2003

Ten Years of Change in Beech Stand in North Central Maine Long Affected with Beech Bark Disease

Amanda Farrar

TEN YEARS OF CHANGE IN A BEECH STAND IN NORTH CENTRAL MAINE LONG AFFECTED WITH BEECH BARK DISEASE

By

Amanda Farrar

B.A. University of Maine Farmington, 1998

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Forestry)

The Graduate School

The University of Maine

August, 2003

Advisory Committee:

William D. Ostrofsky, Assistant Professor of Forest Resources, Advisor

William H. Livingston, Associate Professor of Forest Resources

Alan J. Kimball, Associate Professor of Forest Resources

TEN YEARS OF CHANGE IN A BEECH STAND IN NORTH CENTRAL MAINE LONG AFFECTED WITH BEECH BARK DISEASE

By Amanda Farrar

Thesis Advisor: Dr. William D. Ostrofsky

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
(in Forestry)
August, 2003

In Maine, northern hardwood stands long affected by beech bark disease often still have high numbers of beech trees. This is mostly due to sprouting, and most new stems become severely infected with the disease. Beech that are resistant to the scale insect, *Cryptococcus fagisuga* Lind., the inciting factor for the disease complex, do exist and often occur in clumps of root sprout origin. In 1989 a long-term study of the effects of commonly used seasonal harvesting regimes on regeneration initiation and survival was established in north central Maine. Treatments included harvest season (winter or summer) and intensity (clearcut or partial cut). Resistant trees were paired with nearby susceptible trees that were of similar height and diameter, and then the trees were randomly chosen as a pair to be cut or left standing. The numbers of seedlings and sprouts that occurred in 174 15-foot radius plots around these study trees were counted annually from 1992-1994. The annual growth of over 3100 sprouts and seedlings were

monitored. Initial results showed that the season of harvest, degree of overstory removal, and the cutting or leaving of trees had no effect on the numbers of sprouts initiated as a result of harvesting.

In the summer of 2002, the original plots were re-established to determine sprout mortality associated with seasonal harvesting regimes. Out of the 174 original study trees, 172 were located, and the total number of sprouts and seedlings that occurred within the plots were recorded. Height and diameter measurements were taken on the monitored sprouts, seedlings within each plot.

Summer harvests, and clearcut treatments, resulted in the highest regeneration mortality; 71% mortality in the summer harvests and 69% mortality in the clearcuts. By 2002, resistant study trees that originally were left after harvest had 67% mortality in winter clearcuts and 78% mortality in summer clearcuts, suffering no mortality in any of the partial cut or uncut stands. This demonstrates the importance of protecting resistant trees with uncut "islands" to insure their survival. Understanding the consequences of seasonal harvesting practices on root disturbance and resistant trees may hold the key to improving the quality of beech in stands affected with beech bark disease.

ACKNOWLEDGEMENTS

I would first like to thank my advisor, Bill Ostrofsky for his help and guidance over the past two years. I would also like to thank the members of my committee, Al Kimball and Bill Livingston. Al was particularly helpful in the GPS and GIS portion of this project, and in swapping fishing and hunting stories. Bill was always available to me, and his input and encouragement throughout this process were invaluable. I want to extend my appreciation to Dave Houston, without the maps and information he provided, this would not have been possible. I would also like to thank Bill Halteman, who was extremely helpful in the statistical analysis portion of this project.

The study area was located on land owned by the Maine Bureau of Parks and Lands, and I would like to extend my appreciation to them. My field work would not have been nearly as much fun without my field assistant, Maggie Burke, who always kept me laughing. Speaking of field assistants who made me laugh and kept me sane, I would like to thank my dog Bailey who kept the squirrels, bears, and rabbits at bay throughout the summer, and kept my feet warm under my desk in Nutting Hall all winter.

My friends and family are who made this possible. Thanks go to all of my friends, particularly the graduate and undergraduate students, and the professors that I met in Orono. I would particularly like to thank Steph, Dan, and Tucker Phillips for their help, laughter, and encouragement. My mother, Mary, spent time with me in the field and makes a darn good lunch. My father, Bob, instilled in me my love of the outdoors and always kept me thinking about going on that next fishing trip. My grandparents, Mary and Charlie, always taught me to believe that the only limits I had were the ones that I put on myself.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: INTRODUCTION

Beech bark disease is an introduced disease complex that affects American beech (*Fagus grandifolia* Ehrh.) throughout much of its range in North America The disease was first found in Maine's forests in 1931 (Ehrlich 1934, Houston 1994a). Beech bark disease is incited by the beech scale insect (*Cryptococcus fagisuga* Lindinger), which feeds on the living phloem of the host tree. The feeding alters the bark tissue and predisposes the tree to infection by one of several species of canker fungi in the *Nectria* genus including *N. coccinea* var *faginata* Lohm., Watson, and Ayres, *N. gallingena* Bres., and *N. ochroleuca* (Schweinitz) Berkeley. The scale insect and most likely *N. coccinea* var. *faginata* were first introduced to North America in Halifax, Nova Scotia around 1890 on imported ornamental beech from Europe (Ehrlich 1934, Spaulding et al. 1936, Cotter and Blanchard 1981, Houston and O'Brian 1983, Houston 1994b).

This disease has had numerous detrimental effects on northern hardwood stands containing American beech. In contrast to other introduced diseases such as chestnut blight, which largely eliminated the host tree from its range, beech bark disease has not caused widespread, consistent declines in beech abundance. Instead, the disease has led to an increase in the percentage of beech in many stands in terms of basal area and stems per acre (Houston 1994b). This increase in abundance in response to beech bark disease can be attributed to the species powerful sprouting ability after experiencing root disturbance and ability to persist due to its extreme shade tolerance.

Even in stands that have been affected by beech bark disease for years, a few beech that are free of insects and disease can often be found. Experiments on trees that had remained free from natural infestation confirmed that some trees were resistant to *C. fagisuga* (Houston 1982, 1983a). Later studies determined that approximately one percent of the population of beech is resistant to the disease (Houston and O'Brien 1983, Houston 1997, Houston and Houston 1987, 1994, 2000). Due to the vegetative reproductive habits of the species, resistant trees are often clustered together in genetically related groups (Houston 1983a, Houston and Houston 1987). Isozyme studies have shown that such trees are closely related or identical genetically (Houston and Houston 1994, 2000).

There have been numerous studies concerning the biology of the disease (Ehrlich 1934, Shigo 1964, 1972, Houston 1975, 1983a, 1994a), fewer have considered the long-term effects of different harvesting regimes on beech abundance. Mielke et al. (1986) and Ostrofsky and Houston (1988) discussed harvesting alternatives for stands affected by beech bark disease, stressing that harvesting levels will affect the amount of beech regeneration in the aftermath stand that will become diseased.

Jones and Raynal (1988) found that root sprouting was influenced by the season of injury and is influenced by light exposure and higher temperatures. Houston (2001) found that the season of harvest, degree of overstory removal, and the cutting or leaving of trees had no effect on the numbers of sprouts initiated as a result of harvesting. These results were measured shortly after harvest. The long-term survival of beech regeneration after seasonal harvesting regimes has not been studied. In addition, the condition of resistant trees after various harvesting regimes has not been studied.

Understanding the consequences of the season and intensity of harvest on root disturbance and the survival of resistant beech may hold the key to improving the quality of beech in stands affected with beech bark disease. Determining the long-term effects of different harvesting practices will allow forest managers to evaluate the potential effects of harvesting on stands affected with beech bark disease and make management decisions that will encourage the survival and propogation of resistant trees.

This paper presents the results of a study that investigated the effects of forest practices on beech regeneration survival ten years post harvest and the effects of various harvesting practices on residual resistant trees. Three hypotheses were tested:

$H1_0$: Ten years after harvest, there is a difference in American Beech sprout mortality between summer and winter cuts.

$H2_0$: American beech regeneration survival is greater around resistant than around susceptible trees.

$H3_0$: Different harvesting levels have a different affect on the survival of residual resistant beech.

CHAPTER 2: LITERATURE REVIEW

Beech Bark Disease

Beech bark disease is a decline disease involving inciting, predisposing, and contributing factors (Manion 1991). This introduced disease complex affects American beech (*Fagus grandifolia* Ehrh.) throughout much of its range in North America, and was first found in Maine's forests in 1931 (Ehrlich 1934, Houston 1994a). Beech bark disease is incited by the beech scale insect (*Cryptococcus fagisuga* Lindinger), which feeds on the living phloem of the host tree by inserting its stylet into the bark. The feeding alters the bark tissue and predisposes the tree to invasion by one of several species of canker fungi in the *Nectria* genus including *N. coccinea* var *faginata* Lohm, Watson, and Ayres, *N. gallingena* Bres., and *N. ochroleuca* (Schweinitz) Berkeley.

The scale insect and most likely *N. coccinea* var. *faginata* were first introduced to North America in Halifax, Nova Scotia around 1890 on imported ornamental beech from Europe (Ehrlich 1934, Spaulding et al. 1936, Cotter and Blanchard 1981, Houston and O'Brien 1983, Houston 1994a). This disease has had numerous detrimental effects on northern hardwood stands containing American beech, but in contrast to other introduced diseases such as chestnut blight, which largely eliminated the host tree from its range, beech bark disease has not caused widespread, consistent declines in beech abundance (Houston 1994b). In fact, the number of beech stems has increased. United States Forest Service forest inventory reports recorded 86 million beech stems in 1984 and 146 million beech stems in 1996 (Powell and Dickson 1984, Griffith and Alerich 1996). The increase

in these stems provides a challenging problem for management. The high stem density of the shade tolerant beech prohibits the regeneration of other, more valuable species, and the stems become quickly diseased, defective, slow growing, and susceptible to future infection with beech bark disease (Kelty and Nyland 1981).

Biology of the Insect and Fungus

The first sign of beech bark disease is the presence of the scale insect, which appears as white wooly spots on the bark. The white wool is a waxy secretion produced by the insect that covers and protects it. The tiny, soft-bodied adult beech scale insect reproduces parthenogenetically; all insects are females. The only mobile stage of the insect is the first instar nymph or crawler stage. Crawlers are primarily dispersed by wind, but are occasionally dispersed long distances by small mammals or by humans (Ehrlich 1934, Brown 1934, Wainhouse and Gate 1988, Houston 1994a). Once the insect inserts its stylet and begins to feed, it becomes an immobile, second-instar nymph. It remains in this stage throughout the winter. The insect changes the bark tissue by altering the tree's natural defenses, which allows insects to feed for an extended period of time without the tree producing a wound periderm (Manion 1991, Wainhouse and Gate 1988). It is in these areas the *Nectria* fungi are able to gain entrance to the tree.

