

2006

## Resistance of forest community types to structural and compositional change following beech bark disease infestation

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Resistance of Forest Community Types to Structural and Compositional Change  
Following Beech Bark Disease Infestation

An Honors Thesis

Presented to

The Faculty of the Department of Biology

Colby College

in partial fulfillment of the requirements for the

Degree of Bachelor of Arts with Honors

by

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May 17, 2006

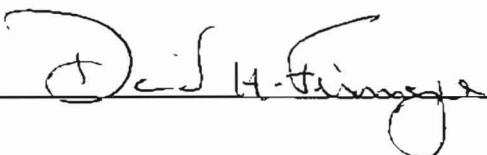
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## **Abstract**

Pathogens change forest composition and structure by selectively eliminating susceptible individuals and species. Caused by a complex between an exotic scale insect and fungi, beech bark disease has infected mature American beech (*Fagus grandifolia*) trees through most of the species range. Before succumbing to the disease, infected trees generate root sprouts, transforming beech from a dominant canopy species into an abundant subcanopy species. Root sprouting can create dense beech thickets that interfere with the regeneration of other species. Exclusion of species from the understory has ecological and economic implications. This study compared forest community types for their resistance to compositional and structural change from beech thickets. The expansion and density of beech sprouts, as well as the density of other species in the thickets were measured in seven different forests in central Maine. Mixed hardwood forests, specifically an ash-birch-maple forest, tend to be most resistant to change, while a hemlock-pine-oak forest was least resistant. This information may be useful for managers to prioritize forest community types in which to control beech thickets.

## Introduction

Disturbances significantly affect forest ecosystem composition, structure, and function (Barnes et al. 1998). By altering the direction and rate of forest succession, disturbances change species distribution and occurrence. For example, catastrophic disturbances such as volcanism, landslides, and floods shape landscapes by initiating secondary succession. Several forest ecosystems rely on natural fire disturbance regimes to regulate processes such as competition and reproduction. Wind alters species composition by creating canopy gaps in which shade tolerant understory species are favored, or by destroying large areas of forest in which early successional species regenerate.

Disturbances from disease-causing pathogens differ from abiotic disturbances because pathogens selectively affect susceptible species and the less vigorous or genetically unfit individuals (Costello and Leopold 1995). Pathogens may eliminate species or individuals directly by decreasing their fecundity and viability, or indirectly by infecting herbivores, pollinators, or seed dispersers (Dobson and Crawley 1995). In addition, diseases may alter the life-history strategies of their hosts by inducing vegetative reproduction. For example, *Cyperus virens* individuals that are infected by a fungus can grow up to four times the size of uninfected plants (Dobson and Crawley 1995).

Like abiotic disturbances, diseases regulate forest ecosystems and drive succession (Barnes et al. 1998). By changing the life history traits or ability for individuals to compete, diseases alter and modify species relationships. For example,

diseases can limit the population size of susceptible species, which may enhance diversity rather than allowing competitive exclusion to occur (Gilbert 2002, Le Guerrier 2003). Disease induced mortality can also create canopy gaps that facilitate regeneration. These gaps may be necessary to maintain diversity in some mature forests (Costello and Leopold 1995, Krasny and DiGregorio 2001). In some instances, pathogens have completely eliminated dominant species across their entire range, leading to widespread species replacements and forest composition changes (Costello and Leopold 1995). This was the case with the chestnut blight and Dutch elm diseases.

Beech bark disease (BBD) has infected American beech trees (*Fagus grandifolia*) through most of the species range (Houston 1994). The disease is caused by a complex between the exotic scale insect, *Cryptococcus fagisuga*, and either *Nectria coccinea* var. *faginata*, an exotic fungus, or *Nectria galligena*, a native fungus. The infection is initiated when *C. fagisuga* feed on vascular fluids in the tree by inserting their stylets through the bark into the phloem (Wiggins et al. 2004). After the scale dies, the pathogenic fungi infect the phloem from the feeding wound in the bark, causing localized death of the vascular tissue. The tree develops cankers and is eventually killed when numerous areas of mortality girdle the tree (Wiggins et al. 2004). Although BBD may slow growth rates by more than 40%, beech trees can survive decades of infestation (Gavin and Peart 1993).

The beech scale was first observed in Europe on European beech, *Fagus sylvatica*, in the mid-1800's. BBD was accidentally introduced to North America from ornamental European beeches that were brought to the Halifax Public Gardens, Nova Scotia in 1890 (Houston 1994). The disease, unchecked by natural controls and

transported long distances by the wind, migratory birds, and possibly humans, spread south, and by the 1940's was well established from southern Maine to the Catskill Mountains in New York (Griffin et al. 2003). The disease has since extended as far south as Tennessee and as far west as Michigan (Houston 1994, Latty et al. 2003) and is likely to eventually become established everywhere within the range of beech (Tainter and Baker 1996). The susceptibility of American beech to BBD suggests that the spread of the disease may be ultimately checked only by the natural distribution of beech (Griffin et al. 2003).

The spread of BBD has been subjectively divided into three phases: the "advancing front" is characterized by large populations of *C. fagisuga* and low *Nectria* levels; the "killing front" constitutes areas with high fungal and insect populations and beech mortality; and the "aftermath zone" in which BBD is widespread (Shigo 1972). New England forests, in which some stands have lost more than 50% of the beech trees that are greater than 25 cm diameter at breast height (dbh) and most remaining beech trees are severely damaged, are in the aftermath zone (Houston 1994, Griffin et al. 2003). Annual beech mortality rate estimates in aftermath zones range from 6.7% to 38.6% (Twery and Patterson 1984, Runkle 1990).

There are local differences in BBD severity within the aftermath forests due to variable individual and forest community characteristics. Although some individuals are immune to BBD, mature trees with >25 cm dbh are more susceptible to infection because these trees have more suitable habitat for the scale insect, such as branch scars, bark fissures, and callused areas around wounds (Jones and Raynal 1986, Gavin and Peart 1993, Houston 1994). Mature trees also tend to have large crowns, which increase the

probability of infection because they capture more insects (Latty et al. 2003). Trees that have high bark nitrogen concentrations are also more susceptible to BBD because of the greater nutritional quality for the scale insect. At the community level, the nitrogen availability and relatively large trees in old growth forests make them more susceptible to infection (Latty et al. 2003). Stands with high beech density are also more susceptible to BBD because the disease is transmitted rapidly and there are larger populations of the scale insect and fungi (Twery and Patterson 1984). The severity of infestation is also higher in eastern hemlock stands, perhaps because the dense shade and moist conditions in these stands favor scale fecundity.

Several studies have documented compositional and structural changes following BBD infestation (Twery and Patterson 1984, Runkle 1990, Houston 1994, DiGregorio 1999, Forrester et al. 2003, Hane 2004). BBD transforms beech from a dominant canopy species into an abundant subcanopy species, where the decline of large beech stems are balanced by dense thickets of small stems (Forrester et al. 2003, Le Guerrier et al. 2003, Latty 2004). These drastic structural changes are due to the physiology of beech. Mature American beech trees under stressed conditions, such as BBD infestation, generate root sprouts in a circular distribution (Jones and Raynal 1986, 1987; Hane 2004). The spatial distribution and number of sprouts produced may depend on the characteristics of the parent tree. For example, parent trees that are more severely damaged from BBD tend to produce more sprouts (Hane 2004). However, if the damage from infestation is equal among trees, the trees with lower vigor may produce fewer sprouts (Jones and Raynal 1986). Parent diameter is also positively correlated with sprout number and the distance from the parent to the sprouts (Jones and Raynal 1986, 1987). Although root sprouts do

not become functionally independent from the parent until they mature, the sprouts will persist as the parent slowly dies (Ward 1961, Jones and Raynal 1986). As an extremely shade tolerant species, beech sprouts survive for decades in the deeply shaded understory, creating dense thickets of beech (Jones and Raynal 1987, Hane 2004).

Changes to forest structure are accompanied by major compositional changes in the understory (Twery and Patterson 1984). Dense beech thickets are fierce competitors with other species in the understory, mainly because shade from the thickets inhibits the regeneration of other species (Krasny and DiGregorio 2000, Lei et al. 2002, Ricard et al. 2002, Hane 2003). This competition has resulted in understories that are overly rich in beech and impoverished in other species (Houston 1994). If beech thickets exclude species from the understory, those species will eventually be absent and the composition and succession of the forest will drastically change. A similar compositional change has also been observed in southern Appalachian forests because the shade from *Rhododendron maximum* thickets inhibits the regeneration of canopy trees (Nilsen et al. 2001, Lei et al. 2002).

The structural and compositional changes following BBD infestation have implications for ecosystem function and forest management. For example, the exclusion of sugar maple, a species that contributes to nitrification, will alter nitrogen cycles (Lovett and Mitchell 2004). Not only has American beech lost most of its commercial value because of the mortality of large stems, but beech thickets interfere with the development of commercially viable species such as sugar maple (Bohn and Nyland 2002). Although extremely costly, it is possible to eliminate beech thickets to facilitate the growth of economically important species. Managers must set management priorities

by determining in which forests the beech thickets are most likely to decrease the regeneration success rates of other species (Bohn and Nyland 2002).

The extent of structural and compositional change in the understory from beech thickets may differ between forests with different species compositions. Forest response to the chestnut blight and oak wilt also varied between forests with different initial species compositions (Menges and Loucks 1984, Stephenson 1986, Costello and Leopold 1995). Identifying which forest community types are least resistant to change from BBD would be useful for managers to prioritize forests in which to focus their efforts. This information complements studies that have focused on how BBD alters canopy replacement and gap dynamics in various forest community types, but that have not explicitly considered the role of beech thickets in changing forest composition and structure (Twery and Patterson 1984, Runkle 1990, Krasny and DiGregorio 2001). Comparing resistance to change across different forest communities could be used to predict landscape level changes across the range of beech, complementing models that predict long term changes from BBD in various forests (Le Guerrier et al. 2003, Evans et al. 2005). Also, understanding which species beech thickets tend to exclude would help to infer the resistance of forest community types in which these species are dominant.

