 350	0.71109 0.0001 328
SCLS7	0.27321 0.0001 319	0.34762 0.0001 325	0.30763 0.0001 325	0.53946 0.0001 201	0.44581 0.0001 284	0.72857 0.0001 326	0.81807 0.0001 327
SCLO1	1.00000 0.00000 375	0.78459 0.0001 366	0.75934 0.0001 357	0.56825 0.0001 209	0.33031 0.0001 309	0.27507 0.0001 343	0.21639 0.0001 323
SCLO2	0.78459 0.0001 366	1.00000 0.00000 373	0.82551 0.0001 364	0.63396 0.0001 215	0.39938 0.0001 316	0.32398 0.0001 349	0.27251 0.0001 329
SCLO3	0.75934 0.0001 357	0.82551 0.0001 364	1.00000 0.00000 364	0.67218 0.0001 215	0.49208 0.0001 315	0.31397 0.0001 349	0.21679 0.0001 329
SCLO4	0.56825 0.0001 209	0.63396 0.0001 215	0.67218 0.0001 215	1.00000 0.00000 216	0.61777 0.0001 171	0.63144 0.0001 211	0.53773 0.0001 202
SCLO5	0.33031 0.0001 309	0.39938 0.0001 316	0.49208 0.0001 315	0.61777 0.0001 171	1.00000 0.00000 317	0.57578 0.0001 307	0.44419 0.0001 287
SCLO6	0.27507 0.0001 343	0.32398 0.0001 349	0.31397 0.0001 349	0.63144 0.0001 211	0.57578 0.0001 307	1.00000 0.00000 351	0.81471 0.0001 329
SCLO7	0.21639 0.0001 323	0.27251 0.0001 329	0.21679 0.0001 329	0.53773 0.0001 202	0.44419 0.0001 287	0.81471 0.0001 329	1.00000 0.00000 331
NECN1	0.16688 0.0012 375	0.01847 0.7239 368	-0.00192 0.9711 359	-0.03485 0.6147 211	-0.03041 0.5925 312	-0.03081 0.5679 346	-0.03818 0.4921 326
NECN2	0.14840 0.0040 375	0.01633 0.7532 373	-0.00273 0.9586 364	-0.04171 0.5421 216	-0.03916 0.4872 317	0.03850 0.4722 351	0.03096 0.5746 331

	SCLO1	SCLO2	SCLO3	SCLO4	SCLO5	SCLO6	SCLO7
NECN3	0.24201 0.0001 375	0.05448 0.2940 373	-0.00420 0.9364 364	-0.05878 0.3900 216	-0.05914 0.2938 317	-0.03966 0.4589 351	-0.05147 0.3506 331
NECN4	0.31852 0.0001 274	0.06888 0.2576 272	0.07785 0.2065 265	-0.00514 0.9401 216	-0.06561 0.3327 220	-0.03789 0.5446 258	-0.02489 0.6995 243
NECN5	0.14681 0.0044 374	0.10514 0.0427 372	0.05557 0.2910 363	-0.02997 0.6614 216	-0.05585 0.3216 317	0.03493 0.5142 351	0.03160 0.5673 330
NECN6	0.14656 0.0045 374	0.15668 0.0024 372	0.21800 0.0001 363	0.06159 0.3677 216	0.09106 0.1056 317	0.07465 0.1628 351	0.03056 0.5802 330
NECN7	0.17878 0.0005 373	0.21215 0.0001 371	0.21450 0.0001 362	0.17711 0.0091 216	0.07465 0.1863 315	0.07295 0.1739 349	0.06062 0.2715 331
NECS1	0.20457 0.0001 375	0.02122 0.6849 368	0.03141 0.5531 359	0.01173 0.8655 211	-0.04415 0.4371 312	-0.00693 0.8977 346	0.00143 0.9794 326
NECS2	0.16192 0.0017 375	0.00809 0.8762 373	-0.00240 0.9636 364	0.01269 0.8528 216	-0.03916 0.4872 317	0.07767 0.1465 351	0.07131 0.1956 331
NECS3	0.26106 0.0001 375	0.06690 0.1974 373	-0.00361 0.9452 364	0.00383 0.9554 216	-0.05610 0.3194 317	-0.02024 0.7056 351	-0.02496 0.6509 331
NECS4	0.24489 0.0001 274	0.08792 0.1482 272	0.05137 0.4049 265	-0.00435 0.9493 216	-0.06515 0.3362 220	-0.02607 0.6768 258	-0.03787 0.5569 243
NECS5	0.04851 0.3495 374	0.11337 0.0288 372	0.07446 0.1569 363	-0.03540 0.6048 216	-0.05020 0.3730 317	0.09415 0.0781 351	0.10328 0.0609 330
NECS6	0.10411 0.0442 374	0.18163 0.0004 372	0.22162 0.0001 363	-0.01352 0.8434 216	0.07783 0.1669 317	0.14361 0.0070 351	0.07801 0.1574 330
NECS7	0.05166 0.3197 373	0.09097 0.0801 371	0.08121 0.1230 362	-0.00384 0.9553 216	-0.00843 0.8816 315	0.10870 0.0424 349	0.10074 0.0672 331