Three species of *Nectria* fungi are associated with beech bark disease in North America. *Nectria galligena* is a native pathogen that causes perennial cankers on many hardwood species, including yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), and sugar maple (*Acer saccaharum* Marsh) (Spaulding et al 1936, Cotter and Blanchard 1981). It rarely affects beech, however, unless the beech scale is present (Houston 1994b). An exotic pathogen, *N. coccinea* var. *faginata*, is believed to

have been introduced from Europe at the same time as the scale. Often, the native *Nectria* species is the first to invade trees infested by beech scale, followed by the slower spreading exotic *Nectria* species (Meilke et al. 1986, Houston 1994b). The third known *Nectria* species found in association with the beech bark disease complex is *N. ochroleuca* (Houston 2002). The *Nectria* fungi kill tree tissue for sustenance and the cankers that form from infection eventually girdle and kill the tree. Since trees must be attacked by the scale insect before *Nectria* spp. can infect them, factors that determine scale establishment also determine *Nectria* infection (Houston et al. 1979, Burns and Houston 1987, Wainhouse and Gate 1988). *Nectria* fungi usually follow 5-10 years after initial scale infestation (Manion 1991).

Early signs of *Nectria* spp. infection include a brownish fluid oozing from dead tarry spots on the trunk (slime-flux). In the later stages of the disease, both the native and exotic fungi produce fruiting bodies called perithecia. The perithecia are tiny, bright red, lemon-shaped clusters found on the living or dead bark. Each perithecium is filled with sacs of spores. These spores are the sexual stage of the fungus. Spores are released from perithecia and are carried by wind. On some infected trees perithecia are abundant, causing large areas of the bark to appear red (Ehrlich 1934, Shigo 1972, Houston 1994a). The asexual stage of the fungi, (sporodochia), appear as small white spots on the bark (Shigo 1972).

Another scale insect, *Xylococculus betulae* (Perg.) Morrison causes a serious defect in beech, and seems to increase in abundance in areas long affected by beech bark disease (Shigo 1964). *Xylococculus betulae* is a large, orange-pink soft-bodied scale insect that establishes itself deep in the bark and can be identified by the waxy tube it

excretes which protrudes from the bark. The true abundance and distribution of this insect is not known, nor is its direct relationship with the beech bark disease complex (Houston 1975). It causes defects on the bark of young trees normally too small to be infested with *C. fagisuga*, which increases the susceptibility of host trees to *C. fagisuga* by creating spatial niches for the insect. Once the beech scale is present, it promotes the establishment of *Nectria* (Shigo 1964, Houston 1975, Sinclair et al. 1987).

Tree Resistance

American beech is unique among temperate hardwood species in that the outer bark is thin, and under normal circumstances remains smooth into old age. This characteristic makes it particularly susceptible to sucking insects (Tubbs and Houston 1990). In stands that have been affected by beech bark disease for years, a few beech that are free of insects and disease can often be found. Experiments on trees that had remained free from natural infestation confirm that some were resistant to *C. fagisuga* (Houston 1982, 1983a). Later studies confirmed that approximately one percent of the population of beech is resistant to the disease (Houston and O'Brien 1983, Houston 1997, Houston and Houston 1987, 1994, 2000). Due to the powerful vegetative reproductive habits of beech, resistant trees are often clustered together in genetically related groups (Houston 1983, Houston and Houston 1987). Isozyme studies have shown that such trees are closely related or identical genetically (Houston and Houston 1987, 1994).

Resistance involves bark structure and chemistry that make certain trees unsuitable as hosts for the beech scale. European beech resistance to beech bark disease has been found to be associated with genotype in planted orchards (Wainhouse and Deeble 1980). Dübler et al. (1997) looked at the bark phenols of European beech, *F.*

sylvatica L., and found when being attacked by the scale insect, European beech emits a higher concentration of certain bark phenols. These phenols are thought to be either toxic to the scale insect, or limiting to certain enzymes the scale needs for nutrition. It is believed that this is a defense reaction European beech has developed in response to scale attack; a trait thought to be a result of a coevolutionary relationship (Krabel and Petercord 2000). Similarly, it has been found that the bark of resistant American beech has significantly lower concentrations of some amino acids and nitrogen than does uninfested bark of susceptible trees. Amino nitrogen is a significant limiting factor to sucking insects such as the beech scale. This suggests that bark structure and chemistry make certain individuals unsuitable as hosts for the beech scale, but why this happens in some trees and not in others is unknown (Wargo 1988).

Isozyme patterns unique to resistant trees have not been found and the control of resistance is believed to be multigenic, or caused by more than one gene (Houston and Houston 1994, Morris et al. 2002). Attempts have been made to use *in vitro* propagation to conserve American beech with resistance to beech bark disease. Because a resistant genotype has not yet been located, this is done by going into forests affected with beech bark disease, identifying resistant trees, and collecting shoot tips and root sprouts from them. One of the barriers to propagating resistant beech is that the shoots have a very low survival rate. Barker et al. (1997) attempted to propagate juvenile and mature beech, and only had 6 out of the 41 shoots survive to be planted in a growth room.

One of the most important management recommendations that has come forth since the onset of this disease is to retain resistant trees in stands slated for harvesting (Burns and Houston 1987, Manion 1991, Patton 1997, Houston 2001). Knowledge of the

genetic structure of forests can provide valuable insights for forest managers as they make silivicultural decisions for forests impacted by beech bark disease. More genetic research is needed throughout the range of beech to better understand the genetics of resistance of American beech and to understand the potential roles of genetic resistance and chemical defense to beech bark disease. Efforts to identify and select resistant or partially resistant trees will be a critical part of reducing the long-term vulnerability of beech to beech bark disease.

Other Organism Interactions

Other organisms colonizing beech bark may interact with scale populations and thereby influence the course of the disease. Some bark epiphytes growing of beech offer valuable spatial habitats for *C. fagisuga* (Ehrlich 1934, Houston et al. 1979). Colonies often develop initially beneath patches of moss and lichen, which offer some protection to the insect. However, not all epiphytes enhance infestations. In some stands in Nova Scotia that are on steep, south facing slopes, beech were found that are free of disease. Other trees in the general area were severely affected with beech bark disease. Houston (1983b) found that the disease free trees were heavily colonized by mosaics of crustose lichens, which appear to be antagonistic to scale establishment. A fungus, *Ascodichaena rugosa*, colonizes the outer bark of some beech, preventing scale establishment. Because this fungus does not cover the entire bark surface, both organisms are often found on the same tree (Houston 1997).

There are no known invertebrate parasites of *C. fagisuga*, but other organisms affect both *C. fagisuga* and *Nectria* species. The twice-stabbed ladybird beetle, *Chilocorus stigma* Say, feeds on the scale but has not been shown to reduce scale

numbers at a stand level. It is thought that its effectiveness at controlling scale populations is limited by three main factors: its propensity to disperse, its failure to feed on all life stages of the scale, and by the high rate of scale reproduction (Mayer and Allen 1983). It is also thought to be a vector for *Nectria* spores (Shigo 1964, Houston 1994a). A fungus, *Nematogonum ferrugineum* (*Gonatorrhodiella highlei*), parasitizes the *Nectria* fungi, but is not extremely effective as a biological control agent (Houston 1983b)

Effects on Stand Composition and Structure

Beech bark disease swept through Maine and the rest of New England between 1930 and 1970, moving westward and southward at an estimated 10 kilometers a year (Mielke et al. 1986). The disease presents itself in different ways depending on the amount of time that it has been in an area. Shigo (1972) identified three stages of beech bark disease: the advancing front, the killing front, and the aftermath forest. In the advancing front, scale populations are introduced, build and spread but *Nectria* spp. are not yet involved. In this stage, there are healthy, mature trees in the overstory. Maine experienced the advancing front from the late 1920's to the late 1950's (Ehrlich 1934, Spaulding et al. 1936, Houston 1994a). Stands can be infested with beech scale for several years before *Nectria* infection is widespread, generally 5-10 years.

The killing front is characterized by high levels of scale infestation, severe *Nectria* outbreaks, and high tree mortality. Maine experienced the killing front between the 1940's and 1960's, losing 85% of the mature beech (Houston et al. 1979). The aftermath forest refers to stands that have experienced the first wave of beech mortality with most of the residual beech defective or declining and endemic populations of the scale and *Nectria* fungi present. Some large trees remain, many of which either escaped

scale infestation or are at least partially resistant. Also present in the aftermath forest are large numbers of slow growing beech sprouts, which usually became established as a result of salvage cuttings (Houston 1975, 2001, Burns and Houston 1987).

Beech has a powerful ability to produce root sprouts when the root system sustains injury. Natural ground disturbancesuch as freezing and thawing can cause root injury and stimulate beech roots to sprout. Because of the sprouting ability of beech when it incurs injuries to the root system, harvesting stimulates even more sprouts than are stimulated under natural circumstances (Jones et al. 1989). Root sprouts are clones of the parent tree, and are equally susceptible to beech bark disease. These sprouts can succumb to beech bark disease as they mature (Houston 1975, Houston and Houston 1987, 2001). Several things have encouraged the growth of beech root sprouts and saplings of seedling origin, including the highgrading of other more desired species leaving beech residuals, partial harvesting without understory treatment, and the occurrence of beech bark disease. This has resulted in stands with even a higher proportion of beech. Beech bark disease has had the greatest impact in these stands (Mielke et al. 1986).

In uncut stands, fewer sprouts are produced around low-vigor beech trees compared to high-vigor beech stands, although there was no difference in the vigor of the sprouts themselves. In addition, parent trees with larger diameters have been found to have more sprouts around them (Jones and Raynal 1986, 1987). Jones et al. (1989) found no consistent, significant difference in height growth between beech sprouts or seedlings. Sprout initiation, growth and survival may decrease when only scattered parent beech trees decline in stands where beech density is low (Twery and Patterson 1984). Sprout

initiation or growth is often stimulated when trees decline and die in beech dominated stands (Houston 1975, Ostrofsky and McCormack 1986). Root sprouting has been found to be influenced by season of injury. Jones and Raynal (1988) discovered that fewer sprouts were initiated when roots of uncut trees were wounded in the fall than in the spring; they found that roots injured in the fall had less vigorous callus formation. In addition, they found that roots that were exposed stimulated more bud initiation than those that were underground.

Stand age and density, tree size, and species composition affect disease severity, especially in forests affected for the first time. Older stands with a high component of large beech trees are most vulnerable and in such stands tree mortality can be very high (Valentine 1983). Older, weaker trees with large, broken branches, or suffering from attack by decay fungi often die quickly once *Nectria* becomes established (Mize and Lea 1979). Twery and Patterson (1984) found that in forests in Massachusetts and New Hampshire stands rich in hemlock were especially vulnerable to beech bark disease.

In the Allegheny hardwood forest of Pennsylvania, DiGregorio et al. (1999) and Krasney and DiGregorio (2001) found that beech was the most common gap maker. The standing dead or fallen trees making these gaps had been infected with beech bark disease. In old-growth forests, many of the gaps were created by beech and were a result of the effects of beech bark disease (Chokkalingam 1998). Beech was also found to dominate the sapling layer in old-growth forests of Maine, suggesting that even in areas in which harvesting has not played a part, the disease has increased the beech component (Chokkalingam 2000).

