

# **FOUR DECADES OF CHANGE IN AN OLD- GROWTH BEECH-MAPLE FOREST IN INDIANA**

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of Missouri-Columbia

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In Partial Fulfillment of the Requirements for the Degree

Master of Arts

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by  
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December 2006

**The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled:**

**FOUR DECADES OF CHANGE IN AN OLD-GROWTH BEECH-MAPLE  
FOREST IN INDIANA**

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**A candidate for the degree of Master of Arts in Geography**

**And hereby certify that in their opinion it is worthy of acceptance.**

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## ABSTRACT

Hoot Woods is a 6.6 ha old-growth beech-maple forest. Fully censused every decade since 1965, the forest is one of the most intensively monitored permanent plot stands in the eastern deciduous forest. Although it is set in a highly fragmented agricultural landscape, the stand largely escaped direct anthropogenic effects during Euro-American settlement of the region during the mid-1800s. Currently, natural processes of competitive development, windthrow, gap replacement, and decomposition operate undisturbed. Tornadoic disturbance in 1980 influenced several portions of the stand. This study reports findings from the fifth inventory in 2005, discusses patterns of vegetation dynamics over the past 40 years, and assesses patterns of species mortality, recruitment, and persistence in both spatial and temporal dimensions, to examine whether the stand can be characterized as demonstrating compositional stability.

Stand density increased by nearly 100 stems per hectare between 1965 and 2005, from 204.3 to 305.2 stems/ha. Stand basal area fluctuated between 27.6, 30.0, 24.7, 26.0, and 26.6 m<sup>2</sup>/ha for the respective census years. Importance values of sugar maple increased steadily over the course of the study period, while those for American beech progressively decreased. Between 1965 and 1975, sugar maple increased by 53.2 and 32.5 percent in density and basal area, respectively. The majority of sugar maple stems occurred in small size classes, indicating consistent regeneration. Beech, meanwhile, displayed a unimodal distribution, typical of a non-replacing population. The importance of beech gradually declined from a high of 40.5% in 1965 to a low of 22.6% in 2005.

The 1980 tornado, in concert with the biological attributes of the codominants, seem to account for the decline of beech. Mortality rates by size class reveal that beech

was particularly hard-hit by the tornado disturbance. In 1985, mortality rates exceeded 30% in all size classes greater than 50 cm dbh. A similar pattern prevailed in the 1995 and 2005 censuses. The loss of so many sizable stems severely dampened the species' reproductive capacity and opened tremendous holes in the canopy. These canopy openings mainly benefited sugar maple.

# CHAPTER ONE

## INTRODUCTION

Over the past forty years, investigators have carefully documented contemporary vegetation change in Hoot Woods, an old-growth, beech-maple forest in south-central Indiana. While the surrounding landscape was cleared and converted to agricultural landuse during the nineteenth century, this 25.9 ha (64 acre) stand escaped direct anthropogenic alteration (Petty & Lindsey 1961). In 1965, a 4.4 ha (10.9 acre) portion of Hoot Woods was first fully censused. An additional 2.2 ha (5.4 acre) was mapped in 1975 (Abrell & Jackson 1977). The resulting 6.6 ha plot was re-censused in 1985, 1995, and for this study in 2005. Stand composition and structure have changed markedly over this ecologically brief time period, with the stand's two most prominent species, American beech and sugar maple, changing in abundance. Most notably, sugar maple has increased in abundance, while American beech has declined. This study documents these changes, and attempts to explain them in the context of vegetation change theories, stand history, and environmental change.

### Theories of Vegetation Change

Vegetation dynamics are a focal point of biogeographic research, with the goal of tracking changes in biotic communities over time. Vegetation structure, composition, and pattern reflect the interaction of numerous biotic and physical factors, and countless events in the history of a specific site. Microsite differences in resource abundance,

competitive interaction among trees, and disturbance regimes all play critical roles in shaping a forest's structure. Research on vegetation dynamics within forests is concerned with shedding light on the processes by which trees occupying a site either maintain their dominance, or give way and become replaced by other species.

Studies of vegetation change must overcome the limitations of time and spatial scale. Changes in species composition appear locally at first, particularly in the vegetative structure and population characteristics of vulnerable species (Bakker et al. 1996). The variation that occurs across larger scales in topography, soil type, and disturbance history interact with small scale phenomena to create composition and structure among vegetative communities (Chen 2004). Further complicating studies of forest dynamics is the matter of time. The ecological processes that determine the characteristics of forest composition rarely operate within time frames easily observed during a human lifetime. In order to investigate ecological variables that operate on long time horizons, such as tree succession, a study must encompass decades if not centuries or millennia. Observations of the successional characteristics of specific forest stands over protracted time periods are, therefore, inherently difficult to make. As the duration of a study is extended, investigators are able to draw increasingly resolute conclusions concerning the dynamics of forests. But until such time that an adequate database of vegetation change has been acquired, researchers must make inferences from incomplete data collected at divergent scales. A large body of literature exists concerning forest dynamics, and a variety of competing theories have been developed to explain patterns of tree replacement. The task of evaluating these theories on their merits is complicated by

the varied methodologies of forest dynamics studies and the unique properties of forest communities.