This study aims to compare the resistance of different forest community types in central Maine to structural and compositional changes in the understory from beech thickets. Two questions are addressed: 1) Does resistance to structural and compositional change in the understory from beech thickets differ among forest community types? and 2) Which species compete well or poorly with beech thickets? To address the first question, the ability for thickets to spread, develop and become denser,

and to exclude other species are compared among forest community types. The growth stage at which beech thickets exclude other species is also compared. To address the second question, the tendency for beech thickets to exclude or to reduce the density of specific species is considered. Communities in which hemlock is dominant may be most resistant to understory change because hemlock is extremely shade tolerant and a strong competitor with beech (Twery and Patterson 1984). Also, communities where sugar maple is abundant may be less resistant to change because several studies have reported that beech thickets interfere with sugar maple regeneration, possibly because sugar maple is less shade tolerant (Beaudet et al. 1998, Hane 2003).

## **Methods**

### **Study sites**

The study was conducted in seven public forests in Kennebec County, Maine (Figure 1). The study sites included: Vaughn Woods, Hallowell; Mt. Pisgah Conservation Area, Winthrop; Sander's Hill, Rome; The Mountain, Belgrade; Alonzo H. Garcelon Wildlife Management Area, Vassalboro; Perkins Arboretum, Colby College, Waterville; and Runnals Hill, Colby College, Waterville. These forests are well distributed throughout Kennebec County to represent a range of forest community types. All forests are managed for recreational use and are in the aftermath phase of BBD infestation (Houston 1975). Study sites are flat or gently sloping and soils range from till to silty clay loam (United States Department of Agriculture 1978).

Central Maine has cool summers (68° F mean) and cold winters (20° F mean). Average annual precipitation is variable, ranging from 33- 60 inches with 25- 90 inches

of snowfall (National Oceanic and Atmospheric Administration National Weather Service 2005). The elevation ranges from 200 ft- 400 ft.

### **Sampling**

Four 125 m transects spaced 160 m apart were used to sample each forest. The first transect was perpendicular to the trail and the other three transects were parallel to the first. A random number generator randomized the distance from the trailhead to the first transect. The diameter at breast height (dbh) and BBD severity were measured for every American beech within 3 m of the transects. Only beech trees between 15-30 cm dbh and with BBD severity between 2-3, based on the BBD severity classification in Latty et al. (2003), were considered. The dbh and BBD severity were controlled because they affect the number of beech sprouts and the distance from the parent tree to the sprouts (Jones and Raynal 1986, 1987; Hane 2004). These dbh and BBD severity specifications were chosen because they were the most common parent tree characteristics during reconnaissance at the sites.

Beech trees meeting the dbh and BBD severity specifications were plot centers. Eight meter radius plots were established around the parent beech trees because most sprouts are located within 8 m of the parent (Jones and Raynal 1986; Figure 2). All beech stems within 8 m of the parent were assumed to be sprouts because most seedlings are more than 8 m from the parent (Jones and Raynal 1986). These sprouts comprise the beech thicket. Care was taken to establish plots around parent trees that were at least 20 m from any other beech >10 cm dbh because beech sprouts can be as far as 10 m from the parent and would overlap in both plots if the parents were close together (Jones and Raynal 1986).

Some sites, including Sander's Hill, Garcelon, Vaughn Woods, and The Mountain, had large beech thickets that were formed by stands of beech trees. If the transects intersected these stands, only parent trees on the edge of the stand were sampled because this study is interested in the thicket-forest interface. For the purposes of this study, the edge of the thicket was defined as the farthest sprout from the parent where the parent was at least 20 m from any other beech >10 cm dbh (Jones and Raynal 1986). An 8 m radius plot was established around the parent tree where the transect entered the thicket (Figure 3). A second plot was established around a parent on the same edge of the thicket but at least 20 m from the first parent. Two more plots were established on the other side of the thicket.

### **Indicators of Resistance**

Three parameters were measured within each 8 m radius plot as indicators of forest resistance to compositional and structural change from beech thickets: distance from the parent tree to the farthest beech sprout; number of beech stems; and number of nonbeech stems. Beech sprouts and nonbeech stems were tallied in two size classes, <1 m tall (seedling) and >1 m tall and <10 cm dbh (sapling), and by species. The distance from the parent to the farthest sprout was measured to indicate the ability for beech thickets to expand, the number of beech stems was tallied to measure the ability for beech thickets to develop and become denser, and the number of nonbeech stems was counted to assess species exclusion. Stems were recorded in two size classes to determine if beech thickets interfere with the regeneration of seedlings and saplings differently. These measurements were recorded even if no thicket was present because other species may have prevented the thicket from establishing.

## **Forest Composition**

To determine the forest composition at each site, a 5 m radius subplot was established adjacent to the 8 m radius plot. Subplots were located in a random direction from the edge of the plot. The subplots adjacent to beech stands were located in a direction away from the thicket. The dbh and species of all stems >10 cm dbh within the subplot were recorded.

## **Forest Composition Analyses**

The importance values (IV) of each species in the 5 m radius subplots were used to compare the species compositions of the forests between the seven sites. IV's were calculated by averaging the relative frequency, relative density, and relative dominance of each species in the subplots at each site. The IV's rank species at each site based on commonness (relative frequency), number of stems per plot (relative density), and the amount of forest area per hectare, or basal area, occupied by the species (relative dominance).

The IV of each species was compared between all seven sites to measure the dissimilarity between the forest compositions quantitatively. Polar ordination was used to order the forests on an axis (Bray and Curtis 1957). The distances on the axis between each forest were based on the measures of dissimilarities in species compositions. The two most dissimilar forests are on either end of the axis and forests with similar species compositions are located close together. Names were assigned to each forest based on dominant species according to IV's. These designations were compared to the Maine Natural Areas Program natural community profiles as a point of reference (Gawler 2000).

The most similar forests, based on their locations on the ordination, were grouped to form three different forest community types.

**Question 1 Analyses: Does resistance to structural and compositional change from beech thickets differ among forests and forest community types?**

The dependent variables that were used to indicate resistance to structural and compositional change were compared among all seven forests. As a complement to analyzing each site separately, dependent variables were also compared among the three broad forest community types by combining data from the sites that comprise each community type. Combining data from the sites enabled a broad comparison between general community types because of the great variability in species compositions between the sites.

All statistical analyses were performed using the Stata 8.0 statistical package (StataCorp 2003). Kruskal-Wallis tests were used to compare the distance from the parent to the farthest sprout, beech stem density (stems/ha), and the ratio of beech stem density/density of nonbeech stems (stems/ha) in the thicket across the seven forest sites. Mann-Whitney U tests, corrected for multiple comparisons, were used for the pair-wise comparisons of the dependent variables between the three forest community types. A two-way ANOVA was used to compare the ratio of beech stem density/density of nonbeech stems in the thicket for two size classes among all seven sites. The beech/nonbeech stem density by size class data were not compared among the three community types because these data are extremely variable among individual forests. Vaughn Woods data for the ratio of beech sprout density/density of nonbeech stems were not included in comparisons between the forests or forest community types because the

nonbeech stem data are incomplete. Relationships between the dependent variables and the mean basal area, density, and biodiversity (Simpson index) of trees in the subplots were also considered.

### **Question 2 Analyses: Which species compete well or poorly with beech thickets?**

Linear regressions were used to test for relationships between the density of beech stems and the density of other species (stems/ha) in the thicket. Beech sprout and nonbeech stem density data were combined from forests comprising the forest community types. Regressions were calculated between beech and species that were present in all the forests that comprise the forest community types, including: hemlock, red maple, sugar maple, white ash, yellow birch, balsam fir, red oak, and striped maple.

### **Index of Resistance**

To comprehensively compare the resistance of each forest to structural and compositional change, each forest was ranked by its relative resistance to change based on the dependent variables. For each dependent variable, the forest that was least resistant to change was ranked first and the forest that was most resistant was ranked last. For example, the forest in which the mean distance from parents to the farthest sprouts was the greatest was ranked 1. The site with the highest mean beech sprout density was also ranked 1, as was the site with the greatest ratio of beech density/ density of nonbeech stems. Forest community types were also ranked by relative dependent variable values. Forests and forest community types with higher means of these rankings are generally more resistant to structural and compositional change resulting from the formation of beech thickets.

## **Results**

### **Forests**

The most important species at each forest site based on IV's were used to name the forest. The forest names and locations include ash-birch-maple (Mt. Pisgah), aspen-pine-ash (Perkins Arboretum), maple-oak (Runnals Hill), oak-maple (Garcelon), hemlock-maple-birch (Sander's Hill), hemlock-pine-oak (The Mountain), and hemlock (Vaughn Woods) forests (Table 1, Figure 1). As a reference, the most similar Maine Natural Areas Program community profile designations include maple-basswood-ash, aspen-birch, oak-pine, red oak- northern hardwoods, hemlock, hemlock-oak-pine, and hemlock forests, respectively (Gawler 2000).

### **Forest Community Types**

Based on the matrix of dissimilarities between forests, the ash-birch-maple and hemlock forests are the most dissimilar (Table 2). These forests are at opposite ends of the ordination axis, and the other forests are ordered based on their distances from the ash-birch-maple forest (Figure 4). Based on the distances between forests, the ash-birch-maple and aspen-pine-ash forests are most similar, the maple-oak, oak-maple, and hemlock-maple-birch forests are similar, and the hemlock-pine-oak and hemlock forests are closest on the ordination. The most similar forests are grouped to form the forest community types including the mixed hardwood, red maple/red oak, and conifer forest community types, respectively.

**Question 1: Does resistance to structural and compositional change from beech thickets differ among forests and forest community types?**

*Does resistance to beech thicket expansion differ among forests and forest community types?*

The distances from parent beech trees to the farthest sprouts differed significantly among forests ( $H = 20.1$ ,  $df=6$ ,  $p = 0.0027$ ; Figure 5a). Beech sprouts were generally found within 5.6 m of the parent tree, and were closest in the hemlock forest and farthest in the maple-oak and hemlock-pine-oak forests ( $mean_1 = 2.7 \text{ m} \pm 0.85$ ,  $mean_2 = 5.6 \text{ m} \pm 0.48$ , and  $mean_3 = 5.6 \text{ m} \pm 0.76$ ). There is no linear trend in the parent-farthest sprout distance along the ordination; the farthest sprouts in the two most dissimilar forests, the ash-birch-maple and hemlock forests, are similar distances from parents. The distance from the parent to the farthest sprout tended to be greater at forests in the middle of the ordination.