Management

The effects of disturbance caused by beech bark disease have long-term management implications. Many hardwood stands have been rendered less productive as a result of high levels of defective, susceptible beech and dense thickets of beech reproduction (Ostrofsky and McCormack 1986, Manion 1991, Houston 2001). The lack of soil disturbance and dense shade created by beech saplings create unfavorable conditions for seedling regeneration of other species (Jones et al. 1989). Stands affected by beech bark disease are managed for a variety of uses, so it is important to understand the ways in which harvesting, severity of beech bark disease, and beech abundance are related.

Houston (1975) suggested that past management practices, such as highgrading, left stands dominated by beech. Beech was often left as more valuable species were cut from the stand. In addition, he pointed out that attempts to rid the forest of beech in response to beech bark disease have actually increased the amount of beech in the aftermath forests of Maine. Meilke et al. (1986) concurs with Houston, agreeing that both highgrading and salvage operations are responsible for the increased beech abundance but he adds that partial harvesting, without herbicide treatment, has also helped to increase the number of beech stems present in the forest today.

There have been a number of studies that have found that ground-applied foliar herbicide treatment prior to or in combination with harvesting helps to reduce beech sprouting and encourages the growth of other more desirable hardwood species (Kelty and Nyland 1981, Horsley and Bjorkbom 1983, Ostrofsky and McCormack 1986). Kelty and Nyland (1981) and Horsley and Bjorkbom (1983) recommended the treatment of

beech understories with ground-applied herbicides prior to harvest to increase the regeneration of other more valuable hardwood species. Ostrofsky and McCormack (1986) used herbicides to control dense advance regeneration and root sprouts that resulted after a harvest in northern Maine. In this study, resistant trees were left as a component of the residual overstory, along with sugar maple, red maple, yellow birch and paper birch. They were able to reduce the beech component in the understory, while increasing the abundance of other, more desired species. Using ground applied herbicide treatments to control beech regeneration is costly and labor intensive. Other methods for improving stand composition and quality in areas affected by beech bark disease need to be developed and tested.

Harvesting alternatives in stands affected by beech bark disease were studied in the Bartlett Forest in New Hampshire. Filip (1978) examined a harvesting study on a beech stand that was managed under the single-tree selection system from 1952-1976, when the peak of the killing front was sweeping through the area. The rational behind this system was to remove the defective beech from the overstory in an attempt to minimize the impact of the disease in the stand. He recommended group selection cutting in conjunction with single tree selection as an alternative where the objective is uneven-aged management. He believed that the combination of cuttings would help to regain control of stand development in areas that had been decimated by beech bark disease.

Jones et al. (1989) considered the effects of selection cutting on beech seedlings and sprouts. They found that 38-65% of all the beech seedlings and sprouts in the understory were advance regeneration (established before the harvest) and were

significantly taller than regeneration established after the harvest. Patton (1997) found that when stands were not harvested, beech would out compete yellow birch. In contrast, in partial cuts and clearcuts, beech was out-competed by yellow and paper birch. In these situations, beech bark disease defect was less common but more severe on individual trees, than in the no-cut situation. Burns and Houston (1987) suggested that harvesting all or most of the mature, defective beech and leaving beech with smooth or blocky bark, may work to reduce the proportion of the beech understory after harvest.

The season of harvest may be an important factor in sprout initiation and development. Jones and Raynal (1988) found that there was more sprouting on roots that were injured in the fall than on those that were injured in the spring. It has long been assumed that winter harvests result in fewer sprouts than summer harvests due to the protection that the snow cover provides to roots. Houston (2001) looked into harvesting methods that would improve stand quality by reducing the number of susceptible beech and increasing the number of resistant beech. He monitored the effects of different harvesting systems on susceptible and resistant beech. Stands were partially cut or clearcut in the summer or in the winter. He found that 2-3 years after treatment, there were significantly more sprouts around resistant trees than around susceptible trees with winter clearcut harvests and summer partial cuts enhancing the sprout development around resistant trees. The long-term effects of seasonal harvesting regimes on beech regeneration have not been studied.

CHAPTER 3: METHODS

Study Area

The study area was located on the Maine Public Lands, Sebois Unit, in southern Piscataquis County in north central Maine. This area is part of the western foothills region of Maine (McMahon 1990, Figure 3.1). Initially established in 1989 by Houston (2001), the study area consisted of 15 10-acre blocks located on a hardwood ridge running from north to south and ranging in elevation from 495 ft to 760 ft (Figure 3.2). The forest in this area is dominated by American beech. Other species in the stand include sugar maple, yellow birch, red maple, striped maple and white ash.

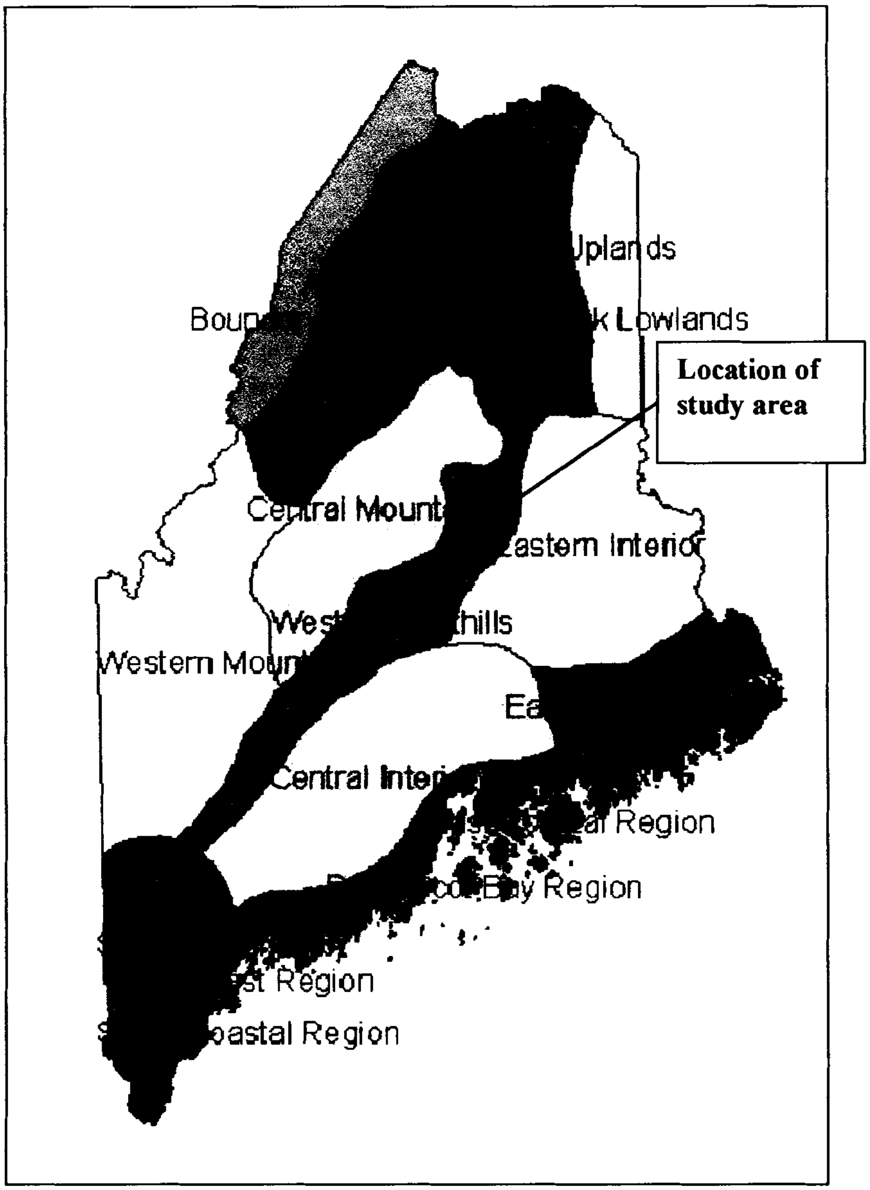

Figure 3.1. Location of study area within Maine's biophysical regions

In the original study, 5 block-level seasonal harvest treatments were assigned to the 15 blocks, with each treatment replicated 3 times: summer clearcut blocks (SC), summer partial cut blocks (SP), winter clearcut blocks (WC), winter partial cut blocks (WP), and no cut control blocks (NC). Harvesting was done with chainsaws, with hand crews and skidders. Block corners were marked with 2 ft lengths of 1 in diameter PVC pipe driven into the ground. The original data was collected in both metric and English units, and this study followed the original protocol. In 2002, the block boundaries were re-established using maps from the original study in combination with a compass and a GPS unit. The original maps were scanned, then digitized using MapInfo 6 software. The UTM coordinates were later loaded into a Garmin GPS III GPS unit to facilitate the location of the block corners. A total of 43 of the 44 original block corners were located.

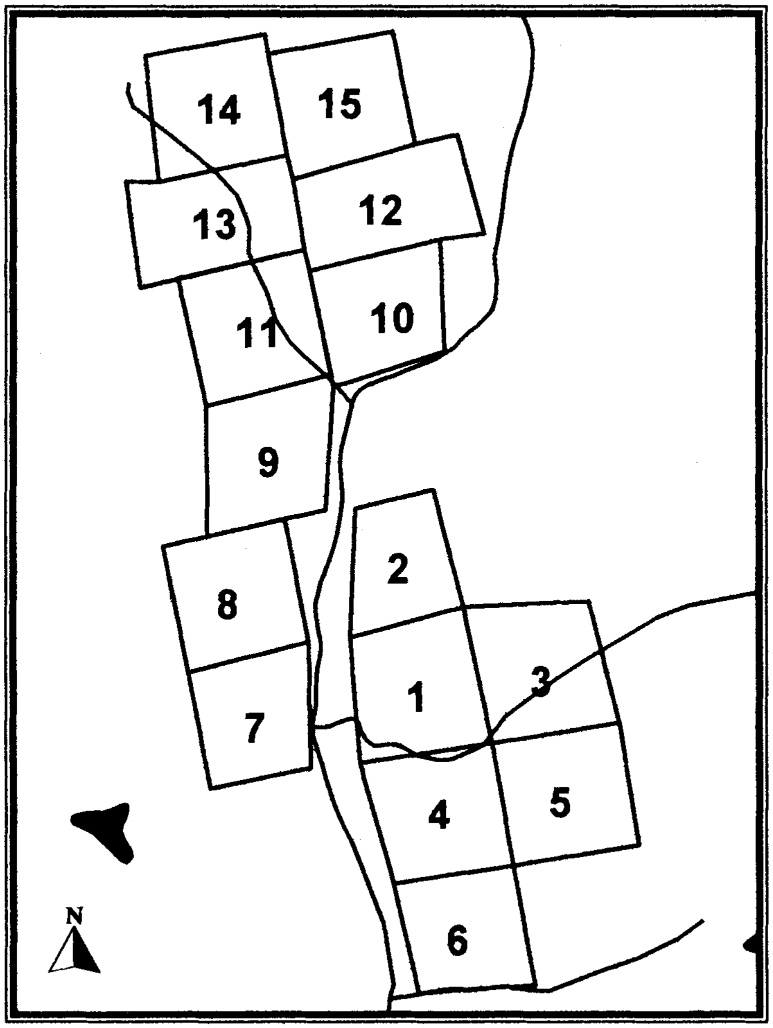

Figure 3.2. Harvest treatment blocks: SC = summer clearcuts (Blocks 11, 12, 13); SP = summer partial cuts (Blocks7, 8, 14); WC = winter clearcuts (Blocks 3, 5, 6); WP = winter partial cuts (Blocks 1, 2, 4); NC = no cut controls (Blocks9, 10, 15).