Early twentieth century scientific theories of vegetation dynamics were best articulated by ecologists Frederic Clements, Henry Gleason, and Henry Cowles. Clements was the first researcher to fully develop the idea of “plant succession.” In his 1916 book on the subject, Clements denoted “succession” to mean the life cycle of an individual biotic community. The crux of his argument was the idea that vegetation cover exists in a balance with determinant climate conditions, unless altered by disturbance or occupying previously unvegetated sites. Succession described the development of vegetation on these sites as an orderly process proceeding in linear stages and ending in the establishment of a “climax” community. Competitively advantageous plant communities supplant their predecessors and, in so doing, change the local conditions of their own habitats. Once reached, climax communities were thought to maintain themselves, relatively unchanged, until such time that the climate might change enough to favor a different type of climax (Clements 1916). At around the same time, Cowles produced a similar theory related to vegetation dynamics, but one more related to environmental change other than climate. Cowles argued that there were cycles of vegetation similar to those for erosion. In the first stage young vegetation and rapid transformations predominate. The ensuing phases, of which there could be many, were stages of maturation characterized by moderate transformations. In the final stages, vegetation was characterized by slow transformations and stability. For Cowles, vegetation change was linked both to long- and short-term environmental change, such as geology, climate change, and landform development (Cowles 1899; 1901). His deductive

approach sought to simplify complex biotic phenomena and aid other researchers in their efforts to evaluate vegetation dynamics (Cowell & Parker 2004).

In 1926, Gleason presented a very different version of vegetation development. He replaced the historical community-based stages envisioned by Cowles and Clements with individualistic life histories and geographies of specific tree species. Gleason questioned the usefulness of the climax premise and the attendant notion of species associations. He argued that Clements' identification of particular kinds of vegetation associations, such as beech-maple, assumed an unrealistic degree of predetermined homogeneity. Gleason lent more credence to the chance nature of tree distributions and offered an alternative to the plant association concept based on the occurrence and abundance of individual tree species. This "individualistic" interpretation of vegetation dynamics views plant communities in the context of their morphological and geographical histories and considers every species an autonomous actor (Gleason 1926). Although a peer of Clements and Cowles, Gleason's contributions were not immediately noticed within biogeography or ecology. Indeed, it took until the early 1950s before they were meaningfully recognized. The trio of Clements, Cowles, and Gleason constitute the primary originators of modern vegetation dynamics research, and their ideas have had a long-lasting impact on successive generations of investigators (Cowell & Parker 2004).

By the mid-twentieth century, some studies had begun to seriously question the validity of these models of succession. Raup (1942) worried that these theories were too weak to serve as the entire foundation of biogeographical research. Instead, Raup advocated empirically-based, inductive explanations of vegetation pattern. Because of the potential of countless environmental factors to cause change in vegetative

communities according to their different combinations in different places, he argued that succession theories were too simplistic. Strahler (1972) echoed the sentiments of Curtis and McIntosh (1951) and Gleason (1926) before them by contending that forests would be better classified as statistical assemblages in which some species occur more often than others, dependent on variation in environmental factors. He applied statistical methods to uncover the role of topographic controls on tree species distribution within forests. Strahler (1972) acknowledged the tendency of tree species to occur in definable groupings because of their similar environmental demands, but suggested that individual species respond independently to variation in environmental controls.

While these views assume that change is a part of biotic communities, coexistence theories assume that stability prevails. Coexistence describes a long-term phenomenon whereby two or more tree species share dominance of forest stands. This scenario has been used as an alternative to succession to describe the composition of old-growth, beech-maple stands (Vankat 1975). Coexistence theories contend that environmental heterogeneity promotes species coexistence rather than competitive exclusion. In these scenarios, several species are allowed to coexist because each species is a superior competitor in certain microsites due to natural fluctuations in the distribution of environmental resources (Bakker et al. 1996). There is some evidence to support the coexistence theory. Several studies have found forest communities in non-directional states of coexistence in whereby two or more species have remained co-dominant for decades or even centuries (Poulson & Platt 1996).

The theories of succession and coexistence rely on autogenic criteria to relate spatial patterns to the unique form of each species. They assume that the evolutionary

attributes of trees, such as size, longevity, seed production cycle, rooting structure, and phenology are the direct determinants of spatial pattern and the indirect causes of responses to disturbance and competition (Chen 2004). Species-specific biological characteristics, such as shade tolerance, leaf-litter, root parasite susceptibility, and longevity are used to infer successional habits. Mortality is an autogenic factor that weighs heavily in succession hypotheses. Stand structure, maximum size and age of trees, formation rates for snags, logs, and canopy gaps are all impacted by mortality rates. Large trees are the most susceptible to death, and are more likely to suffer the effects of windthrow during storms because wind speeds are greater at the top of the canopy. In addition, larger trees have been shown to be more at risk to threats from pathogens and insects (Lorimer 2001).

Disturbance regimes and patch dynamics emerged as prevailing successional concepts within ecology in the late 1970s. Earlier theories of vegetation dynamics began to give way to more dynamic models that considered instability an intrinsic part of vegetative communities. Currently, postmodern ideas of uniqueness, diversity, and disorder predominate. Vegetation dynamics are considered difficult to predict, non-linear, and multi-scale. As such, they require complex explanations that can account for temporal irregularities in disturbances and the responses by species to those events (Cowell & Parker 2004).