The distances from the parents to the sprouts also differed significantly among forest community types. The sprouts were significantly farther from the parents in the red maple/red oak forest community than in the mixed hardwood forest community ( $mean_1 = 5.0 \pm 0.27$ ,  $mean_2 = 3.6 \pm 0.38$ ;  $N_1 = 32$ ;  $N_2 = 15$ ;  $U = -2.9$ ,  $p = 0.0041$ ; Figure 5b). The distance from parent-farthest sprout did not differ significantly between the conifer and red maple/red oak forests.

*Does resistance to beech thicket development and ability to become denser differ among forests and forest community types?*

The density of beech sprouts in the beech thickets differed significantly between

the forest sites ( $H = 37.4$ ,  $df=6$ ,  $p = 0.0001$ ; Figure 6a). The beech sprouts were most dense in the hemlock-maple-birch forest and least dense in the ash-birch-maple forest ( $mean_1 = 3366.3 \pm 420.1$ ,  $mean_2 = 517.0 \pm 153.2$ ). The beech densities were most similar in the ash-birch-maple and hemlock forests, which are at opposite ends of the axis. The beech thicket density tended to increase along the ordination, but the density decreased in the hemlock forest.

The trend of more dense beech thickets in intermediate forests is also seen across the forest community types (Figure 6b). The beech thickets are significantly less dense in the mixed hardwood forests than in either the red maple/red oak or conifer forest communities ( $mean_1 = 1009.5 \pm 193.8$ ,  $mean_2 = 2264.1 \pm 252.6$ ,  $mean_3 = 1808.9 \pm 276.3$ ;  $N_1 = 15$ ,  $N_2 = 32$ ,  $N_3 = 18$ ;  $U = -3.283$ ,  $p = 0.001$ ,  $U = -2.1$ ,  $p = 0.038$ , respectively). The beech thickets are most dense in the red maple/red oak community, but thickets in the conifer community are not significantly less dense.

*Does the exclusion of other species in the thicket differ among forests and forest community types?*

The ratio of the density of beech sprouts/ density nonbeech stems in the thickets differed significantly across the forests ( $H = 29.8$ ,  $df=6$ ,  $p = 0.0001$ ; Figure 7a). The relative density of beech was lowest in the ash-birch-maple forest and highest in the hemlock-pine-oak forest ( $mean_1 = 0.4 \pm 0.09$ ,  $mean_2 = 2.7 \pm 0.41$ ). Beech sprout density tended to increase relative to nonbeech stem density along the ordination.

The ratio of beech sprout density/ density of nonbeech stems differed significantly between the mixed hardwood, red maple/red oak, and conifer forest communities (Figure 7b). Beech had significantly lower relative density in the mixed hardwood forests than in

the red maple/red oak and conifer forests ( $\text{mean}_1 = 0.7 \pm 0.14$ ,  $\text{mean}_2 = 1.3 \pm 0.16$ ,  $\text{mean}_3 = 2.7 \pm 0.41$ ;  $N_1 = 15$ ,  $N_2 = 32$ ,  $N_3 = 8$ ;  $U = -2.4$ ,  $p = 0.0168$ ,  $U = -3.9$ ,  $p = 0.0001$ , respectively). Beech had a significantly greater relative density in the conifer community than in the red maple/red oak community ( $U = -3.4$ ,  $p = 0.0008$ ).

*At what growth stage are other species affected most by beech thickets?*

The ratio of beech sprout density/ density of nonbeech stems in the thickets differed significantly by size class,  $<1$  m (seedling) and  $>1$  m and  $<10$  cm dbh (sapling), among the forests ( $F = 5.5$ ,  $df=6$ ,  $p = 0.0002$ ; Figure 8). The ratio of beech/ nonbeech stem density was greater for the seedling size class than the sapling size class in most forests. Beech sprout density was highest relative to the seedlings in the aspen-pine-ash forest and lowest in the similar ash-birch-maple forest ( $\text{mean}_1 = 9.0 \pm 3.74$ ,  $\text{mean}_2 = 0.3 \pm 0.11$ ). Although beech sprouts had a higher relative density than the seedlings but not the saplings in the aspen-pine-ash forest, beech sprouts had a higher relative density than the saplings but not the seedlings in the hemlock-maple-birch forest.

## **Question 2: Which species compete well or poorly with beech thickets?**

Red maple is the only species in beech thickets in which the stem density is significantly correlated with the beech thicket density. Red maple density in the red oak/red maple community type is negatively correlated with beech thicket density ( $r = -5.6$ ,  $p = 0.024$ ; Figure 9). Although less clear, there is also a significant negative relationship between red maple and beech stem densities in the conifer community ( $r = -9.2$ ,  $p = 0.008$ ).

## **Index of Resistance**

If all dependent variables are weighted equally, the hemlock-pine-oak forest is least resistant to compositional and structural change (Table 3). Compared to the other forests, the distance from the parent to farthest sprout was greatest in this forest, the beech sprout density was relatively high, and the ratio of beech sprout density/ nonbeech stem density were the greatest. The two most dissimilar forests, the ash-birch-maple forest type and the hemlock forest, are both relatively resistant to change. However, the hemlock forest resistance rank should be considered cautiously because this rank is based on only two of the three variables.

When comparing the relative resistance among communities, the mixed hardwood forest community type is most resistant to change. This community has the shortest parent-sprout distance, lowest beech stem density, and lowest ratio beech density/ density of nonbeech (Table 4). The red maple/red oak community type is the least resistant.

## **Discussion**

**Question 1: Does resistance to structural and compositional change from beech thickets differ among forests and forest community types?**

*Does resistance to beech thicket expansion differ among forests and forest community types?*

Although the distances from the parents to the farthest sprouts differed significantly between forests, there is no clear linear trend along the ordination. The forests that are most resistant to beech thicket expansion (in which the parent-sprout distance is relatively short), the ash-birch-maple and hemlock forests, are the most

dissimilar forests. Since beech sprouts from the roots of the parent, the extent of the beech thicket likely reflects the extent of the parent root system, and the thicket may be able to spread if the parent tree can extend its roots (Bohn and Nyland 2003). These sprouts may continue to expand until competing plants are encountered (Jones and Raynal 1986).

Beech thickets may be least likely to spread in hemlock forests because of root competition between parent beech trees and mature hemlock trees. Hemlock and beech both have shallow, wide-spreading, extensive root systems, and competition can change the vertical stratification and spatial distribution of beech roots (Harlow and Harrar 1958, Schmid and Kazda 2000). For example, root competition may constrain the beech roots and limit beech thicket expansion. Hemlock roots may also overtop the beech roots so that sprouts cannot surface, or if hemlock roots are just beneath the beech sprouts, the sprouts would not be able to form their own roots and would not establish. Thicket expansion may also be limited in the ash-birch-maple forest because of competition from white ash and yellow birch, which both have shallow, wide spreading roots (Harlow and Harrar 1958).

Beech thickets may be most able to expand in the maple-oak and hemlock-pine-oak forests because red oak has a deep root system (Harlow and Harrar 1958). There may be less underground competition between red oak and beech because the roots of these species grow at different depths. The lack of competition may allow beech roots to spread farther into forests dominated by red oak than in the hemlock and ash-birch-maple forests. It is also less likely that red oak roots will grow over beech roots.

The interactions between beech and other species are not consistent across all forests, and the extent of the beech thicket expansion likely depends on interactions between several other species, as well as abiotic and edaphic factors. For example, despite the codominance of hemlock in the hemlock-pine-oak forest, this forest is susceptible to beech thicket expansion. Beech thickets may be able to expand in this forest because codominants, such as red pine, have moderately deep root systems that do not compete with the beech roots.

In terms of broad forest community types, the conifer and mixed hardwood community types may be relatively less susceptible to beech thicket expansion primarily because dominant species such as hemlock and white ash are strong root competitors with beech. However, because of the especially strong root competition between beech and hemlock, it would be expected that beech thicket expansion would be lowest in the conifer community type.

*Does resistance to beech thicket development and ability to become denser differ among forests and forest community types?*

As with thicket expansion, beech sprout density may have differed significantly across the seven forests because of root competition between the parent beech and other mature trees. The number of sprouts each parent produces depends on parent vigor and root size, density, and depth (Ward 1961, Jones and Raynal 1986). Interspecific root competition can affect all of these parent tree characteristics (Schmid and Kazda 2000).

Beech roots with larger diameters tend to produce more sprouts, and sprouts that are produced by small roots tend to be ephemeral or have low survivorship (Jones and

Raynal 1986). Also, roots with faster growth rates produce relatively more sprouts. Beech sprouts may have been least dense in the ash-birch-maple forest because competition from the shallow, extensive white ash and yellow birch root systems may reduce the growth rates and diameters of beech roots. Competition from hemlock roots may also slow beech root growth in the hemlock forest. A lack of root competition does not explain the dense beech thickets in the hemlock-maple-birch forest, however, because hemlock is also dominant in this forest.

The depth of the parent tree roots also affects the number of beech sprouts that are generated (Ward 1961, Jones and Raynal 1986). Most sprouts are found on roots that are superficial or near the soil surface. Since interspecific competition affects the vertical stratification of roots (Schmid and Kazda 2000), if beech roots are forced to grow at lower soil depths in forests with intense root competition, parents in these forests may not produce as many sprouts. Since the roots of beech and the dominant species in the ash-birch-maple and hemlock forests are all shallow, root competition likely affects the depth at which the beech roots grow and the number of sprouts generated. Similarly, the red maple/red oak community type has relatively dense beech thickets, perhaps because red oak roots are deep and do not interfere with the shallow beech roots.

Lowered parent vigor also reduces sprout production (Jones and Raynal 1986). Even though the severity of BBD infestation was the same in all the forests, parent vigor may have differed because of different interspecific competitors and abiotic conditions. It would be expected that parent vigor would be lowest in forests where hemlock is dominant because of competition for moisture and stressors such as low light; hemlock canopies attenuate the most light out of several canopy species (Canham et al. 1994,

Canham 1994). This expectation is supported by Twery and Patterson's (1984) findings that the highest rates of beech mortality from BBD occur in stands dominated by hemlock. Runkle (1990) also reported that hemlock most commonly replaces beech, suggesting that these species are fierce competitors. If this is the case, it would be expected that beech stems would be least dense in the forests dominated by hemlock. However, although hemlock was codominant in the hemlock-maple-birch and hemlock-pine-oak forests, beech thickets were relatively dense in these forests. Perhaps only pure hemlock stands lower parent vigor, which explains why thickets in the conifer community were not the least dense. Parent vigor may have also been relatively low in the ash-birch-maple forest because of the relative abundance of sugar maple, which is a strong competitor with beech when the species are mature (Forrester 2003). Competition from sugar maple may also explain why thicket density is lowest in the mixed hardwood forest community.