Stand Plots: Overstory Data

After the original blocks were located, the original transect points were re-established. Transect points ran diagonally from corner to corner through each block. There were 5 transect points per block for a total of 75 (Figure 3.3). As with block corners, transect points were marked with labeled 2-ft PVC pipes driven into the ground. Data on overstory composition and structure were obtained using point samples centered on these points. Species, diameter at breast height, and crown class were recorded for trees selected using a BAF 10 prism. The estimated percent live crown, severity of scale infestation, presence of *Xylococculous betulae*, and severity of defect of all beech trees selected by the prism were also noted. In addition, the UTM position of the transect point was recorded with the Garmin GPS.

Stand Plots: Regeneration Data

Data on regeneration were obtained in nested 1-m and 2-m plots located in the middle three of the five transect points in each block. The plot centers for each of the plots was located 40.5 ft from the transect points in the 4 cardinal directions (Figure 3.3). There were 12 of each type of plot in each block, for a total of 180 nested plots. The plot centers were marked with labeled, 2-ft lengths of PVC. In the 1-m plots, all species < 2.5cm diameter at 10 centimeters from the ground were counted and recorded. The saplings were split into 3 height classes: < 25 cm, 26-50 cm, and > 50 cm. In the 2-m plots, trees that were 2.5-10 cm diameter at 10 cm from the ground and > 1 m tall were counted and sorted. On beech stems recorded in the 2-m plots, any scale or defect present was noted.

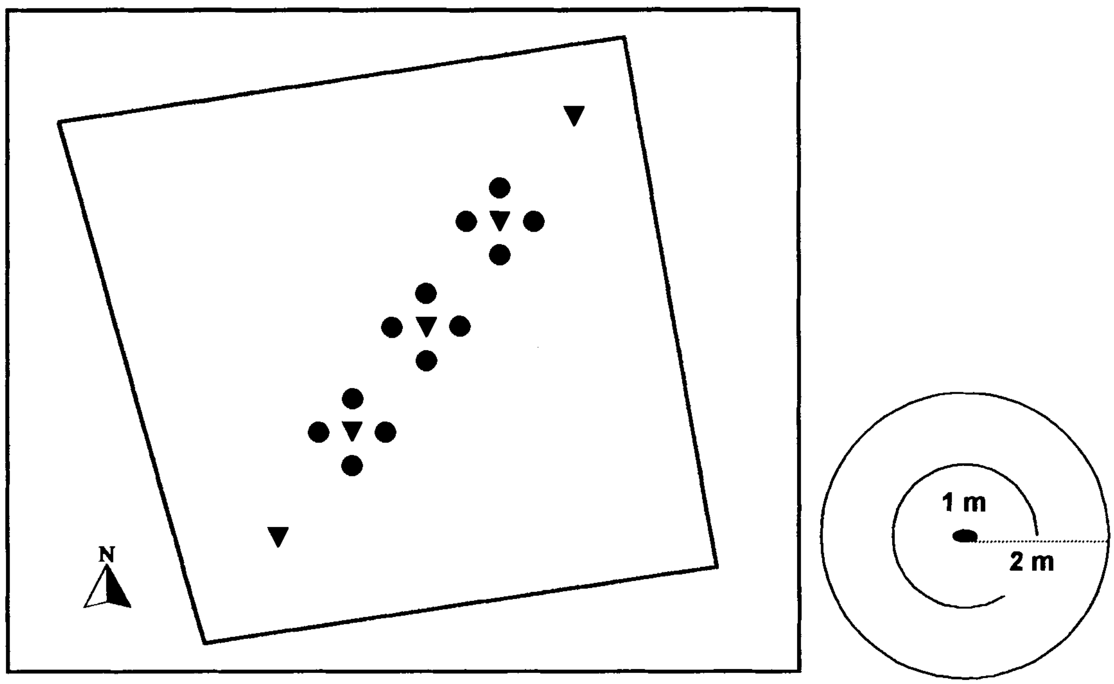

Figure 3.3. Sample regeneration plots (circles), transect points (triangles), and nested regeneration plot (right)

Long-Term Study Plots

In addition to the stand plots, additional plots were established for long term observation. In the original study (Houston 2001), 87 resistant beech trees were selected and paired with a nearby susceptible tree, allowing for 174 study trees total. Trees were cut or left as pairs. Houston established discrete, 15-foot radius plots around each of these trees, and 20 sprouts or seedlings were selected and tagged for long-term study. For the follow-up study, 171 of the original 174 study plots were located and re-established. In each plot, the UTM coordinate of the center tree or stump was recorded with the Garmin III GPS unit. Sprout maps from the original study were used to relocate the original 20 tagged sprouts and seedlings. It was recorded whether or not the original sprout or seedling was alive or dead, and the maps were updated to reflect any mortality found. Sprouts or seedlings were retagged and recorded separately. The diameter in mm at 2 cm from the ground and the height in cm were also noted. Point of origin of each sprout was recorded as being from the top, bottom, or side of the parent root. The diameter of the parent root was recorded in mm at the point of sprout origin. Within the 15-ft radius plot, the total number of sprouts and seedlings within the plot were counted and recorded.

Statistical Analysis

All data were analyzed using Systat 10.2 software. Mortality data acquired in the 15-ft radius study plots were pooled within blocks to determine the number of living regeneration. Percent living regeneration was calculated by dividing the total number of tagged sprouts found alive in the study plots by the total number sprouts that were there originally. A 3-way ANOVA was used in conjunction with Systat's general linear model

to determine differences among main effects: harvest treatment, resistance/susceptibility of study tree, and cut/leave status of study tree against the response variable percent alive. Due to lost degrees of freedom because of the lack of cut trees in the control blocks, a general linear model was run with the same data, and hypothesis tests were done on each factor level. Two other 3-way ANOVAs were examined to determine if there were main effects associated with season of harvest and type of cut (clearcut or partial cut). Pearson's correlation was used to test for normality and a Levine's test was done to test for constant variance in all cases. Standing study trees from the long term treatment plots were separated by treatment block and their resistant or susceptible status, and a percentage survival per treatment was determined.

CHAPTER 4: RESULTS

Site Characterization

Slope and elevation did not vary considerably among treatments (Table 4.1). Slope ranged from 7.58% in the winter partial cut blocks to 14.12% in the winter clearcut blocks. Elevation ranged from 186 feet in the winter partial cut blocks to 227 feet in the summer partial cut blocks. Aspect was mostly northwest in the clearcut and control blocks, and was predominantly south in the other treatments.

Table 4.1. Mean site conditions for each treatment

	% Slope		Aspect (azimuth)		Elevation (ft)	
	mean	range	Mean	range	mean	Range
No cut control	9.2	7-10.7	307 (NW)	270-322	221	169-290
Summer clearcut	8.6	7-9.2	286 (NW)	273-295	189	173-215
Summer partial cut	11.2	7-13.9	233 (SW)	233-238	227	192-290
Winter clearcut	14.1	11-15.8	136 (SE)	129-145	246	199-293
Winter partial cut	7.6	5-9.3	130 (SE)	96 -148	186	170-199

Overstory Composition

The 15 10 acre blocks differed in overstory composition and structure. The mean basal area per acre by species for each of the treatment blocks was calculated from the data collected along the transect points in each of the treatment blocks. Beech was dominant in all treatments, being less prevalent in the summer and winter clearcuts (Table 4.2). Mean block basal area ranged from 50 to 128 ft^2/acre. Most of the blocks had small amounts of yellow birch, striped maple, and sugar maple. Other hardwoods and softwoods were present throughout the treatments at low levels.

Table 4.2. Mean basal area (ft^2/acre) for species by treatment[a,b]

Species	WC		WP		SP		SC		NC	
	Treatment									
American beech	33	(9.8)	94	(4.6)	67	(3.5)	24	(5.4)	81	(5.4)
Yellow birch	17	(5.5)	5	(.67)	15	(2.7)	9	(1.4)	13	(1.7)
Striped maple	13	(2.6)	7	(1.0)	16	(3.2)	7	(1.5)	6	(1.5)
Sugar maple	8	(5.0)	4	(.89)	4	(.58)	3	(5.8)	18	(3.0)
Other hardwoods	5	--	--	--	12	--	38	--	4	--
Softwoods	--	--	5	--	13	--	3	--	8	--
Total	76		110		114		81		122	
Percent Beech	49%		85%		59%		30%		66%	

[a] Standard errors are in parentheses
[b]Total basal area per species per block is available in Appendix B
Empty values indicate species not present

Regeneration Composition

Beech was present in the regeneration in all blocks (Table 4.3) but was not dominant in all blocks, nor was it equally prevalent in all treatments. In the 1-m radius regeneration plots in which smaller regeneration was tallied, summer clearcuts were dominated by species such as trembling aspen, sugar maple, hobblebush, balsam fir, and yellow birch, with beech making up only a minor component of the regeneration. Beech was also a minor component of the regeneration in the winter clearcuts. No trembling aspen, big-toothed aspen, or balsam fir were present. Summer partial cuts were also dominated by beech with other species such as striped maple, sugar maple, and yellow birch making up a large portion of the regeneration. Winter partial cuts overall were dominated by beech, with hobblebush and sugar maple composing much of the understory. The uncut blocks, although dominated by beech regeneration, had a strong presence of sugar maple, yellow birch and white ash.

Table 4.3. Regeneration stems per acre in 1m[a] and 2m[b] plots (in thousands of stems)[c]

	NC		SC		SP		WC		WP	
Species	**1m**	**2m**	**1m**	**2m**	**1m**	**2m**	**1m**	**2m**	**1m**	**2m**
American beech	12.4	.8	3.4	.9	11.0	1.0	4.3	.7	18.4	.8
Balsam fir	3.4	7.1	12.9	2.5	4.3	1.4	.6		1.3	
Big tooth aspen			2.1	.3						
Hobblebush	7.4		10.4		3.6	.6	5.2	1.3	12.6	
Hophornbeam	2.6	.3			2.6		1.6		2.6	
Red maple	11.5		2.9	2.8	7.9		5.3	.9	3.6	
Red spruce	1.3			.3	2.9		1.9		1.1	
Striped maple	4.8	1.2	2.9	1.4	8.2	1.2	2.9	1.2	2.9	.8
Sugar maple	10.9		5.9	2.1	8.9		11.7	.8	10.1	
Trembling aspen			9.5	1.7						
White ash	11.2		3.0	1.9	1.3		2.2	1.3	1.3	
Yellow birch	12.0		7.3	1.7	7.8		3.9	.9	5.6	.3

[a]1m plots include all stems < 1" dia and <1m tall

[b]2m plots include all stems > 1" dia and < 5" dia and > 1m tall

[c]Individual regeneration data per block and standard errors in Appendix B

Empty values indicate species not present

The 2-m radius regeneration plots were used to assess older and larger regeneration. Beech did not dominate the larger regeneration in any treatment. Striped maple was present in all treatments, as was beech and yellow birch. There was a high proportion of balsam fir in the no cut control blocks.