Much of the contemporary research surrounding vegetation dynamics and species composition has been framed by the concept of disturbance regimes. Disturbance regimes refer to natural events that affect the mortality of vegetation. Fire, floods, disease, windthrow, and insects are the most commonly cited sources of disturbance.



Low levels of disturbance appear to favor superior competitors, while intermediate to high levels of disturbance appear to ensure the coexistence of several plant species (Zaczek et al. 2002). In some modern-day landscapes, however, many of these disturbances have been eliminated or reduced in importance to mere stresses (Cowell & Dyer 2002). Plant species adapted to conditions of persistent stress can gain the upper hand in these communities, to the detriment of both disturbance-favored and competitive communities.

Allogenic influences, such as human induced decreases in fire frequency have created fortuitous opportunities for shade tolerant species and provided a window via which exotic species may increase their presence (McCune 1985). Fire is widely acknowledged as a major controller of vegetation pattern in presettlement midwestern landscapes (Guyette et al. 2002). In most reconstructions of pre-European settlement, a mosaic of prairie, savanna, and upland oak forests dominate the Midwest (Cowell & Jackson 2002). Studies of current-day forest stand dynamics often indicate successional patterns caused by post-settlement fire suppression. The characteristics and composition of contemporary forests can be quite different from their predecessors. In many of the region's once oak-dominated forests, mesophytic species, such as sugar maple have come to dominate (Abrams, 2003). The common wisdom is that these species possess characteristics that are favored by the human-altered landscape. Sugar maple is shade and temperature tolerant, but is quite susceptible to fire. With the elimination of fire as a major form of disturbance, they have begun to thrive. The current landscape is dominated by agricultural land and scattered second-growth forests. In this setting, stands without evidence of logging or other human disturbance are a rare ecological

finding, and the few that do exist are a source of great research interest (McCune & Menges 1986). Despite their pristine old-growth status, the species composition of even these dwindling tracts often fails to reflect their composition at the time of settlement (Zaczek et al. 2002).

### Old-growth Forests

No universal definition exists for the term “old-growth” forest (Ziegler 2004). Indeed, the Food and Agricultural Organization of the United Nations (FAO) lists 105 proposed definitions for old-growth forests, eighty-six of which are noticeably dissimilar (Diggins & Kershner 2005). Most frequently, the presence of overstory canopy trees older than 150 years, minimal evidence of human disturbance over the past eighty to 100 years, an abundance of snags and coarse woody debris, mid- or late- successional tree species in the canopy, late-successional trees in the understory, uneven-age structure among canopy trees, high diversity of large canopy trees, a canopy structured in multiple layers, a mosaic of all-aged canopy gaps, and significant numbers of standing and downed dead trees are cited as indicators (Parker 1989; Diggins & Kershner 2005). These criteria represent descriptive features that are expected, but not necessarily found, in all old-growth forest ecosystems. There is a tendency among definitions of old-growth to favor forests that reflect natural ecological processes and disturbance regimes. Individual old-growth stands often represent an undisturbed condition where the influence of geomorphology, soils, and natural disturbances, in conjunction with plant reproductive processes and animals, constrain the development of plant communities (Goebel et al. 2005). However, in practice, it is quite difficult to differentiate those

features that are natural from those that may have been impacted by humans. Despite the many different attempts to define old-growth, there remains an erroneous conception which still is held by many persons that these forests consist of large tracts of mostly massive trees. In reality, there are a wide range of tree sizes and ages, a higher proportion of small trees than large trees, and more young trees than old trees (Potzger 1942).

Old-growth forests are important to researchers because they are among the rare sites experiencing minimal human alteration. Old-growth forests developed under prior environmental conditions and thus, some believe, provide a window to the past. These natural areas provide baseline information from which scientists can measure the effects of human actions elsewhere and to help maintain biological diversity. It has long been believed that ecosystem processes such as nutrient cycling and biodiversity remain undisturbed in old-growth forests. This sentiment has been used as a primary justification for the protection of these wilderness areas. As such, many remnant old-growth forest stands have been protected with the goal of studying and preserving their unique characteristics. In this sense, remnant woodlots are analogous to museum archives.

Some, however, question the ability of old-growth forests to reveal landscape conditions at the time of European settlement (Parker 1989). A common presumption is that old-growth remnants mirror presettlement forest in their dynamics (Forrester & Runkle 2000), but there is increasing evidence that the effects of disturbance on stand composition and structure vary throughout stand history (Zaczek et al. 2002). Many isolated old-growth stands are in a state of transition due to landuse practices in the