Abiotic factors that are specific to each forest type but which were not measured for this study could affect beech sprout survivorship and beech thicket density. For example, although beech stems are extremely shade tolerant, low light conditions under the hemlock canopy could contribute to beech sprout mortality because root sprouts need some light to develop (Jones and Raynal 1986). The acidic soils that are typical of hemlock stands may also affect survivorship because soil nutrient status can influence low-light survivorship (Kobe et al. 1995).

*Does the exclusion of other species in the thickets differ among forests and forest community types?*

The ratio of beech sprout density/ nonbeech stem density in the thickets increased

along the ordination from the ash-birch-maple to the hemlock-pine-oak forest. The relative density of beech tended to increase as light transmission through the forest canopy decreased; forests dominated by white ash and red oak allow the greatest light transmission, red maple forests cast intermediate levels of shade, and hemlock canopies attenuate the most light (Canham et al. 1994.) If more light is attenuated by the forest canopy, the shade cast by the beech thickets in the understory will also be denser.

Shade has been identified as an important mechanism by which beech thickets interfere with the regeneration of other species, and shade tolerance determines which species can compete with beech thickets (Kobe et al. 1995, Hane 2003). In general, it is more likely that beech sprouts affect the density of nonbeech stems in the thicket (rather than nonbeech stems affecting beech sprout density) because beech sprouts have a competitive advantage over seedlings, and because sprout density is influenced mostly by parent tree characteristics (Jones and Raynal 1987, Beaudet et al. 1999, Hosaka et al. 2005). Bohn and Nyland (2003) also found that young stems of other species did not affect the development of beech thickets.

The relatively great light transmission through the ash-birch-maple canopy may allow shade intolerant species in this forest, including white ash, paper birch, and black cherry, to compete with beech. As a shade tolerant species, beech grows relatively slowly in high light conditions in comparison to shade-intolerant species (Kobe et al. 1995). Also, the growth rates of shade tolerant species in this forest, such as yellow birch and sugar maple, are faster than beech sprouts if light levels are slightly above the optimum for beech (Nyland 2006). This suggests that as long as the canopy doesn't attenuate too much light, species will be able to compete with beech in the understory.

This may also suggest that the shade intolerant species comprising early successional forests may be able to compete with beech thickets if light is abundant.

The relative density of beech may have been the greatest under canopies dominated by hemlock, which transmit the least light, because of its shade tolerance and competitive advantage (Canham et al. 1994). It is possible that only the most shade tolerant species in the hemlock-maple-birch and hemlock-pine-oak forests, such as beech and hemlock, would be able to grow under these low light conditions (Kobe et al. 1995). Beech sprouts likely exclude hemlock stems because sprouts benefit from parent subsidies, which can compensate for extremely low light conditions, and because sprouts do not need to allocate resources to construct a root system (Beaudet et al. 1999, Hosaka et al. 2005). Kobe et al. (1995) also found that beech has higher survivorship under low light than other species, perhaps because sprouts have a competitive advantage.

The same trend, in which the relative density of beech increases as light levels decrease, is clear when comparing the forest community types. The density of nonbeech species in the mixed hardwood community may have been relatively high because these species are able to take advantage of the relatively high light levels. Beech was likely more dense than other species in the conifer community because beech has a competitive advantage under low light conditions.

Lei et al. (2002) also found that shade tolerance creates interspecific differences in the ability for young stems of other species to compete under the dense shade of a *Rhododendron maximum* thicket. The order of mortality of species under the thicket, black cherry>red oak>hemlock, correlates with increasing shade tolerance. Although the present study compared the relative density of beech sprouts across canopies that transmit

different amounts of light, within each forest the most shade tolerant species likely compete better with the thickets than the shade intolerant species.

*At what growth stage are other species affected most by beech thickets?*

Comparing the ratio of nonbeech seedlings and saplings to beech can be used to determine at what growth stage beech thickets interfere with nonbeech regeneration. In most forests, beech sprouts were more dense than nonbeech seedlings but were not more dense than nonbeech saplings. Beech thickets may affect nonbeech seedling density by excluding seed or preventing germination of other species, or by affecting nonbeech seedling survivorship. Both possibilities require further study. Also, beech sprouts < 1 m may simply be more abundant than nonbeech seedlings (Jones and Raynal 1987).

Nonbeech sapling density may have been less affected by thickets because nonbeech seedlings may be recruited to the larger size class more often than the beech sprouts.

The relative density of beech compared to nonbeech seedlings may have been greatest in the aspen-pine-ash forest because the dominant species in this forest, trembling aspen and white ash, are relatively shade intolerant so their seedlings may have low survivorship in the low light conditions under beech thickets. In fact, models show that white ash regeneration is often inhibited by beech thickets (Le Guerrier et al. 2003). Conversely, since nonbeech saplings are much more dense than beech sprouts in this forest, this may suggest that nonbeech seedling mortality is low and nonbeech stems tend to move up to the sapling size class. If this is the case, the beech sprouts < 1 m may simply be relatively abundant in this forest.

Nonbeech seedlings may have been more dense than beech in the ash-birch-maple and hemlock-maple-birch forests because of the relative abundance of shade tolerant

species such as hemlock, yellow birch, and sugar maple. These species can likely persist as seedlings in the thicket. Nonbeech saplings may have been less dense than beech in the hemlock-maple-birch forest because beech sprouts may outcompete less shade tolerant species like white ash, hemlock, yellow birch, and red maple over time so that these stems are not recruited to the sapling size class.

Understanding whether thickets have a greater affect on the establishment or growth and survivorship of other species is helpful to determine the mechanism of regeneration interference. Although Lei et al. (2002) found that *Rhododendron maximum* thickets affect the survivorship of species in the thicket rather than the arrival or germination of seeds, to my knowledge the mechanism of regeneration interference has not been studied for beech thickets. While the effect of beech thickets on the survivorship of nonbeech seedlings and saplings seems to differ among forests, controlled experiments may required to study the mechanism of interference.

## **Question 2: Which species compete well or poorly with beech thickets?**

Understanding which species are able to compete with beech thickets and which species tend to be excluded can help to predict the degree of resistance in forest communities in which they are dominant. Red maple is the only species in which stem density in the thicket is significantly correlated with the beech thicket density. As the beech thicket density increases in the red maple/red oak community, the red maple stem density decreases, suggesting that red maple competes poorly with beech thickets. The negative correlation is less clear in the conifer community. There were no red maple stems in the relatively less dense beech thickets, perhaps because these thickets are in

areas with very dense shade where understory growth is suppressed. However, in thickets in which red maple is found, their density tends to decline with increasing beech density. Red maple stem density did not correlate with the beech thicket density in the mixed hardwood community; this indicates that species interactions affect the ability for red maple to compete and illustrates why it may be beneficial to study species interactions at the community level.

Red maple may compete poorly with beech thickets because it is a relatively shade intolerant species. However, studies have documented the positive effects of intact vegetation on red maple survival (Berkowitz et al. 1995) and red maple attributes such as large seeds with dormancy mechanisms that enable them to germinate with minimal light (Houle 1994). This suggests that shade tolerance is an important life history trait affecting the survivorship of species in beech thickets.

### **Index of Resistance**

When the three dependent variables, parent-sprout distance, beech sprout density, and ratio of beech sprout density/ nonbeech stem density, are all compared across the forests and forest community types, the mixed hardwood community, specifically the ash-birch-maple forest is one of the most resistant to change. This forest is the most resistant to the exclusion of other species and the ability for thickets to develop and become denser. Compositional change may be least likely in this forest because other species in the understory are able to compete.

Although the conifer community type is less resistant to change than the mixed hardwood community, the hemlock forest is one of the most resistant forests. However,

this measure of resistance must be considered cautiously because the data are incomplete. As expected, the hemlock forest is most resistant to beech thicket expansion and thicket development. Interestingly, although hemlock is codominant in the hemlock-pine-oak forest, this forest is the least resistant to change, especially in regards to beech thicket expansion and the exclusion of other species.

The red maple/ red oak community type is the least resistant to change. The forests comprising this community type tend to be relatively more resistant to the exclusion of other species and less resistant to beech thicket expansion. Again, it is interesting that the forest in which hemlock is codominant, the hemlock-maple-birch forest, is the least resistant to change.

These results are not entirely consistent with previous studies. To my knowledge studies have not yet explicitly quantified structural and compositional changes in the understory from beech thickets. However, studies have reported that beech thickets tend to exclude mixed hardwood species such as sugar maple and yellow birch, while conifer species such as hemlock, red spruce, and species with similar ecological attributes will be able to regenerate (Twery and Patterson 1984, Beaudet, et al. 1998, Hane 2003). Models have also predicted that hardwoods such as sugar maple and white ash will be most severely affected by change following BBD, while hemlock will benefit because of its shade tolerance (Le Guerrier et al. 2003). If results from the present study were consistent with previous studies, the mixed hardwood community type should be least resistant to change, while the conifer community type should be most resistant to change. Conversely, the relatively low resistance of the red oak/ red maple community type is consistent with a study by Lorimer et al. (1994) in which red oak tended to be excluded

by thickets, albeit not a beech thicket. However, most of the studies mentioned above were based on observations at the species level. The present study compares the effects of beech thickets at the community level, where interactions between several species could complicate the results of previous studies.

### **Conclusions**

Resistance to structural and compositional changes from beech thickets differs among forests and forest community types. The ability for thickets to expand and become denser may differ among forests because of competition between the parent beech tree and various species. The propensity for thickets to exclude other species may differ because of the different shade tolerances of the species in the understory. Beech thickets may tend to dominate the seedlings of other species more than saplings, but controlled experiments to determine the mechanism by which beech thickets interfere with regeneration would complement these observational data. Controlled experiments to study interactions between beech and other species may also help to confirm why red maple competes poorly with beech thickets.

Although forests in which hemlock is dominant were expected to be most resistant to change from beech thickets, the mixed hardwood community is most resistant. Forests in which hemlock is codominant, with the exception of the hemlock forest, tend to be relatively less resistant. Although this study attempts to explain resistance to beech thickets using the ecological and life history characteristics of certain species, these results may be explained by species interactions and other conditions specific to each forest that are beyond the scope of this study.