Beech Regeneration Survival, Ten Years Post Harvest

The general linear model using harvest treatment, resistance/susceptibility of study tree, and cut/leave status of study tree against the response variable percent alive met the assumptions of constant variance ($p=.04$). Survival had a significant response to harvest treatment ($p=.01$) but not with other main effects or interactions. The average survival of beech regeneration in the summer harvests was 29%, and the mean survival in winter harvests was 44% (Figure 4.1). The 3-way analysis of variance using season of harvest, resistance/susceptibility of study tree, cut/leave status of study tree against percent survival ($\alpha=.05$) was tested for normality using Pearson's correlation ($r = .987$), and a Levine's test was used to test for constant variance. Main effects were found with season of harvest ($p = .001$). Survival was lowest in summer harvest treatments. No significant interactions were found.

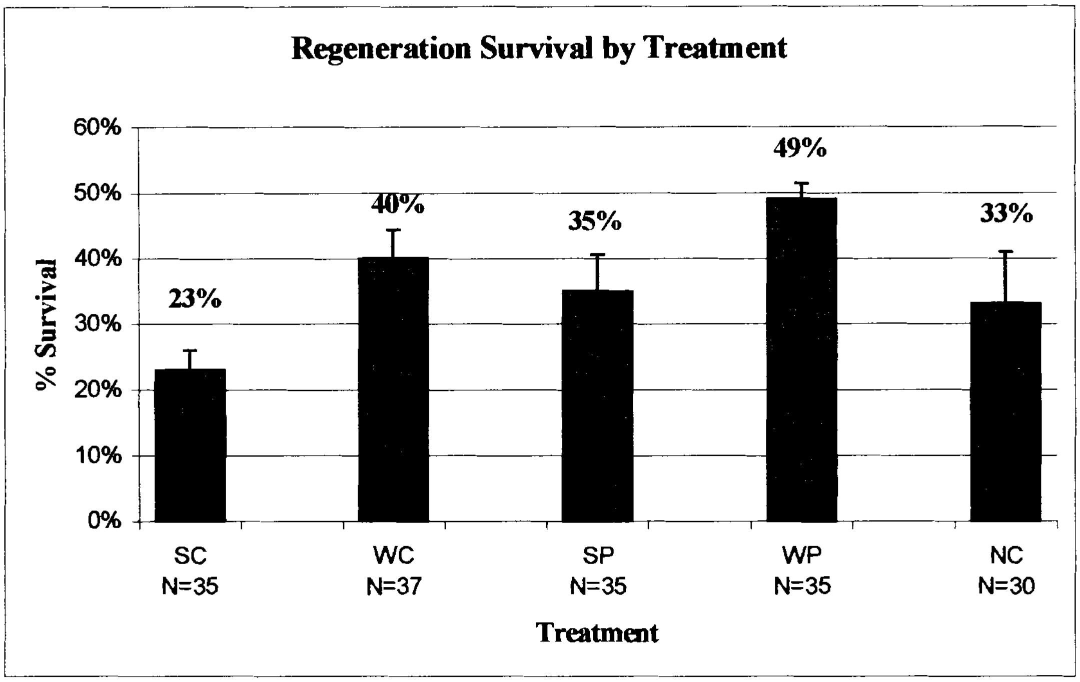

Figure 4.1. Beech regeneration survival by treatment

The average beech survival in clearcuts was 31%, while the average survival in partial cuts was 42%. The 3-way analysis of variance using type of cut (partial cut or clear cut), resistance/susceptibility of study tree, cut/leave status of study tree against percent survival (α=.05) was tested for normality using Pearson's correlation (r = .990). Constant variance was tested using the Levine's test. Main effects were found associated with type of cut (p=.029). Survival was lowest in clearcut treatments. No significant interactions or other main effects were found.

Study Tree Survival

Survival data on study trees left standing were pooled by treatment to detect differences in mortality among resistant trees. Resistant study trees suffered 78% mortality in summer clearcut blocks and 67% mortality in winter clearcuts (Figure 4.2). Resistant trees suffered no mortality in summer or winter partial cuts or in the control blocks. Due to lack of variation, ANOVA could not be calculated.

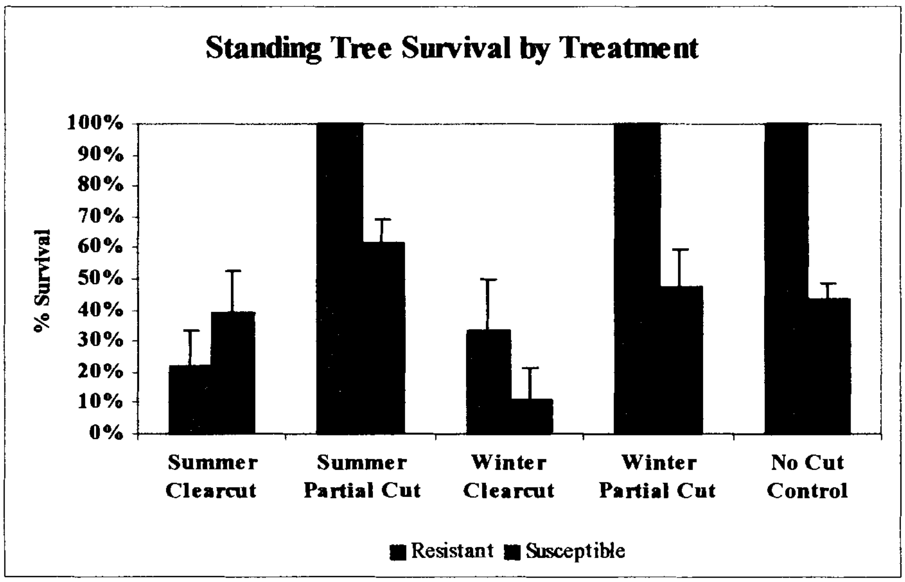

Figure 4.2. Standing tree survival by treatment
(Number of standing trees per treatment in Appendix B)

CHAPTER 5: DISCUSSION

Since its introduction to North America, beech bark disease has had a significant effect on stand composition and structure. The changes to stands by beech bark disease provides significant challenges to forest managers. Knowing the long-term affects of different harvesting regimes on beech regeneration and the survival of resistant trees may hold the key to improving the quality of beech in stands affected with beech bark disease.

The findings of this study indicate that the intensity of harvest and season of harvest affect regeneration survival ten years post harvest. In addition, there were differences found in standing tree survival among harvest treatments. This variation in regeneration and tree survival can be attributed to the different harvest strategies used, and possibly to site differences.

Site Characteristics

The fifteen, 10 acre blocks in this study varied in their composition and structure, although the differences in basal area among blocks can be attributed to the harvest treatments, particularly the clearcuts. Site variation associated with block location may have influenced the results. In general, the control blocks and the summer clearcut blocks averaged a northwest aspect; where the blocks partial cut and clearcut in the winter and the summer partial cut blocks overall had a southeast aspect. These differences in aspect may be an important factor in the mortality of beech regeneration in this study because slopes that face different directions are exposed to different site conditions.

Beech was not dominant in the summer clearcuts. Other hardwoods such as red maple, trembling aspen, big toothed aspen, and white ash dominated the species composition. This finding agrees with other studies, which have found that the increased light and soil scarification associated with clearcuts create conditions favorable for the establishment of wind dispersed intolerant species (Leak and Smith 1997, Patton 1997). Data acquired in the 1-m regeneration plots revealed that beech regeneration was most prevalent in the winter partial cuts and least prevalent in the summer clearcuts.

Beech Regeneration Survival

Sprout initiation is influenced by exposure to light and to higher temperatures (Maini and Horton 1966, Held 1983, Jones and Raynal 1986). The light level available to regeneration is considered to be the most important influence on growth rates in northeastern forests (Lorimer 1981, Runkle 1984, Oliver and Larson 1996), although a link between light level and long-term survival has not been studied. This study considered regeneration survival ten years post harvest and it is possible that light levels that result after various types of harvest are a factor in regeneration survival. The analysis of the survival of beech regeneration shows that harvest treatment affected regeneration survival. There was little difference in survival between winter clearcut blocks (41%) and winter partial cut blocks (48%). However, summer harvesting had lower survival with summer clearcut blocks (27%) having less survival than summer partial cut blocks (36%). Jones and Raynal (1988) found that callus development is affected by season and by root injury, but exposed roots had limited callus formation and low survival rates. In the summer clearcut blocks, in particular, many of the parent roots were visible above ground. It is possible that this exposure is responsible for the high

mortality rates found in the summer clearcuts, although this does not explain the low survival in the no-cut control blocks (33%).

Fewer sprouts are initiated when roots of uncut beech are wounded in the fall than in the spring. This result is attributed to the high mortality of fall-wounded roots, which have a less vigorous callus formation (Jones and Raynal 1988). Measurements taken shortly after harvest indicated that there were more sprouts in the summer cuts than the winter cuts, but that after three years of measurements, the high mortality found in the summer cuts negated any difference found (Houston 2001). The results of this study show that overall, the mortality of summer regeneration continued over time and in the end, regeneration survival in the summer treatments (29%) was lower than in the winter treatments (41%). Survival of regeneration was highest around cut trees in winter partial cuts (48%), and lowest around cut trees in summer clearcuts (27%). This could possibly be because the nutrient levels in roots are the highest in the late fall and early winter and lowest in the early spring and summer. Extra nutrients may help to increase the survival of sprouts living off of the nutrients that the parent tree provides (Taiz and Zeiger 2002).

Houston (2001) found that the lowest regeneration mortality was in the no-cut control blocks, which also was dominated by seedlings. Interestingly, ten years post harvest, regeneration survival was higher in the winter partial cut blocks (49%), summer partial cut blocks (35%), and winter clearcut blocks (39%), than in the control blocks (33%). This could be because seedlings are known to have a higher mortality than sprouts in some cases (Ward 1961). This could also be a function of site. For instance, the no-cut control blocks have the same aspect (northwest) as the summer clearcut blocks. There have been some studies that found that aspect affects hardwood

regeneration. George and Fisher (1991) looked at the quantity of oak regeneration at the Hoosier National Forest in Indiana, and found that regeneration increased from lower to upper slope positions and from a northeast to southwest aspect. Understanding the differences in soils, site index, and drainage classes between sites would help to better determine whether or not site was a factor in regeneration mortality in this study. Unfortunately, information on the soils and drainage classes for that area are not yet available, and site index for each site was not obtained due to the fact that the majority of the trees in the study area were beech affected with beech bark disease so this was not studied in detail. Regardless of that, the species that were found most commonly in the overstory on the site, American beech, sugar maple, and yellow birch, are generally found on the better quality sites. American beech, for example, is frequently found on mesic soils and does not do well on poorer sites (Tubbs and Houston 1990). Sugar maple grows on a variety of sites, but does the best in fertile, moist well-drained soils (Godman et al. 1990) Yellow birch grows best on well-drained, fertile loams and moderately well-drained sandy loams (Erdmann 1990).