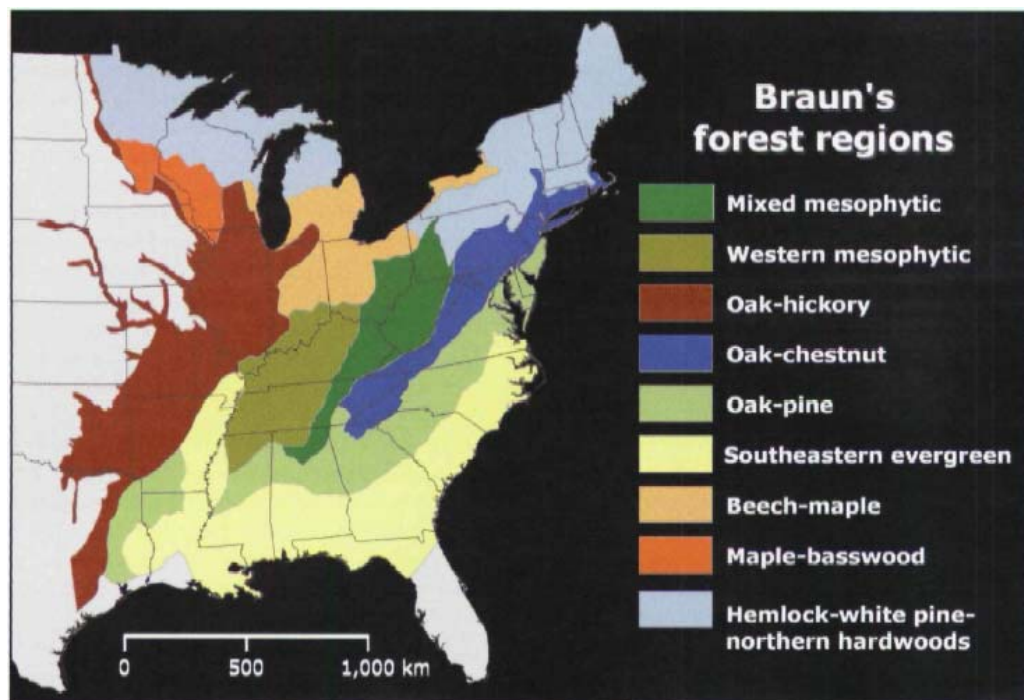
surrounding landscape, such as fire suppression. This process has been occurring for some time in oak-dominated stands, particularly those situated on mesic sites, where oaks have failed to regenerate and been replaced by more shade tolerant species (Parker 1989).

Old-growth forests are quite rare in the Midwestern United States. They have been publicly documented since the late 1800s and discussed in publications since the 1930s. Research at these sites has provided many insights into the ecology and environmental history of the region (e.g., Potzger & Friesner 1934; Cain 1935; Lindsey 1962; Schmelz and Lindsey 1965; Schneider 1966; Vankat 1975). However, many of these woodlands are of such limited area and so fragmented that their long-term viability remains an open scientific question (Parker 1989).

### The Beech-Maple Region

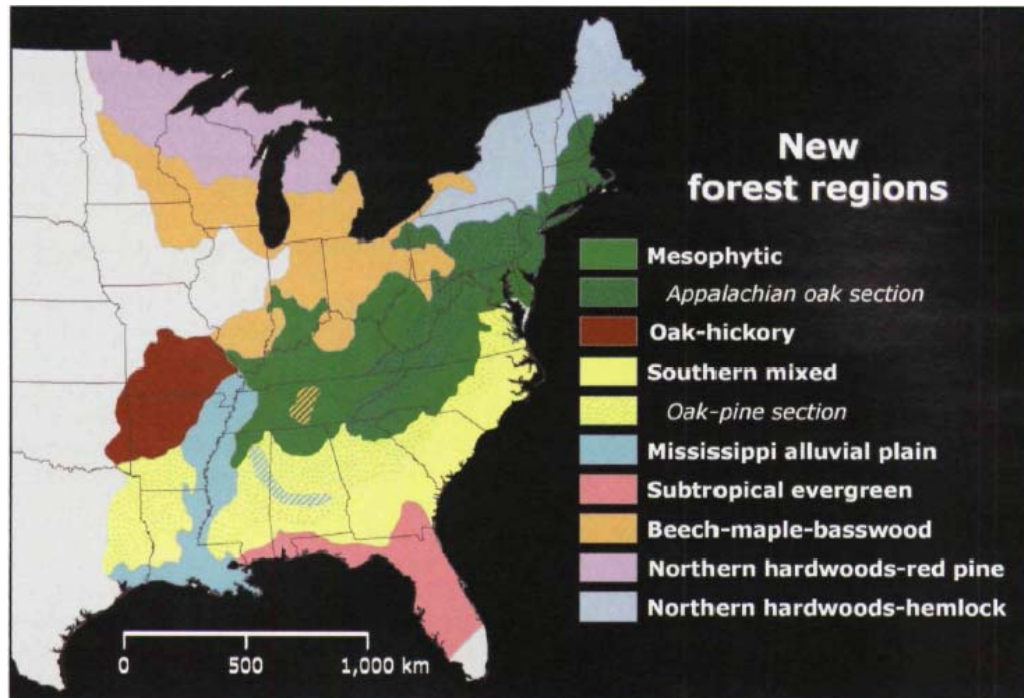
The beech-maple region, with forests co-dominated by American beech and sugar maple, is one of the most widely studied forest types in eastern North America. First recognized in southern Wisconsin in 1877, the unit is centered on the states of Indiana, Ohio, and Michigan and includes the areas surrounding Lake Ontario and the southern half of Lake Michigan (Pell & Mack 1977; Figure 1.1). Considerable research has explored the successional dynamics of beech and maple in these forests. The observation that sugar maple far outstrips beech in reproduction, as evidenced by its large numbers in small size classes, has been almost universal. Other studies have observed that beech saplings are hardier than those of sugar maple and exist in great enough numbers to ensure the maintenance of its codominant status. When taken as a whole, however, prior research appears to uphold the former supposition much more than the latter.