## Acknowledgements

I would like to thank Dr. Judy Stone for her encouragement, generous time, and help with every aspect of this study. I also thank Dr. F. Russell Cole and Dr. David Firmage for their suggestions and support. Thanks also to Dr. Katherine St. Clair for help with the sampling design, the Kennebec Land Trust for suggesting study sites, and to my field companion, Elli Jenkins.

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Table 1. The importance values (percentages) of species in each forest. The most similar Maine Natural Areas Program (MNAP) community profile name is also given.

| Site             | Mt. Pisgah                      | Perkins Arboretum | Runnals Hill | Garcelon         | Sander's Hill       | The Mountain     | Vaughn Woods |
|------------------|---------------------------------|-------------------|--------------|------------------|---------------------|------------------|--------------|
| Forest Type      | Ash-birch-maple                 | Aspen-pine-ash    | Maple-oak    | Oak-maple        | Hemlock-maple-birch | Hemlock-pine-oak | Hemlock      |
| MNAP Forest Type | Maple-basswood-ash              | Aspen-birch       | Oak-pine     | Red oak-hardwood | Hemlock             | Hemlock-oak-pine | Hemlock      |
| Species          | Importance Values (Percentages) |                   |              |                  |                     |                  |              |
| Beech            | 0                               | 0                 | 8.3          | 7.0              | 5.8                 | 2.9              | 4.3          |
| Bigtooth Aspen   | 0                               | 0                 | 9.4          | 0                | 0                   | 0                | 0            |
| Black Cherry     | 2.1                             | 2.2               | 0            | 0                | 0                   | 0                | 0            |
| Grey Birch       | 0                               | 3.3               | 0            | 0                | 0                   | 0                | 0            |
| Hemlock          | 2.5                             | 5.4               | 12.1         | 12.7             | 41.4                | 27.8             | 47.5         |
| Hophornbean      | 2.0                             | 0                 | 0            | 11.1             | 0                   | 0                | 0            |
| Paper Birch      | 13.7                            | 7.5               | 12.5         | 5.0              | 1.5                 | 10.3             | 0            |
| Quaking Aspen    | 12.5                            | 36.1              | 0            | 0                | 0                   | 0                | 2.7          |
| Red Maple        | 4.9                             | 10.6              | 22.7         | 19.5             | 18.1                | 3.0              | 8.2          |
| Red Oak          | 0                               | 0                 | 17.0         | 26.9             | 4.0                 | 26.2             | 21.1         |
| Red Pine         | 0                               | 0                 | 0            | 0                | 0                   | 26.3             | 0            |
| Red Spruce       | 0                               | 0                 | 0            | 0                | 0                   | 3.5              | 0            |
| Sugar Maple      | 13.1                            | 2.9               | 0            | 9.1              | 5.8                 | 0                | 0            |
| White Ash        | 28.5                            | 13.7              | 5.6          | 2.1              | 9.4                 | 0                | 0            |
| White Pine       | 2.1                             | 18.2              | 12.4         | 0                | 0                   | 0                | 14.2         |
| Yellow Birch     | 18.5                            | 0                 | 0            | 6.7              | 13.9                | 0                | 2.0          |

Table 2. The matrix of dissimilarities between forests based on species importance values. (ABM=Ash-birch-maple, APA=Aspen-pine-ash, MO=Maple-oak, OM=Oak-maple, HMB=Hemlock-maple-birch, HPO=Hemlock-pine-oak, H=Hemlock.)

| Forest Composition | ABM   | APA   | MO    | OM    | HMB   | HPO   | H     |
|--------------------|-------|-------|-------|-------|-------|-------|-------|
| ABM                | 0     | 0.518 | 0.632 | 0.677 | 0.620 | 0.841 | 0.858 |
| APA                | 0.518 | 0     | 0.584 | 0.740 | 0.702 | 0.840 | 0.695 |
| MO                 | 0.632 | 0.584 | 0     | 0.373 | 0.528 | 0.546 | 0.459 |
| OM                 | 0.677 | 0.740 | 0.373 | 0     | 0.432 | 0.502 | 0.518 |
| HMB                | 0.620 | 0.702 | 0.528 | 0.432 | 0     | 0.608 | 0.402 |
| HPO                | 0.841 | 0.840 | 0.546 | 0.502 | 0.608 | 0     | 0.452 |
| H                  | 0.858 | 0.695 | 0.459 | 0.518 | 0.402 | 0.452 | 0     |

Table 3. The forest sites ranked by each dependent variable from 1= least resilient to change to 6= most resilient to change. The mean rank is the overall resiliency rank.

| Dependent Variable  | Distance from Parent to Sprout | Beech Sprout Density | Ratio Beech/Non Beech Density | Mean Rank |
|---------------------|--------------------------------|----------------------|-------------------------------|-----------|
| Ash-birch-maple     | 5                              | 7                    | 6                             | 6.0       |
| Aspen-pine-ash      | 4                              | 4                    | 4                             | 4.0       |
| Maple-oak           | 1                              | 5                    | 5                             | 3.7       |
| Oak-maple           | 3                              | 3                    | 3                             | 3.0       |
| Hemlock-maple-birch | 2                              | 1                    | 2                             | 1.7       |
| Hemlock-pine-oak    | 1                              | 2                    | 1                             | 1.3       |
| Hemlock             | 6                              | 6                    | Data not available            | 6.0       |

Table 4. The forest community types ranked for each dependent variable from 1= least resilient to change to 3= most resilient to change. The mean is the overall resiliency rank.

| Dependent Variable | Distance From Parent to Sprout | Beech Stem Density | Ratio Beech/Non Beech Density | Mean Rank |
|--------------------|--------------------------------|--------------------|-------------------------------|-----------|
| Hardwood           | 3                              | 3                  | 3                             | 3.0       |
| Red maple/red oak  | 1                              | 1                  | 2                             | 1.3       |
| Conifer            | 2                              | 2                  | 1                             | 1.7       |

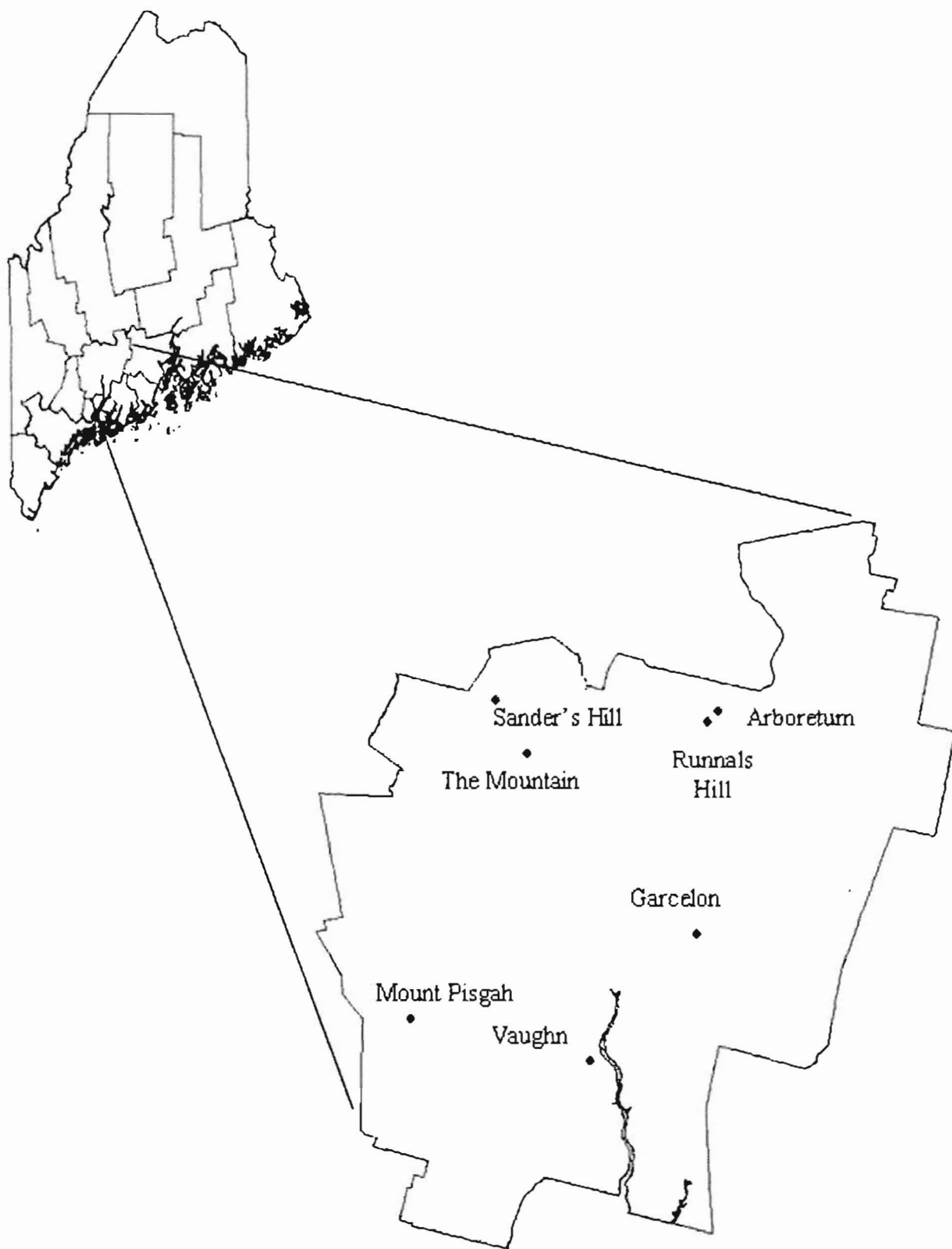


Figure 1. The study site locations in Kennebec County, Maine.