The oystershell scale, *Lepidosaphes ulmi* L., was responsible for a considerable amount of mortality in all blocks when the study was initiated. Indeed, Houston (2001, 2002) stated that it was the most important mortality agent in the study, although he indicated no apparent treatment effects. It is not possible, 10 years later, to determine why many of the sprouts and seedlings died - in most cases they had decomposed and no material was present except a metal tag. In addition, there was a significant amount of moose activity in the summer clearcut blocks. Although moose are not known to browse on beech, many of the study plots in the summer clearcut blocks were trampled by moose

walking through browsing on the trembling aspen, yellow birch and sugar maple on the site. It is also likely that much of the regeneration in the clearcuts was adversely affected by the increased light associated with the sudden removal of the overstory canopy.

The survival of the sprouts in the plots was not related to whether trees were cut or left standing. Overall, there was not a significant difference in survival between monitored sprouts around cut trees (35% survival) than around uncut trees, (37% survival). This finding is different than what Houston (2001) found 3 years after harvest. He found that significantly more sprouts died around cut trees. This most likely is a consequence of the high mortality found in the summer clearcut treatments, where there was a greater disturbance and a different aspect (northwest) than the other treatments.

There was no significant relationship between the mortality of the monitored regeneration and the resistance/susceptibility status of the study plot tree. Overall, 39% of the regeneration around resistant, high-vigor trees survived compared to 34% for those around susceptible, low vigor trees. Likewise, there was no difference in regeneration survival found between sprouts from resistant trees that were cut (39%) and those that were not cut (39%). In addition, there was little difference in survivorship of regeneration around susceptible trees that were cut (32%) and those that were left standing (35%). Unfortunately, this finding provides forest managers with no clear management practice that encourages the survival and propogation of resistant beech regeneration. Regardless of the parent tree's vigor, the sprouting that occurs around the tree and the survival of that regeneration is similar.

Standing Tree Survival

One of the goals of the study was to determine what happened to resistant beech left standing in the various cuts. These trees, which show resistance to the beech scale are the only reliable hard mast producers in many areas, and they are vital to the future of the species. Past management recommendations for landowners conducting harvesting in a beech stand affected by beech bark disease have been to identify and retain resistant trees, even in clearcuts (Houston 2001). The results of this study show that in clearcut blocks, resistant trees that were left standing suffered mortality ranging from 67% - 78%. There was no mortality of resistant trees left standing in any of the partially cut blocks or in the no-cut control blocks. This is a surprising result, because 10 years ago, most of these trees were listed as high-vigor trees in excellent condition (Houston 2002). The majority of the resistant trees in the clearcut blocks were standing dead, suggesting that they had not been dead for a long time. Other resistant trees in the clearcuts that were not dead were declining and had very little live crown. Not a single resistant tree died in any of the other treatment blocks.

Although the reason for the mortality of these trees is not certain, it is most likely that trees left in clearcut blocks suffered sunscald (Houston 2002). Sunscald is a wintertime injury that affects the tree's trunk. It is caused by the wide fluctuation in temperatures that trees with exposed trunks experience in the winter. During the winter months, deciduous trees are without leaves, and night temperatures are usually below freezing. During the day, the winter sun is low in the sky, and the bole of the tree warms, and the cold-hardy bark cells begin to become active. When the temperature drops below freezing and the sun sets, the bark cells are killed. Water flow from roots to the crown is

cut off because dead cells in the trunk cannot conduct moisture. As a result, much of the tree's crown dies back, and the tree becomes susceptible to other organisms, such as fungi and insects. Thin-barked trees, such as beech, are most at risk (Sinclair et al. 1990). Many resistant and susceptible trees that were left in clearcuts were actively being bored by the pigeon tremex, *Tremex columba*, a species of wasp that oviposits eggs into the trunks of dead and dying trees. This insect was not found on any study tree, resistant or susceptible, left in any of the partial cut or control blocks.

As part of the original study, both resistant and susceptible trees were left standing in all treatments. It is not surprising that many of the standing susceptible trees died in clearcuts, as they are suffering from the effects of beech bark disease and mortality was common in every treatment block, including the control blocks. The mortality of susceptible trees left standing was the highest in clearcut blocks, averaging 61% in the summer clearcut blocks, and 89% in the winter clearcut blocks. What is interesting is that in the summer clearcut blocks, a higher percentage of the resistant trees died (78%) than susceptible trees (61%).

Management Implications

Many stands have been rendered less productive as a result of a high level of defective beech and dense thickets of beech reproduction. Unfortunately, this study leads to no clear regeneration strategy to increase the number of resistant beech stems in forests affected with beech bark disease. There was no significant difference found between the harvest-initiated sprouting around resistant and susceptible trees. Because American beech is so shade tolerant, it does not experience rapid mortality when regeneration is left to grow in the understory. It is this way that beech is often able to work its way into the

overstory by taking advantage of gaps that occur over time and by outliving other hardwood species (Lormier 1981). Apparently, as shown in this study, beech will experience mortality if regeneration is left out in the open, as with clearcuts.

Winter partial cuts, while initially causing the least sprouting overall, lead to the highest sprout survival. The decreased sprouting in the winter cut blocks is thought to be the result of the root system being frozen and protected by snow and thus less likely to suffer injury as a result of harvesting (Houston 2001). Sprouts resulting from winter treatments survive longer because the supporting root system has more stored nutrients.

Leaving resistant trees and removing susceptible ones should enhance genetic variation through the sexual reproduction of resistant trees. In addition, large diameter, mature beech have a high wildlife value for the mast they produce (Foss 1997). Past studies have suggested leaving resistant trees in all harvesting situations. However, this study shows that leaving resistant American beech of high vigor in clearcuts without the protection of surrounding trees leaves them susceptible to decline and death from exposure. When implementing management plans, resistant trees should be identified and retained, but care should be taken to ensure that they are protected from sunscald by surrounding trees.

Conclusions

American beech produce populations of root sprouts as a response to injuries that the root system incurs during harvesting. Less sprouting is initiated in winter harvests, but sprouts that are initiated in winter harvests survive longer than those initiated in summer harvests. The type of harvest treatment, season of harvest, and intensity of

harvest all affect regeneration survival. There was a higher level of regeneration survival in the winter cuts than summer cuts and in partial cuts than clearcuts.

Resistant trees experienced mortality, presumably due to sunscald to the bole, in all clearcuts. This suggests that when resistant trees are left, they need to be protected from sunscald, preferably by species other than beech. Understanding the consequences of seasonal harvesting practices on root disturbance and resistant tree survival may hold the key to improving the quality of beech in stands affected by beech bark disease.

LITERATURE CITED

Barker, M.J., P. M. Pijut, M.E. Ostry, and D.R. Houston. 1997. Micropropagation of juvenile and mature American beech. Plant Cell, Tissue and Organ Culture **51**:209-213.

Borror, D.J., and R.E. White. 1995. A Field Guide to the Insects of America North of Mexico. Peterson Field Guide Series. Houghton Mifflin, Boston.

Brown, R.C. 1934. Notes on the beech scale, *Cryptococcus fagi* (Baer.) Dougl., in New England. Journal of Economic Entomology **27**: 327-333.

Burns, B.S., and D.R. Houston. 1987. Managing beech bark disease: Evaluating defects and reducing losses. Northern Journal of Applied Forestry **4**: 28-33.

Chokkalingam, U. 1998. Spatial and temporal patterns and dynamics in old-growth northern hardwood stands and mixed forests of northern Maine. Ph.D. Dissertation. University of Maine, Orono. 227pp.

Chokkalingam, U., and A.S. White. 2001. Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. Plant Ecology **156**: 139-160.

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.

DiGregorio, L.M., M.E. Krasney, and T.J. Fahey. 1999. Radial growth trends of sugar maple (*Acer saccharum*) in an Allegheny northern hardwood forest affected by beech bark disease. Journal of the Torrey Botanical Society **126(3)**: 245-254.

Dübler, A., G. Voltmer, J. Lunderstädt, and A. Zeeck. 1997. Phenols from *Fagus sylvatica* and their role in defense against *Cryptococcus fagisuga.* Phytochemistry **45**:51-57.

Ehrlich, J. 1934. The beech bark disease. A *Nectria* disease of *Fagus*, following *Cryptococcus fagi* (Baer.). Canadian Journal of Research **10**: 594-692.

Erdmann, G.G. 1990. *Betula alleghansis* in R.S. Burns and B.H. Honkala (eds). Sylvics of North America, Vol. 2, Hardwoods. USDA, Forest Service Agricultural Handbook. 654pp.

Filip, S.M. 1978. Impact of beech bark disease on uneven-age management of a northern hardwood forest. USDA Forest Service General Technical Report NE-45. 7pp.

George, D.W., and B.C. Fischer. 1991. The occurrence of oak reproduction after clearcut harvesting on the Hoosier National Forest. Northern Journal of Applied Forestry. **8** (4): 144-146.

Godman, R.M., H. W. Yawney, and C. H. Tubbs. 1990. *Acer saccharum in* R.S. Burns and B.H. Honkala (eds). Sylvics of North America, Vol. 2, Hardwoods. USDA, Forest Service Agricultural Handbook. 654pp.

Griffith, D. M., and C. L. Alerich. 1996. Forest statistics for Maine, 1995. Resource Bulletin NE-135. USDA Forest Service. 134 pp.

Held, M.E. 1983. Pattern of beech regeneration in the east-central United States. Bulletin of the Torrey Botanical Club **110**: 55-62.

Horsley, S.B., and J.C. Bjorkbom. 1983. Herbicide treatment of striped maple and beech in Allegheny hardwood stands. Forest Science **29(1)**: 103-112.

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. 1982. A technique to artificially infest beech bark with the beech scale, *Cryptococcus fagisuga* (Lindinger). USDA Forest Service. Research paper NE-507. 7pp.

Houston, D.R. 1983a. American beech resistance to *Cryptococcus fagisuga*, p. 38-42 *in* Proceedings IFURO Beech Bark Disease Working Party Conference. USDA Forest Service General Technical Report WO-37. 140p.

Houston, D.R. 1983b. Effects of parasitism by *Nematogonum ferrugineum* (*Gonatorrhodiella highlei*) on pathogenicity of *Nectria coccinea* var. *faginata* and *Nectria galligena*, p. 109-114 *in* Proceedings IFURO Beech Bark Disease Working Party Conference. USDA Forest Service General Technical Report WO-37. 140p.

Houston, D.R. 1994a. Temporal and spatial shift within the *Nectria* pathogen complex associated with beech bark disease of *Fagus grandifolia.* Canadian Journal of Forest Research **24**: 960-968.

Houston, D.R. 1994b. Major new tree disease epidemics: beech bark disease. Annual Review of Phytopathology **32**: 75-87.