In her seminal work, Braun (1950) chronicled the structure and composition of numerous deciduous forest stands throughout the eastern United States. Based on the results of those inventories, she classified the Eastern Deciduous forest into a series of species associations (Figure 1.1). Trained by Henry Cowles, Braun's work bears the markings of both Clements and her teacher's thoughts. Braun claimed that the beech-maple formation is a seral stage in a successional process towards a climax community composed of several, relatively co-equal, hardwoods species, that she deemed the "mixed mesophytic" region. While the geographic boundaries of the beech-maple region have been modified by subsequent research (Figure 1.2), the core of Braun's classification scheme has been upheld (e.g., Pell & Mack 1977; Dyer 2006).



**Figure 1.1 – Map of Lucy Braun's Forest Regions (Dyer 2006)**

Braun's classification system has been extensively cited, with researchers typically suggesting slight modifications to her scheme based on the results of their own



**Figure 1.2 – Updated Map of Lucy Braun’s Forest Regions (Dyer 2006)**

studies (Petty & Lindsey 1961; Lindsey & Schmelz 1969; Strahler 1972; Diggins et al. 2005). But Braun has also drawn some direct challenges to the basis of her classifications. Pell and Mack (1977) disagreed with Braun’s assessment that no understory species could be considered emblematic of the beech-maple region, arguing that mayapple, Jack-in-the-pulpit, and smooth Solomon’s seal typically offer low levels of coverage. Strahler (1972) and Rogers (1981) criticized the vagueness of her sampling criteria. Curtis & McIntosh (1951) argued against the usefulness of Braun’s classification as a whole. They contended that vegetation cannot be segregated into discrete classifications because community types are never so clear in nature. Rather, they described a set of Wisconsin forests as a continuum of species responding individually to environmental variation. Strahler (1972) critiqued Braun’s map because her species associations lacked sufficient detail. Most criticisms of Braun’s classification

scheme stop short of totally disavowing its utility (Ward 1958), and despite its limitations, Braun's (1950) work remains as one of the few studies to be both quantitative and geographically extensive.

### Codominance

No reports of poor reproduction exist for beech-maple forests. Pell and Mack (1977) described ten "near-climax" beech-maple stands in northeastern Ohio. They noted that the two codominants displayed a negative exponential trend in their size- and age-class distributions, suggesting both species would persist into the foreseeable future. But the authors also observed that sugar maple seedlings occurred in great numbers, describing the density of maple saplings in some stands as "impenetrable." Beech seed reproduction, despite being supplemented by root sprouts, was quite low by comparison. Although they noted the striking disparity in reproductive capacities, the authors attributed the trend to differences in the life histories of the two species and projected no change in beech's canopy composition. This interpretation is emblematic of beech-maple investigations that describe stand dynamics in terms of codominance. Dismissal of sugar maple's high seedling and sapling numbers based on a belief that those numbers are offset by high mortality rates for young trees is the most common element of these types of studies.

Vankat et al. (1975) downplayed superior reproduction by sugar maple at Hueston Woods in western Ohio and identified a mechanism whereby beech replaced itself via seedlings and root sprouts. According to the authors, young beech trees hold a competitive advantage over sugar maple in efforts to occupy canopy openings due to a

faster vertical growth rate and an ability to adapt quickly to increased light intensities by developing a multilayered aspect. Similarly, Kupfer et al. (1997) recognized that the recruitment of species into gap areas is based on the species' nature of replacement and regeneration. Subsequent research has confirmed that young beeches grow quicker than young sugar maples. But this advantage is short-lived, as sugar maple grows more quickly when older ages are reached (Forrester & Runkle 2000).

Warren's Woods in Berrien County, Michigan is an intensively monitored old-growth, beech-maple stand (Cain 1935; Brewer 1980; Poulson & Platt 1996). Cain (1935) concluded that reproduction trends would promote the continuance of a beech-maple association, but identified heavy sugar maple reproduction as one of the stand's "most outstanding features." In 1963 and 1974 Brewer (1980) relocated and resampled, as best he could, the original quadrats used by Cain. Brewer's results indicated that the abundance of several herbaceous species had declined within the woods. He traced the downward trend in herbaceous vegetation to an attendant decline in shade-intolerant species in the canopy, which leaf-out at a later point in spring than their shade-tolerant counterparts. Poulson and Platt (1996) surveyed trees in the area included in Cain's study, but observed little change in composition. They found that the reproductive strategies of American beech and sugar maple were geared towards self-replacement of canopy individuals and concluded that allogenic coexistence best explained the stand dynamics in Warren Woods.