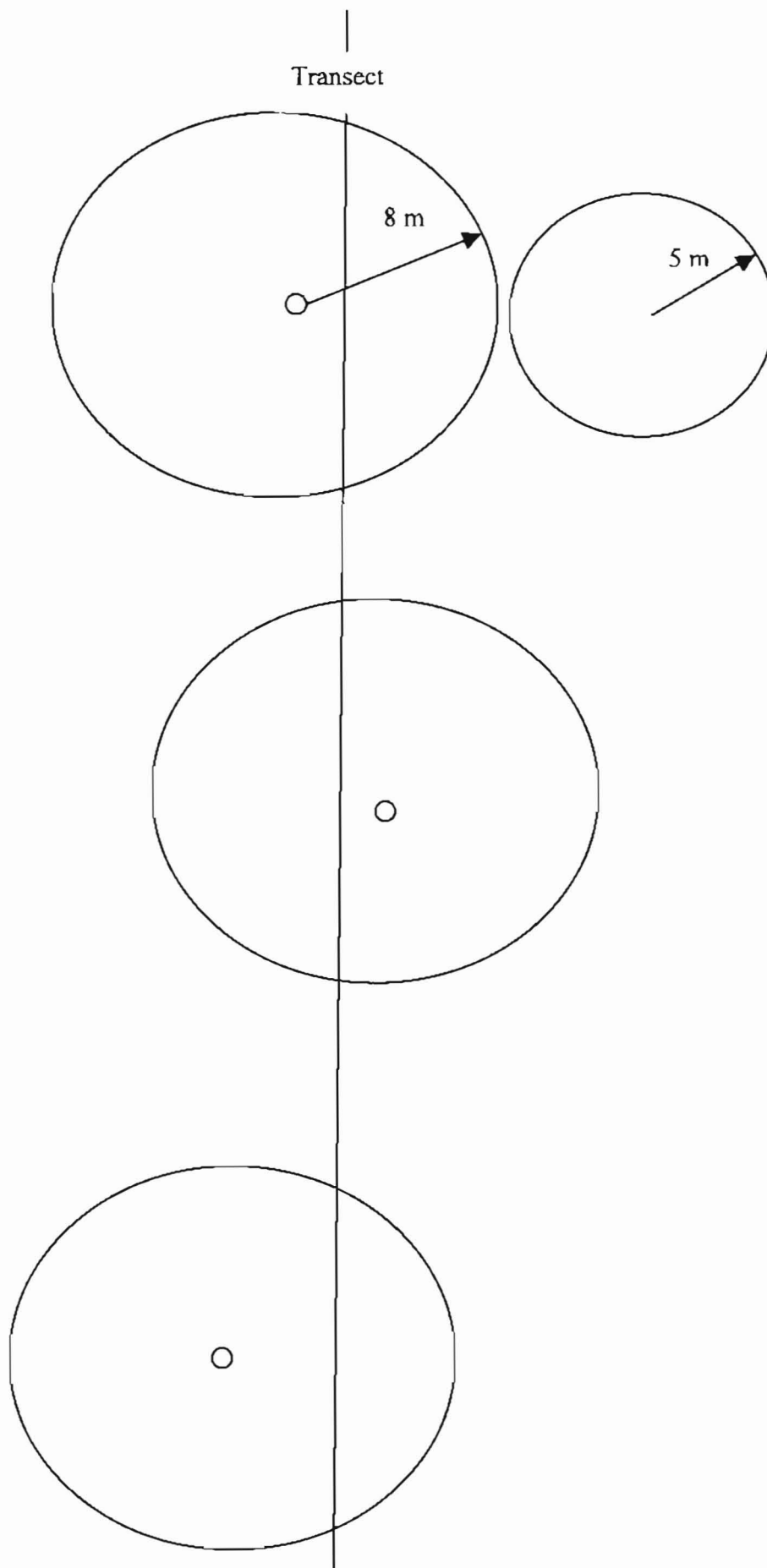


Figure 2. Schematic illustrating sampling methods of thickets produced by individual parent beech trees

Transect

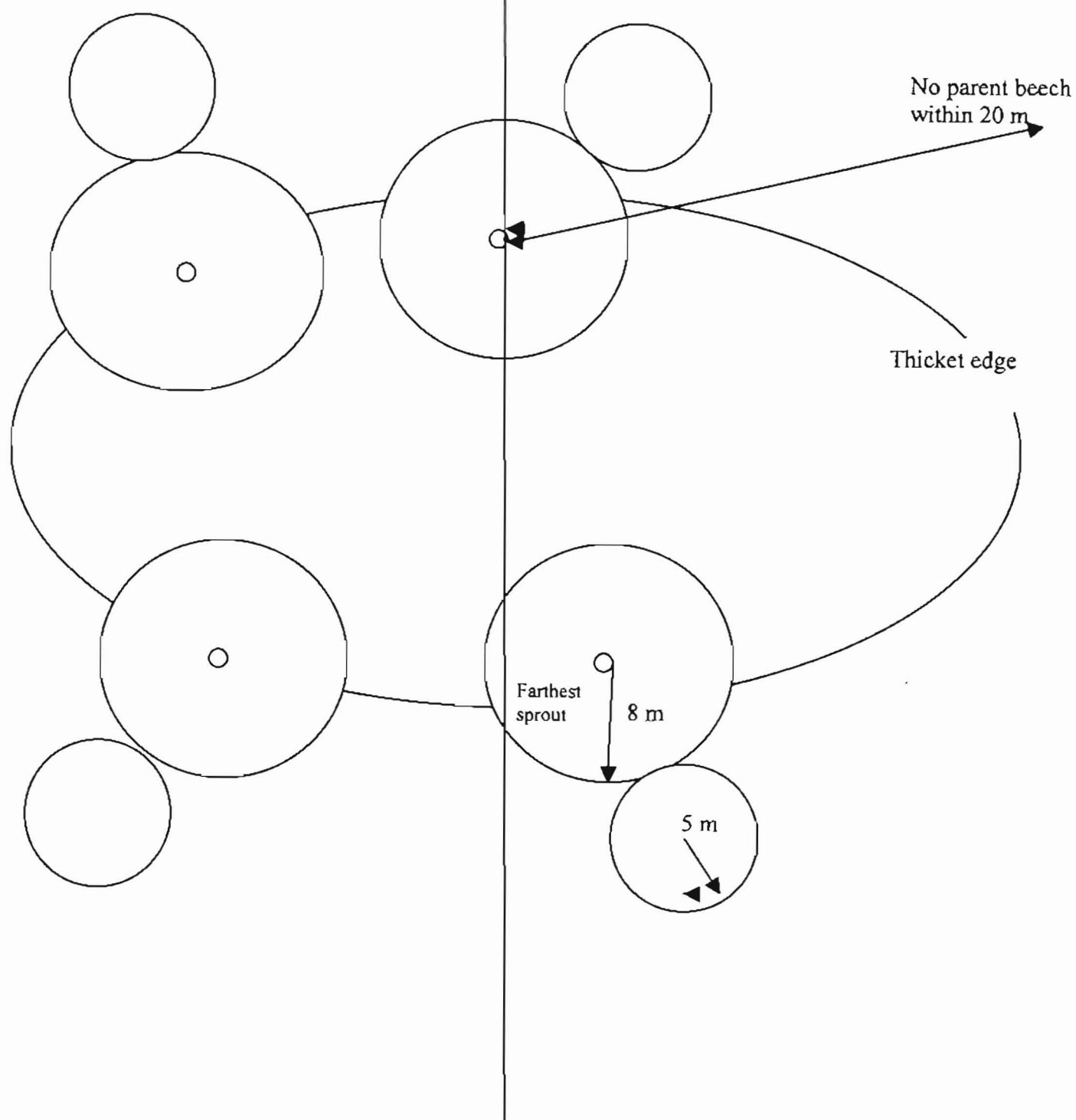


Figure 3. Schematic illustrating sampling methods for thickets produced by beech stands.

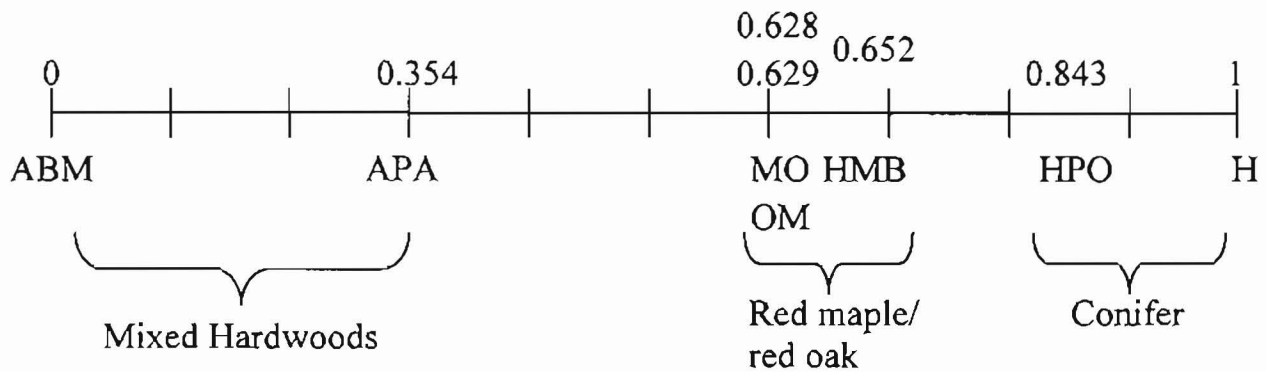
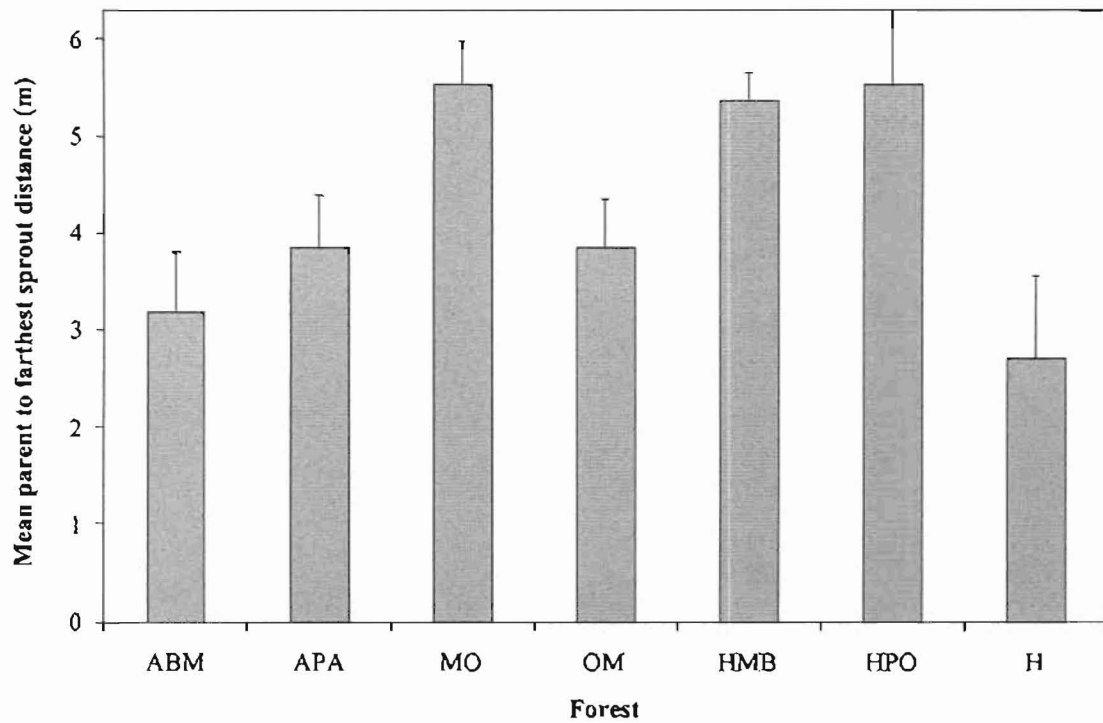