Houston, D.R. 1997. Potential for biologically based control of beech bark disease in the southern Appalachians. p.36-42 *in* Proceedings Southern Appalachian Biological Control Initiative Workshop. Asheville, NC. 7pp.

Houston, D.R. 2001. Effect of harvesting regime on beech root sprouts and seedlings in a north-central Maine forest long affected by beech bark disease. USDA Forest Service, Research Paper NE-717. 20 pp.

Houston, D.R. 2002. Personal communication. Orono, Maine.

Houston, D.R., and D.B. Houston. 1987. Resistance in American beech to *Cryptococculus fagisuga*: Preliminary findings and their implication for forest management. p. 105-116 *in* Proc. 30^{th} Northeastern Forest Tree Improvement Conference, July 22-24, 1986, Orono, Maine.

Houston, D.R., and D.B. Houston. 1994. Variation in American Beech (*Fagus grandifolia* Ehrl.): Isozyme analysis of genetic structure in selected stands. Silvae Genetica **43(5/6)**: 277-284.

Houston D.R., and D.B. Houston. 2000. Allozyme genetic diversity among *Fagus grandifolia* trees resistant or susceptible to beech bark disease in natural populations. Canadian Journal of Forest Research **30**: 778-789.

Houston, D.R., E.J. Parker, and D. Lonsdale. 1979. Beech bark disease: patterns of spread and development of the initiation agent, *Cryptococcus fagisuga*. Canadian Journal of Forest Research **9**: 336-344.

Houston, D.R., and J.T. O'Brian. 1983. Beech bark disease. USDA Forest Service. FILD Leaflet 75. 7pp.

Jones, R.H., and D.J. Raynal. 1986. Spatial distribution and development of root sprouts in *Fagus grandifolia* (Fagaceae). American Journal of Botany **73**: 1723-1731.

Jones, R.H., and D.J. Raynal. 1987. Root sprouting in American beech (*Fagus grandifolia*): Production, survival, and the effect of parent tree vigor. Canadian Journal of Forest Research **17**: 539-544.

Jones, R.H., and D.J. Raynal. 1988. Root sprouting in American beech (*Fagus grandifolia*): Effects of root injury, root exposure, and season. Forest Ecology and Management **25**: 79-90.

Jones, R.H., R.D. Nyland, and D. Raynal. 1989. Response of American beech regeneration to selection cutting of northern hardwoods in New York. Northern Journal of Applied Forestry **6**: 34-36.

Kelty, M.J., and R.D. Nyland. 1981. Regenerating Adirondack northern hardwoods by the shelterwood method and control of deer density. Journal of Forestry **79**: 22-26.

Krabel, D., and R. Petercord. 2000. Genetic diversity and bark physiology of the European beech (*Fagus sylvatica*): a coeveolutionary relationship with the beech scale (*Cryptococcus fagisuga*). Tree Physiology **20**: 485-491.

Krasney, M.E., and L.M. DiGregorio. 2001. Gap dynamics in Allegheny northern hardwood forests in the presence of beech bark disease and gypsy moth disturbances. Forest Ecology and Management **144**: 265-274.

Leak, W.B., and M.L. Smith. 1997. Long-term species and structural changes after cleaning young even-aged northern hardwoods in New Hampshire, USA. Forest Ecology and Management **95**: 11-20.

Lorimer, C.G. 1981. Survival and growth of understory trees in oak forests of the Hudson Highlands, New York. Canadian Journal of Forest Research **11**: 689-695.

Maini, J.S., and K.W. Horton. 1966. Vegetative propagation of *Populus* spp. I. Influence of tempature on formation and initial growth of aspen suckers. Canadian Journal of Botany **44**: 1183-1189.

Manion, P.D. 1991. Tree Disease Concepts. 2nd ed. Pretance Hall Career and Technology. 402pp.

Mayer, M., and D.C. Allen. 1983. *Chilocorus stigma* (Coleoptera: Coccinellidae) and other predators of beech scale in central New York p 89-98 *in* Proceedings IFURO Beech Bark Disease Working Party Conference. USDA Forest Service General Technical Report. WO-37. 140p.

McMahon, J. S. 1990. The biophysical regions of Maine: Patterns in the landscape and vegetation. M. S. Thesis, University of Maine, Orono. 120 pp.

Mielke, M.E., D.R. Houston, and A.T. Bullard. 1986. Beech bark disease management alternatives. p. 272-280 *in* Proc. Integrated Pest Management Symposium for Northern Forests. Univ. Wisconsin, Coop. Ext. Ser., Madison.

Mize, C.W., and R.V. Lea. 1979. The effect of the beech bark disease on the growth and survival of beech in northern hardwoods. European Journal of Forest Pathology **9**: 243-248.

Morris, A.B., R.L. Small, and M.B. Cruzan. 2002. Investigating the relationship between *Cryptococcus fagisuga* and *Fagus grandifolia* in Great Smokey Mountain National Park. Southeastern Naturalist **1**(4): 415-424.

Oliver, C.D., and B.C. Larson. 1996. Forest Stand Dynamics. New York: McGraw-Hill, Inc. 520p.

Ostrofsky, W.D., and D.R. Houston. 1988. Harvesting alternatives for stands damaged by the beech bark disease. p.173-177 *in* Proceedings, 1988 Society of American Forester's National Convention, SAF Publ. 88-01.

Ostrofsky, W.D., and M.L. McCormack, Jr. 1986. Silvicultural management of beech and the beech bark disease. Northern Journal of Applied Forestry **3**: 89-91.

Patton, T.A. 1997. Effects of overstory density and beech bark disease severity on height growth patterns of American beech and associated species. M.S.Thesis, University of Maine, Orono. 98p.

Powell, D.S. and D.R. Dickson. 1984. Forest statistics for Maine: 1971 and 1982. USDA Forest Service. Resource Bulletin NE-81. 194pp.

Runkle, J.R. 1984. Development of woody vegetation in tree fall gaps in a beech-sugar maple forest. Holarctic Ecology **7**: 157-164.

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 United States. Journal of Forestry **70**: 286-289.

Sinclair, W.A., H.H. Lyon, and W.T. Johnson. 1987. Diseases of Trees and Shrubs. Cornell University Press. New York. 576pp.

Spaulding, P., T.J. Grant, and T.T. Ayers. 1936. Investigations of *Nectria* diseases in hardwoods of New England. Journal of Forestry **34**: 169-179.

Taiz, L. and E. Zeiger. 2002. Plant Physiology. Sunderland: Sinauer Associates, Inc., . 690p.

Twery, M. J., and W.J. Patterson III. 1984. Variation in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. Canadian Journal of Forest Research **14**: 565-574.

Tubbs, C. H., and D.R. Houston. 1990. *Fagus Grandifolia* Ehrh. American Beech. *in* R.S. Burns and B.H. Honkala (eds). Sylvics of North America, Vol. 2, Hardwoods. USDA, Forest Service Agricultural Handbook. 654pp.

Valentine, H.T. 1983. An approach to modeling the consequences of beech mortality from beech bark disease p.35-42 *in* Proceedings IFURO Beech Bark Disease Working Party Conference. USDA Forest Service General Technical Report. WO-37. 140p.

Wainhouse, D., and R. Deeble. 1980. Variation in susceptibility of beech (*Fagus* spp.) to beech scale (*Cryptococcus fagisuga)*. Annales Sciences Forestieres **37**:279-290.

Wainhouse, D. and I.M. Gate. 1988. The beech scale p. 67-85 *in* A. Berryman. Dynamics of forest insect populations: Patterns, causes, implications. New York: Platinum Press. 345p.

Ward, R. T. 1961. Some aspects of the regeneration habits of American beech. Ecology **42**: 828-832.

Wargo, P. M. 1988. Amino nitrogen and phenolic constituents of bark of American beech, *Fagus grandifolia*, and infestation by the beech scale, *Cryptococcus fagisuga*. European Journal of Forest Pathology **18**: 279-290.

Appendix A: MAPS

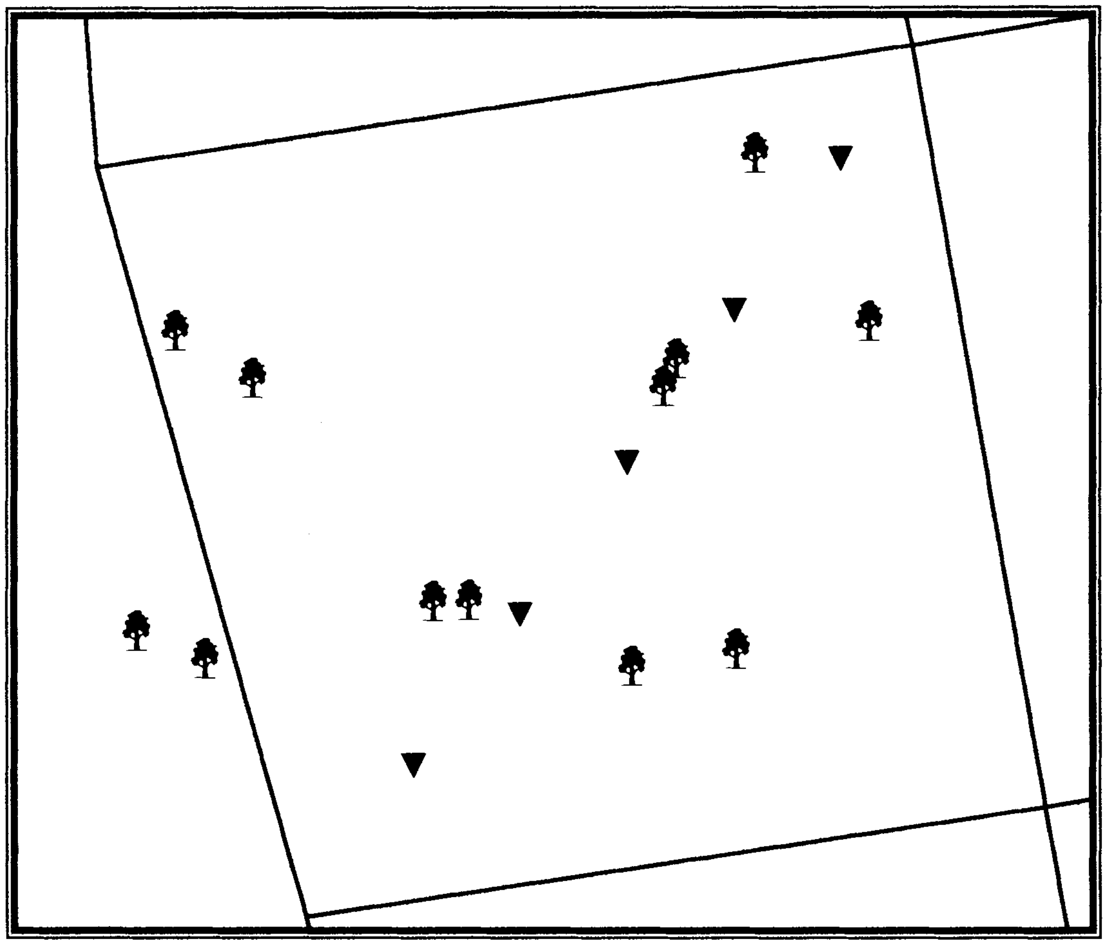

Figure A.1. Sample location of long-term study plots throughout block. Triangles indicate transect points for stand measurements.