#### Sugar Maple Expansion & American Beech Loss

High numbers of sugar maples are a common feature of beech-maple forests. In



some instances sugar maple dominates the canopy and is present in all size classes, leaving little doubt as to the species' preeminence (Schneider 1966). Other studies observe that sugar maple reproduction far exceeds beech and predict a general increase in its stand representation (Williams 1936). But more commonly, studies that observe increasing sugar maple populations stop short of predicting canopy composition change (Seischab 1990; Forrester & Runkle 2000; Medley et al. 2003; Diggins et al. 2005).

Sugar maple's high density is most evident in understories, where it is often ubiquitous. Small sugar maples are typically well-positioned to replace large beech trees. In addition, beech and maple appear to be negatively correlated in terms of their spatial location (Diggins et al. 2005). Beech replacement patterns, meanwhile, often appear insufficient for retaining its codominant status (Forrester & Runkle 2000; Zhang 2000). Ward (1956; 1958) examined the composition of fifteen beech-maple forest stands in Wisconsin, compared them to presettlement data from GLO surveys, and reported high sugar maple sapling densities. Most notably, he observed a general decline in beech in several stands and surmised that beech was in decline. In reported instances of poorly regenerating American beech populations, neither anthropogenic modification to the local environment nor disturbance agents could be blamed for the decline.

The results of studies conducted in several mixed hardwoods stands support the observations made in beech-maple forests (Miceli et al. 1977). Sugar maple domination of understories is reported for several old-growth forests (Buell & Cantlon 1951; Jackson 1968; Schmelz et al. 1974; Rogers 1981; Parker et al. 1985; Cowell & Jackson 2002; Zaczek et al. 2002; Cowell et al. unpublished). Eventual canopy dominance of shade-

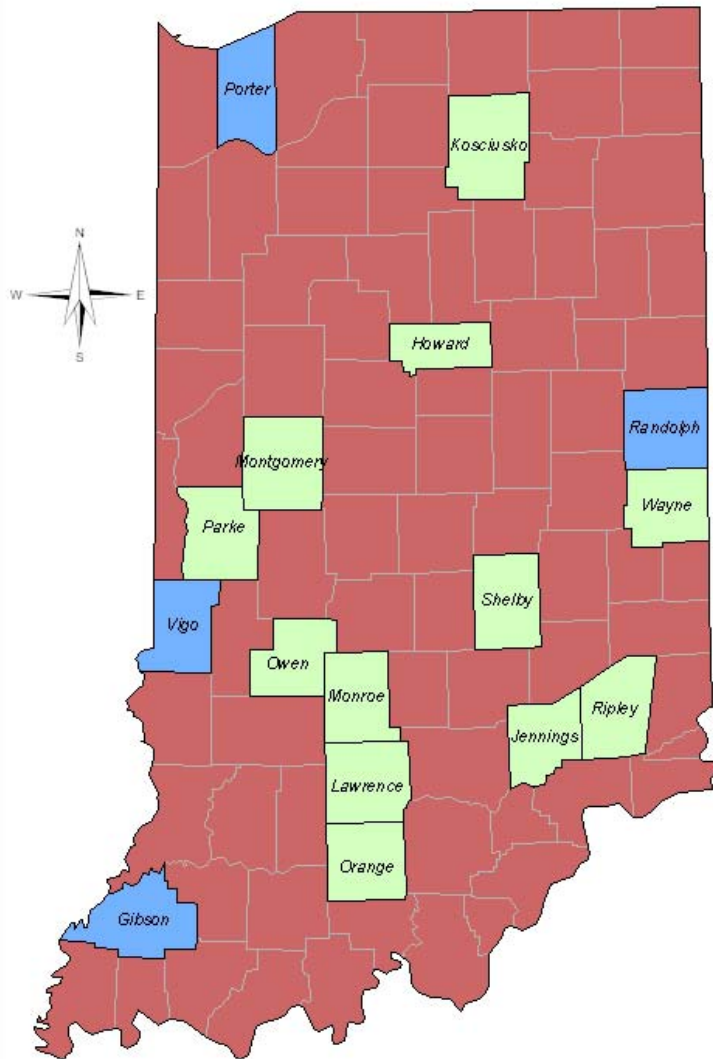
tolerant species, whose intense shading would in turn cause the decline of other hardwoods, is sometimes predicted.

### Beech-Maple Forests of Indiana

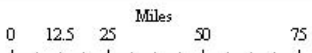
Esten (1932) was one of the earliest researchers to suggest an approaching decline in American Beech for a beech-maple stand in Indiana (Figure 1.3). She reported a substantial increase in sugar maple stems coupled with a very slight increase in beech over a two year period. On average, beech trees greatly exceeded sugar maples in size and age. But sugar maples were denser and more frequent throughout the stand. Similar conditions have been reported for other Indiana beech-maple forests (Potzger 1935; Potzger & Friesner 1943; Beals & Cope 1964; Arnett 1968; Jackson & Allen 1968; Rogers 1980). Remarkable reproduction by sugar maple and its mounting dominance in understories and midstories are, by far, the most consistent observations made by the aforementioned studies. But while many examiners have encountered these circumstances, few have boldly suggested that the trend is a prelude to the species' impending dominance.