Figure 4. The ordination of the forests and forest community types based on the distance from ABM. Distances were calculated from the dissimilarity matrix based on species IV's. (ABM=Ash-birch-maple, APA=Aspen-pine-ash, MO=Maple-oak, OM=Oak-maple, HMB=Hemlock-maple-birch, HPO=Hemlock-pine-oak, H=Hemlock).

A.



B.

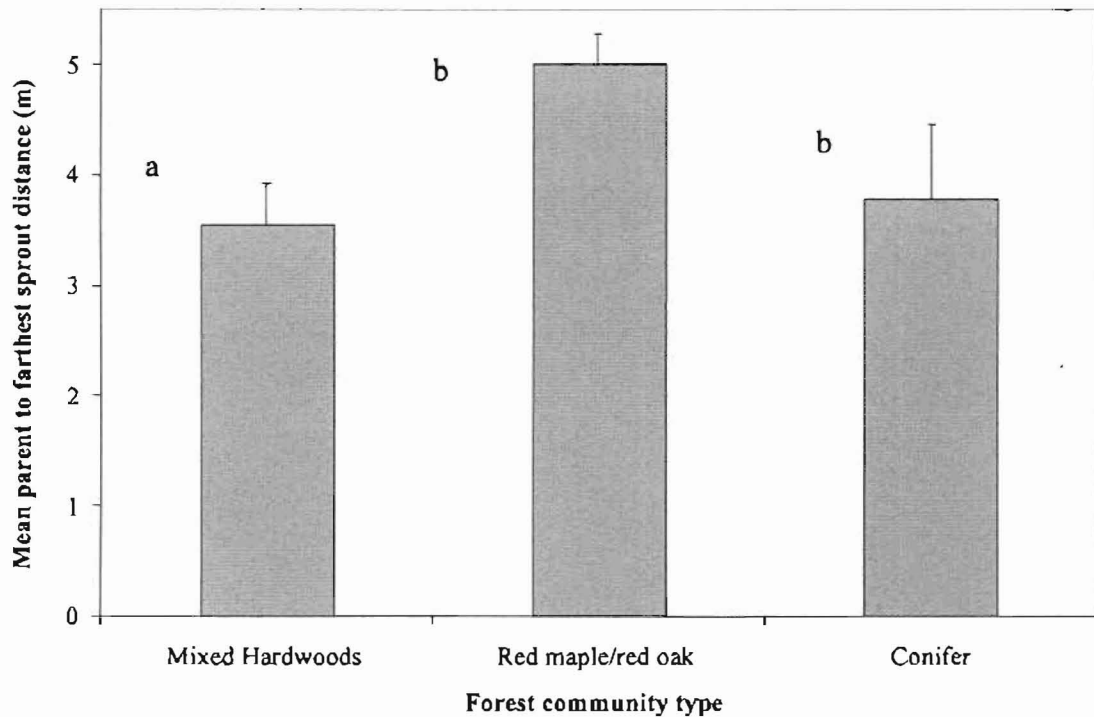


Figure 5. The mean distance ( $\pm$  SE) in meters from parent trees to the farthest beech sprout. A) Forests are arranged by ordination. (ABM=Ash-birch-maple, APA=Aspen-pine-ash, MO=Maple-oak, OM=Oak-maple, HMB=Hemlock-maple-birch, PO=Hemlock-pine-oak, H=Hemlock.) B) Letters indicate statistical differences between forest community types.

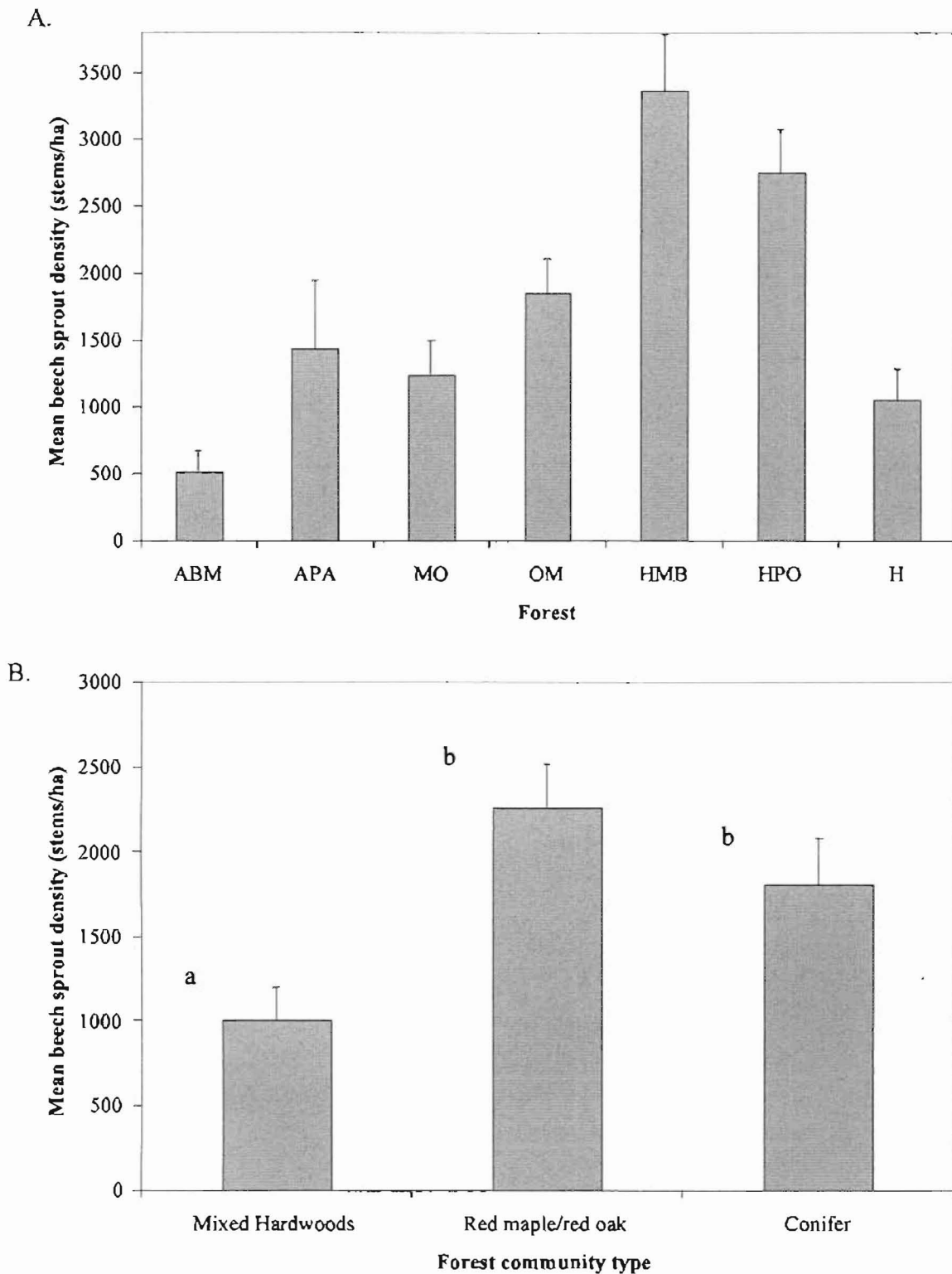
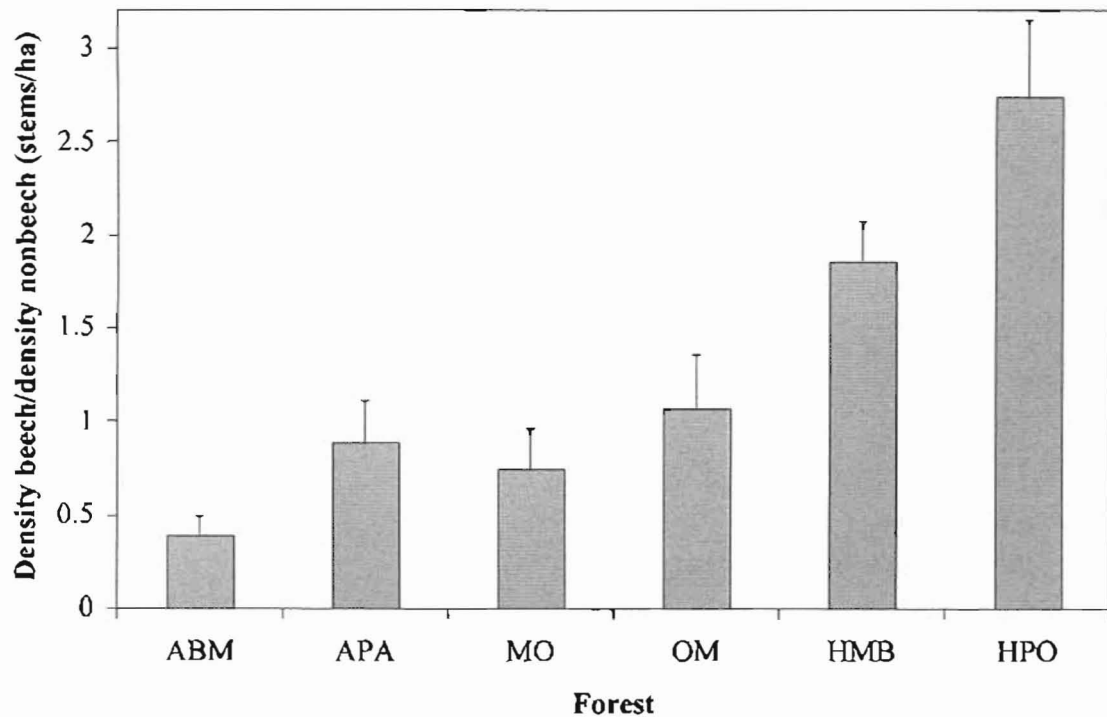


Figure 6. The mean density of beech sprouts in thickets (stems/ ha  $\pm$  SE). A) Forest sites are arranged by ordination. (ABM=Ash-birch-maple, APA=Aspen-ine-ash, MO=Maple-oak, OM=Oak-maple, HMB=Hemlock-maple-birch, HPO=Hemlock-pine-oak, H=Hemlock.) B) Letters indicate statistical differences between forest community types.