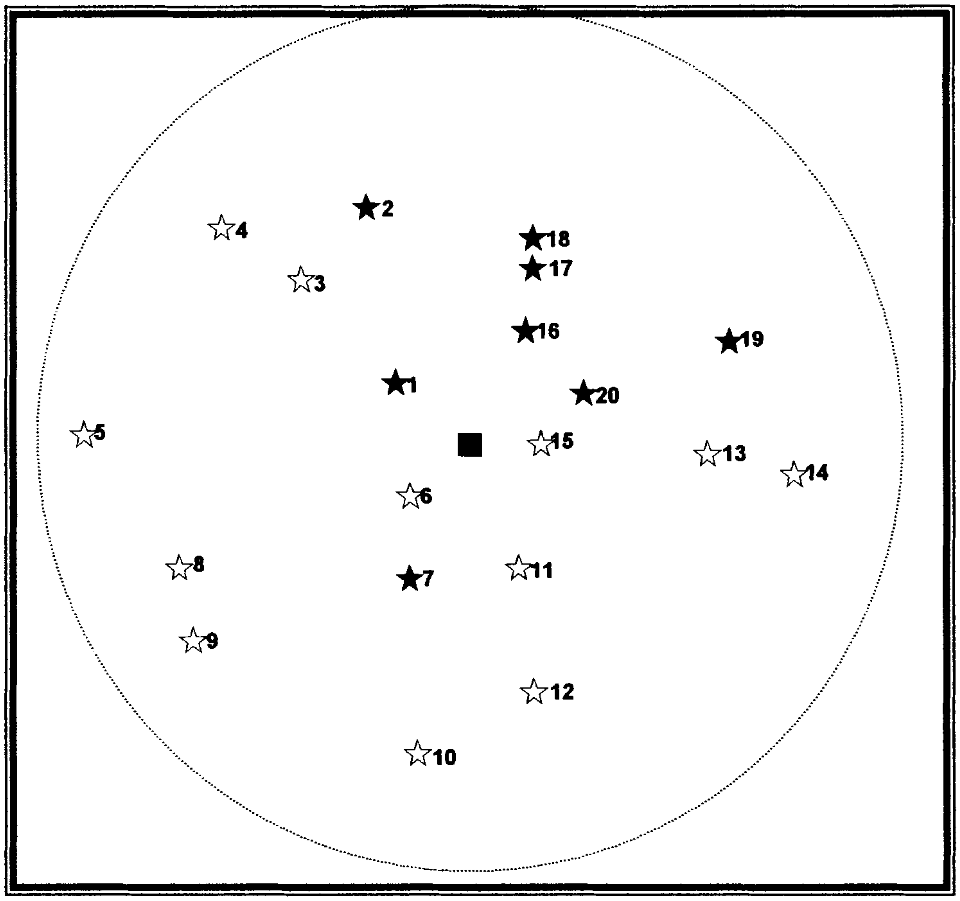

Figure A.2. Sample long term study plot. Red stars signify sprouts, blue stars signify seedlings, and gray stars indicate located dead regeneration.

Appendix B: TABLES

Table B.1. Mean basal area (ft^2/acre) for species in 15 treatment blocks

Species	Block 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
American beech	100	88	34	94	40	26	80	60	90	98	30	8	34	62	56
Yellow birch	4	8	12	2	30	8	4	20	12	8	2	14	10	20	20
Striped maple	4	12	6	6	26	8	6	16	4	12	2	8	12	26	2
Sugar maple	4			4	12	4	4	6			4		2	2	18
Red maple					2	2	12				34		2		4
White ash					4	2					4	12	4		2
White birch							2	2							2
Red spruce	6	6					2		8	2					4
Balsam fir							14	2			2	6	2	2	4
Trembling aspen											6	8	6		
Bigtooth aspen												6	6		
White pine							4	2							
E. white cedar								2	2					2	
Eastern hemlock															
Hophornbeam										2					
Total	118	114	52	108	114	50	128	110	116	122	84	62	78	114	112

*Standard error was computed for dominant species (occurring in 10 or more of the blocks)

Table B.2. Stems per acre (stems < 1" in diameter and <1 meter tall) in thousands of stems

	Block															
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	SE*
American beech	20.9	21.8	2.6	12.6	6.6	3.7	18.2	6.7	25.2	7.7	3.9	1.7	4.7	8.1	4.3	2.0
Balsam fir		1.3				.6	1.3	3.0	2.4	5.8		14.6	11.1	8.7	2.2	1.8
Beaked hazelnut														6.4	30.9	
Big tooth aspen											1.9	2.6	1.8			
Eastern hemlock							1.3									
Hobblebush	3.8	18.8	3.9	5.8	6.9	4.8		5.2	4.3	1.3	4.7	21.9	4.6	2.0	16.8	1.8
Hophornbeam		2.5		2.6		1.6	3.9	1.3		2.6					2.6	
Red maple	2.1	4.8		3.9	7.7	2.9	7.9	7.1	2.0	11.8	4.0	1.3	3.5	9.0	20.6	1.4
Red spruce	1.9	1.2	2.5	.3		1.3	2.9								1.3	
Striped maple	1.9	2.9	2.1	3.8	2.6	3.9	9.5	8.6	5.6	1.9	2.8	1.8	4.1	6.5	6.8	.6
Sugar maple	9.2	2.6	6.4	18.5	16.9	11.7	5.6	10.7	8.7	3.9	1.6	14.8	1.1	10.3	20.4	1.6
Trembling aspen											15.5	3.4	9.7			
White ash	1.3		2.6		1.3	2.7	1.3	1.3	11.6	10.7	2.9	3.1				1.2
White pine							2.1					1.3			1.3	
Yellow birch	9.6	5.7	8.2	1.3	3.4	.9	15.9	1.3	1.3	33.6	7.0	4.3	10.3	4.5	1.3	2.2

*Standard error was computed for dominant species (occurring in 10 or more of the blocks)

Table B.3. Stems per acre (stems > 1" in diameter and >1 meter tall) in thousands of stems per acre

	Block														
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
American beech	.8	1.1	.8	.3	.7	.5	.9	.6	.9	.4	1.1	.8	.8	1.6	2.6
Balsam fir							2.6					3.9	.9	.3	7.1
Big tooth aspen												.3	.3		
Hobblebush						1.3		.6							
Hophornbeam															.3
Red maple						.9					.8	5.7	1.9		
Red spruce													.3		
Striped maple	1.1	.5	1.2	.9	1.2		1.9	1.3	1.4	.6	1.9	1.1	1.2	.3	1.5
Sugar maple					.3	1.3					.9	2.1	3.2		
Trembling aspen											3.		.3		
White ash						1.3					5.6	4.9	.3		
Yellow birch			.9	.3	.5	1.5					.3	2.1	2.7		

*Standard error was computed for dominant species (occurring in 10 or more of the blocks)

Table B.4. Standing tree mortality by treatment

Treatment	N	Mean	Standard Error	95% CI lower	95% CI upper
Summer clearcut					
Resistant	10	.783	.117	.281	1.285
Susceptible	8	.611	.139	.013	1.209
Summer partial cut					
Resistant	9	0.00	0.00	0.00	0.00
Susceptible	10	.383	.073	.017	.696
Winter clearcut					
Resistant	9	.667	.167	-.050	1.384
Susceptible	10	.889	.111	.411	1.367
Winter partial cut					
Resistant	10	0.00	0.00	0.00	0.00
Susceptible	10	.528	.121	.006	1.049
No cut control					
Resistant	12	0.00	0.00	0.00	0.00
Susceptible	12	.566	.056	.316	.795

Table B.5. Regeneration survival by treatment

Treatment	N	Mean	95% CI upper	95% CI lower	Standard Error
Summer clearcut					
Resistant					
Cut	9	.254	.380	.129	.029
Not cut	10	.254	.479	.029	.052
Susceptible					
Cut	8	.137	.273	.002	.032
Not cut	8	.285	.679	-.109	.091
Summer partial cut					
Resistant					
Cut	9	.392	.941	-.158	.128
Not cut	9	.346	.839	-.201	.127
Susceptible					
Cut	10	.286	.794	-.222	.118
Not cut	10	.382	.988	-.224	.141
Winter clearcut					
Resistant					
Cut	9	.438	.895	-.019	.106
Not cut	9	.517	.881	.153	.085
Susceptible					
Cut	9	.332	.626	.038	.068
Not cut	10	.294	.544	.045	.058
Winter partial cut					
Resistant					
Cut	9	.478	.771	.184	.068
Not cut	10	.464	.469	.432	.007
Susceptible					
Cut	9	.515	.732	.297	.051
Not cut	10	.495	.801	.188	.071
No cut control					
Resistant	12	.356	1.014	-329	.159
Susceptible	12	.300	.623	-.023	.075

Table B.6. Analysis of variance table results from long term study plots

Source	Sum of squares	df	Mean square	F-ratio	P
Treatment	1.242	4	.046	5.332	.001
C_L	.001	1	.001	.099	.756
R_S	.004	1	.004	.426	.520
C_L*R_S	.000	1	.000	.001	.981
R_S*Treatment	.061	3	.020	2.351	.095
C_L*Treatment	.012	3	.004	.481	.698
R_S*C_L*Treatment	.038	4	.010	1.105	.375
Error	.224	26	.009		

Table B.7. Analysis of variance results (partial vs. clearcut) from long term study plots

Source	Sum of squares	df	Mean square	F-ratio	P
Cut	.150	1	.150	5.542	.024
R_S	.038	1	.038	1.415	.241
C_L	.010	1	.010	.381	.540
Cut*R_S	.027	1	.027	.989	.326
Cut*C_L	.002	1	.002	.086	.771
R_S*C_L	.002	1	.002	.086	.771
Cut*R_S*C_L	.001	1	.001	.046	.832
Error	1.083	40	.027		

Table B.8. Analysis of variance results (summer vs. winter cuts) from long term study plots

Source	Sum of squares	df	Mean square	F-ratio	P
Season	.287	1	.287	12.112	.001
R_S	.038	1	.038	1.616	.211
C_L	.010	1	.010	.436	.513
Season*R_S	.001	1	.001	.032	.860
Season*C_L	.004	1	.004	.148	.703
Season*R_S*C_L	.024	1	.024	1.025	.317
Error	.948	40	.024		

BIOGRAPHY OF THE AUTHOR

Amanda Farrar grew up in Solon, Maine and graduated from Carrabec High School in North Anson, Maine in 1992. She graduated from the University of Maine at Farmington in 1998. Before attending graduate school, Mandy worked as a whitewater raft guide, fishing guide, and Allagash Ranger. She entered the graduate program in the department of Forest Management at the University of Maine in the fall of 2001.

After receiving her degree, Mandy will be working for the Small Woodland Owners Association of Maine. She is a candidate for the Master of Science degree in Forestry from The University of Maine in August, 2003.