The complex nature of vegetation dynamics has made conservative conclusions a fixture of beech-maple forest studies. Most of the reluctance to proclaim sugar maple a superior competitor to beech can be traced to the history of the two species as associates and the long-standing impression that the species are equally shade tolerant. The trepidation of researchers, particularly those that worked long ago, to make strong claims concerning the relationship between the two species is understandable. But a body of

# Beech-Maple Investigations



Projection: NAD 1983 UTM 16N  
Cartography by: Trent Holmes  
Date: 01/31/06



**Forest Stand Type**

- Beech-Maple
- Mixed Hardwoods

**Indiana**  
 Gibson - Hemmer Woods  
 \* Jackson (1968)  
 Howard - Shenk's Woods  
 \* Friesner & Ek (1944)  
 Jennings - Tribbets & Comiskey Woods  
 \* Jackson & Barnes (1974)  
 Kosciusko - Berkey Woods  
 \* Potzger & Friesner (1943)  
 Lawrence - Donaldson's Woods  
 \* Schmelz, Barton, & Lindsey (1974)  
 Monroe - Salt Creek  
 \* Potzger (1935)  
 Montgomery - Shades State Park  
 \* Rogers (1980)  
 Owen - Hoot Woods  
 \* Abrell & Jackson (1977, 1977)  
 \* Petty & Lindsey (1961)  
 \* Spetich, Parker, & Gustafson (1997)  
 \* Williamson (1975)  
 Orange - Cox Woods  
 \* Potzger, Friesner, & Keller (1942)  
 Parke - Turkey Run State Park & Allee Woods  
 \* Esten (1932) - TRS  
 \* Arnett (1968) - AW  
 Porter  
 \* Harman (1970)  
 Ripley - Jackson & Potzger Woods  
 \* Jackson & Allen (1968)  
 Shelby - Metzger Woods  
 \* Keller (1945)  
 Vigo - Dobbs Park  
 \* Helms & Jackson (1975)  
 \* Cowell, Hoalst-Pullen, & Jackson (Unpub.)  
 Wayne - Lewis Woods  
 \* Beals & Cope (1964)

**Illinois**  
 Hardin - Kaskaskia Woods  
 \* Zaczek & Groninger (2002)

**Michigan**  
 Berrien - Warren's Woods  
 \* Cain (1935)  
 \* Brewer (1980)  
 \* Brewer & Merritt (1978)  
 \* Poulson & Platt (1996)  
 Ingham - Toumey Woodlot  
 \* Schneider (1966)

**Ohio**  
 Cuyahoga - North Chagrin Reservation  
 \* Williams (1936)  
 Geauga - Western Hocking Plateau Subsection  
 \* Goebel, Hix, & Semko-Duncan (2005)  
 Geauga & Lake - Holden Arboretum  
 \* Forrester & Runkle (2000)

**Wisconsin**  
 Multiple Beech Forests in Multiple Counties  
 \* Ward (1956, 1958)

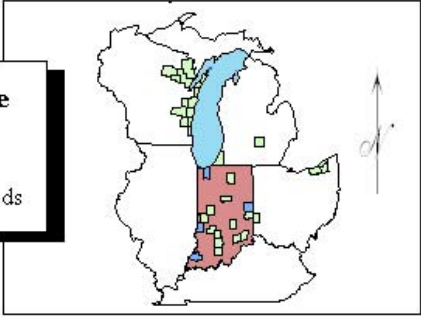


Figure 1.3 – Map of Beech-Maple Investigations Conducted in Indiana

consistent findings provides its own persuasive argument that, at some recent point, the nature of the relationship between beech and maple changed.

### Theories of Beech Loss

Ward (1956) put forward eight possible explanations for decreases in American beech populations. He identified the lowering of water tables following European settlement, selective logging practices, soil impoverishment, climate change, decreased seed production of beech, self-sterility of beech, hybrid vigor in sugar maple, and plant succession as potential answers. Ward himself favored plant succession as a reason for the decline, envisioning a future scenario in which beech maintained moderate representation in beech-maple forests by occasional seedling survival and root sprouts. Later, Ward (1958) postulated that beech may be limited by water availability as it approaches its western limit and soil development as it approaches its northern limit.

Several researchers have augmented or added to Ward's suggestions. Since the decline of beech reproduction roughly coincides with European settlement, faltering beech populations are sometimes attributed to anthropogenic disturbances. Thirty inches of annual precipitation is thought to be a minimum threshold for beech (Beals & Cope 1964). The factors responsible for the rapid increase of sugar maple on mesic sites throughout the beech-maple region are poorly understood, but one suspects they are connected with the factors responsible for beech's decline. The variables used to describe the species' behavior fall into six general categories: edaphic and physiographic controls, species migration, climate change, biological attributes of beech and sugar maple, gap-phase dynamics, and disturbance agents.

### *Edaphic & Physiographic Controls*

The term “edaphic” refers to characteristics of the soil, such as soil type and soil moisture. The term “physiographic”, meanwhile, refers to the form of the land, such as topography, slope, and aspect. In practice, the two factors are so closely intertwined as to render efforts to distinguish between their effects largely futile. Several investigations have noted the importance of the role of edaphic and physiographic factors in the expansion of mesophytic tree species, such as sugar maple (Strahler 1972; Cowell et al. unpublished).