A.



B.

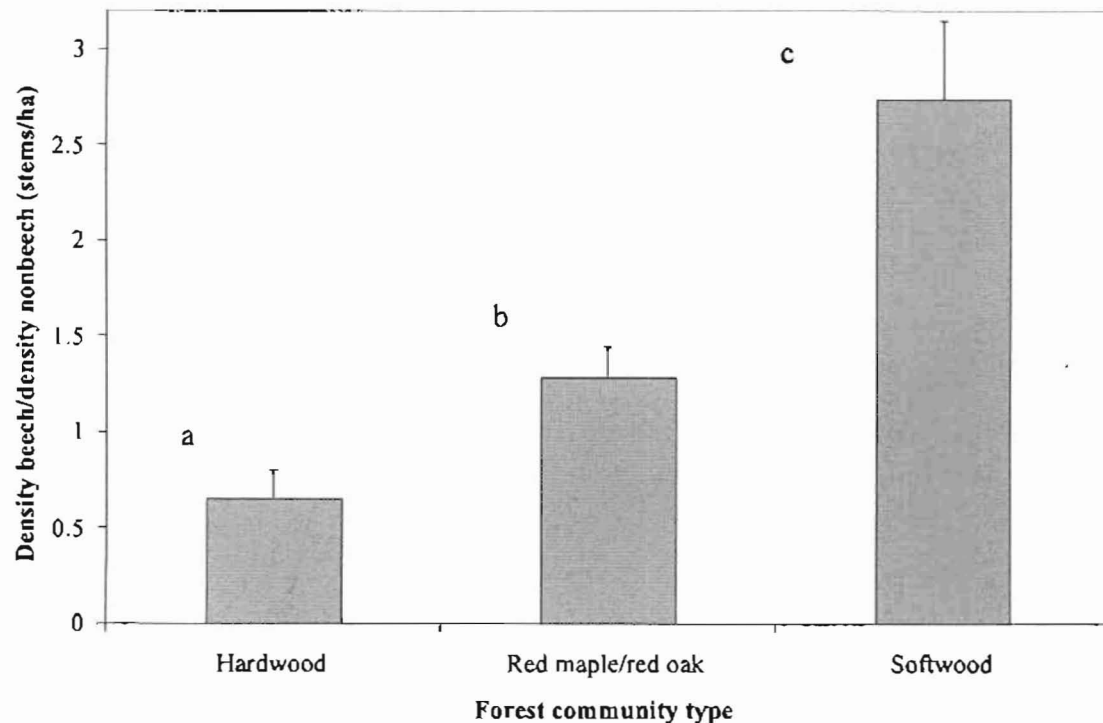


Figure 7. The ratio of the density of beech sprouts/density of nonbeech stems (stems/ ha  $\pm$  SE) in thickets. A) Forest sites are arranged by ordination. (ABM=Ash-birch-maple, APA=Aspen-pine-ash, MO=Maple-oak, OM=Oak-maple, HMB=Hemlock-maple-birch, HPO=Hemlock-pine-oak, H=Hemlock.) B) Letters indicate statistical differences between forest community types.

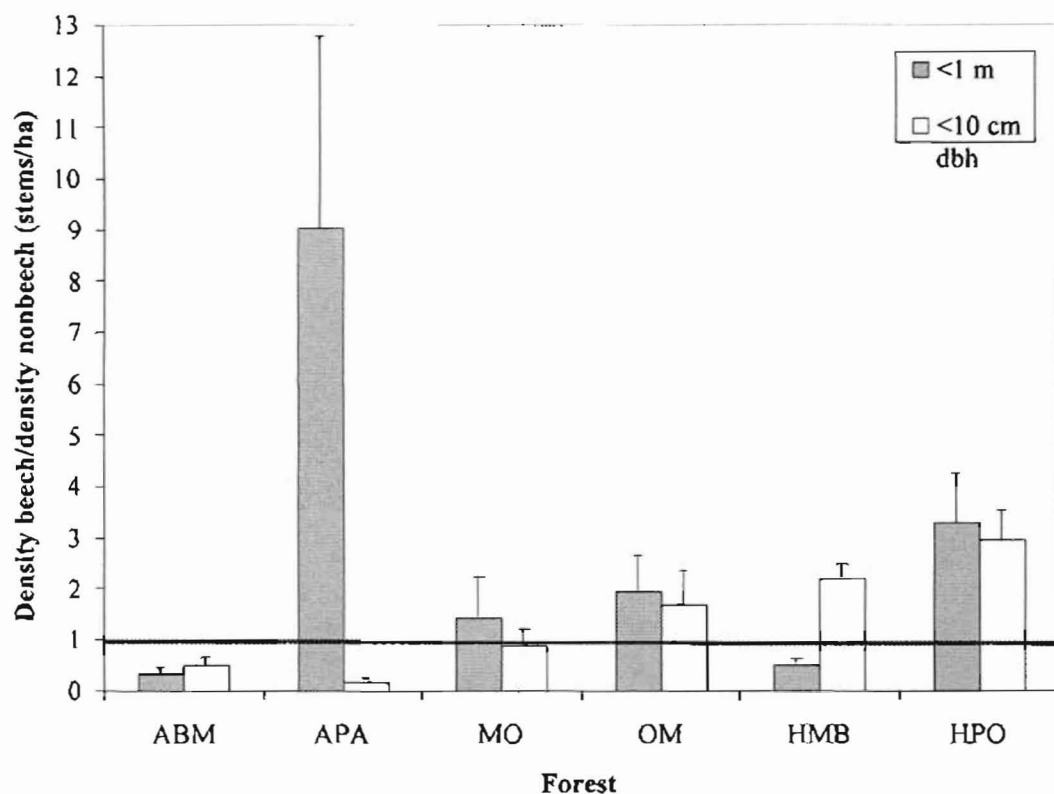


Figure 8. The ratio of beech sprout density/density of non beech stems (stems/ ha  $\pm$  SE) in thickets in two size classes, seedling (<1 m) and sapling (>1 m and <10 cm dbh), across the forest sites. Forest sites are arranged by ordination. (ABM=Ash-birch-maple, APA=Aspen-pine-ash, MO=Maple-oak, OM=Oak-maple, HMB=Hemlock-maple-birch, HPO=Hemlock-pine-oak, H=Hemlock.)

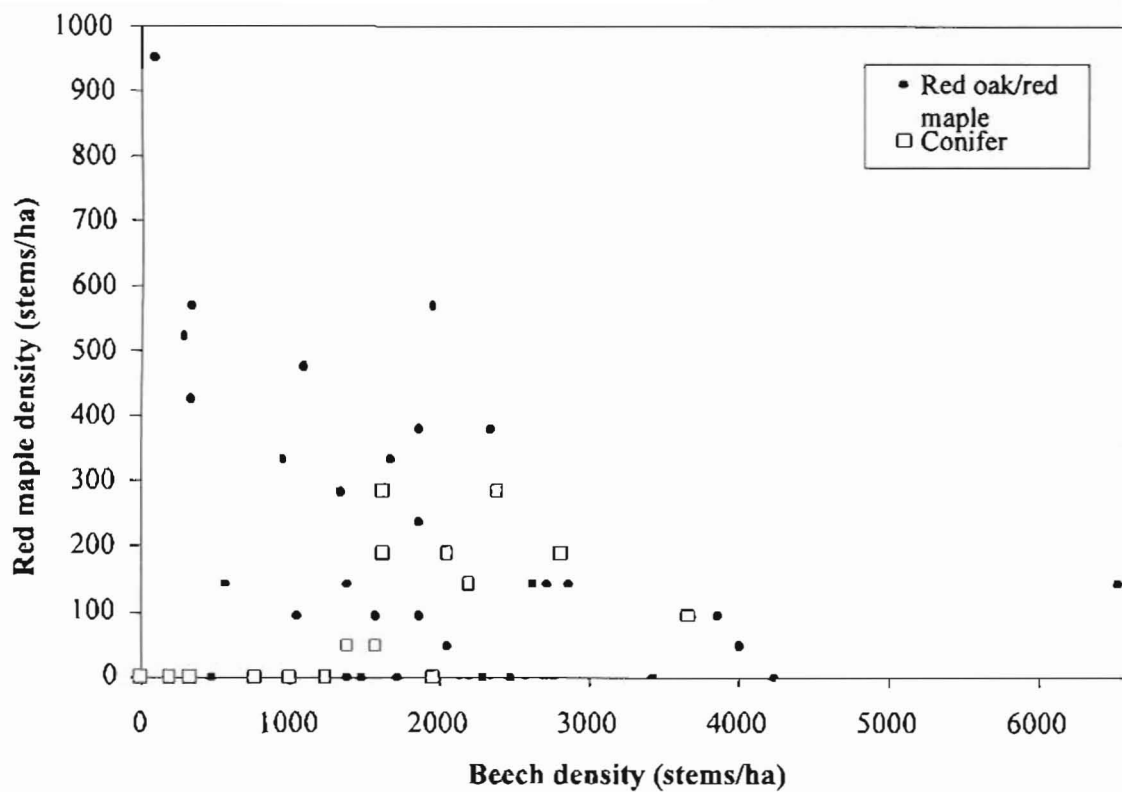


Figure 9. The correlation between red maple stem density and beech sprout density (stems /ha) in thickets in the red maple/red oak and conifer forest community types.