	SCLO1	SCLO2	SCLO3	SCLO4	SCLO5	SCLO6	SCLO7
NECO1	0.18220	0.00423	0.00581	0.00530	-0.06101	-0.00093	-0.01640
	0.0004	0.9356	0.9126	0.9390	0.2827	0.9862	0.7680
	375	368	359	211	312	346	326
NECO2	0.21749	0.02796	-0.01404	0.03538	-0.00764	0.10502	0.14720
	0.0001	0.5903	0.7896	0.6050	0.8922	0.0493	0.0073
	375	373	364	216	317	351	331
NECO3	0.23753	0.06985	-0.01132	0.00602	-0.05255	-0.01020	-0.00295
	0.0001	0.1783	0.8295	0.9299	0.3510	0.8490	0.9574
	375	373	364	216	317	351	331
NECO4	0.28344	0.12294	0.10298	0.02213	-0.06889	-0.00338	0.01555
	0.0001	0.0428	0.0944	0.7464	0.3091	0.9570	0.8095
	274	272	265	216	220	258	243
NECO5	0.17124	0.15876	0.13520	-0.00505	-0.05620	0.04144	0.03950
	0.0009	0.0021	0.0099	0.9412	0.3185	0.4390	0.4746
	374	372	363	216	317	351	330
NECO6	0.17963	0.21020	0.27265	0.09346	0.11612	0.16597	0.07939
	0.0005	0.0001	0.0001	0.1711	0.0388	0.0018	0.1502
	374	372	363	216	317	351	330
NECO7	0.26014	0.34479	0.38757	0.29061	0.19986	0.18938	0.13340
	0.0001	0.0001	0.0001	0.0001	0.0004	0.0004	0.0152
	373	371	362	216	315	349	331

^a SCLN = Scale North, SCLS = Scale South, SCLO = Scale Overall, NECN = *Nectria* North, NECS = *Nectria* South, NECO = *Nectria* Overall

^b Numbers = Sampling Times

VITA

Gregory James Wiggins was born in Harriman, Tennessee, on October 24, 1971. As a child, he lived and grew up around Wilson, North Carolina. He received his high school diploma from Mount Pisgah Academy in Candler, North Carolina, in 1990 and went on to Southern Adventist University in Collegedale, Tennessee. There he received a Bachelor of Arts in Biology in August 1994. In August 1995, he was accepted into the Department of Entomology and Plant Pathology at The University of Tennessee, Knoxville. Under the direction of Dr. Jerome Franklin Grant, he completed the requirements for a Master of Science degree in Entomology and Plant Pathology in December 1997. He is a member of the Entomological Society of America, Tennessee Entomological Society, and Gamma Sigma Delta Agricultural Honor Society.

1119 8651 2
07/21/05 HFB 