The types of soil that underlie forests have received extensive attention. Ward (1956) commented that beech growth proceeded best on soils containing fairly heavy mor humus while sugar maple preferred mull humus (Ward 1956). Peterken and Jones (1987) confirmed this relationship for a European species of beech which excelled on shallow, slightly acidic soils containing mor humus. Soil types that underlie beech-maple forests in other parts of the region include Bethel, Blount, Brookston, Cincinnati, Clermont, Crosby, Eel, Hillsdale, Miami, Morley, Pewamo, Spinks, and Waverly. These soils are described variously as heavy clay loams, silt loams, silt clays, gray-brown podsolics, and plain podsolics. They are characterized by fine loose particles, high silt content, high air content, moderate water content, low wilting coefficients and pH values ranging from 5 to 7.

Sugar maple seems limited by shallow and compact soils that restrict its root system to the top 30.5 cm of the A-horizon. This soil condition prevents the species from guarding itself against the threat of severe windthrow (Williams 1936; Friesner & Ek 1943; Beals & Cope 1964; Schneider 1966; Arnett 1968; Jackson 1968; Jackson & Allen

1968; Lindsey & Schmelz 1969; Parker et al. 1985). European stands of pure beech sometimes possess impoverished soil as the result of calcium deficient leaf litter dropped to the canopy floor by the stand's dominants. Over time, this situation can lead to growing conditions that are unsuitable for beech. But in North America, beech rarely occurs by itself (Ward 1956; Beals & Cope 1964).

Moisture content, by most accounts, has the greatest impact on tree growth of all soil conditions (Potzger 1935; 1942; Cowell 1995). Beech prefers imperfectly drained soils, is capable of invading wet lowlands, and is believed to be sensitive to slight variations in soil moisture. Sugar maple, meanwhile, is considered relatively drought resistant and can invade dry sites (Potzger 1942; Seischab 1990). Moderately moist, mesic sites are considered the optimum locations for both species. The absence of sugar maple on certain sites can be related to poor drainage and aeration (Friesner & Ek 1943; Braun 1950; Helms & Jackson 1977). Beech absence, by contrast, can be linked to increased evapotranspiration rates and drainage improvement (Ward 1956; Lindsey & Schmelz 1969; Seischab 1990). Lumbering and farming practices can lower the water tables of forests, thus harming beech (Cain 1935). Improved drainage of the land surrounding old-growth forest remnants for agricultural purposes, therefore, may favor sugar maple over beech.

Scarcely discernible variations in drainage have proven to be critical to the success of mesic tree species. Appreciable species composition shifts often occur along moisture-topography gradients. American beech is tolerant of wet acidic soils. In hydric environments, beech seedlings are capable of establishing themselves on low mounds and by vigorous root sprouting. The opposite situation occurs on excessively drained slopes,

where beech drops off and sugar maple increases its representation. Sugar maple requires fertile, well-drained soils to thrive. But it can also grow on poor, dry, shallow soils. High tree species richness in some stands has been cited as evidence of heterogeneous soil moisture conditions. In old-growth stands, soil moisture levels in early spring are thought to be a more important determinant of tree species success than late summer and early fall conditions (Beals & Cope 1964; Jackson 1968; Jackson & Allen 1968; Jackson & Barnes 1974; Helms & Jackson 1977). Although important, edaphic controls are typically insufficient to account for all observed forest patterns (Cowell 1995).

Topography heavily influences other environmental factors and has a strong determinative effect on forest types. High species diversity is often observed in landscapes where land surfaces are highly variable. But even in areas of modest relief, topography plays a controlling role (Potzger 1935). American beech and sugar maple occur in areas of scarcely determinable, gently rolling, and strongly undulating relief (Friesner & Ek 1943; Jackson 1968; Jackson & Barnes 1974; Parker et al. 1985).

Slope aspect and position is an important variable in determining species composition (Cowell 1995). Potzger (1942) described the composition of forested areas in the beech-maple region according to slope aspect. North-facing slopes were occupied by mixed hardwoods with a tendency towards beech-maple. South-facing slopes were primarily oak-hickory. Potzger portrayed the transition between beech-maple on north-facing slopes and oak-hickory on south-facing slopes as “abrupt and decisive.” Beech-maple associations prevail on mesic, east- and north-facing middle slopes. Sugar maple sometimes exists on the xeric southern slopes, but beech is almost never present (Seischab 1985; Goebel et al. 2005). In Indiana, sugar maple has been found on all slope

aspects, but with widely varying values for basal area and importance. Western slopes in the state trend towards mixed mesophytic composition (Jackson & Allen 1968).

### *Species Migration*

One of the longest standing theories of species composition change for beech-maple forests relates to Braun's notion of species migration. The beech-maple region is within the area covered by the last, Wisconsinan, ice sheet. This youthful land surface contrasts with older areas of glacial drift, such as Kansan and Illinoian. When Wisconsin-age glaciers impinged on the area today known as the beech-maple region, all native vegetation and soil were destroyed (Braun 1950). As the glaciers gradually retreated, they left behind a barren surface, devoid of life. According to Braun, reestablishment of vegetation followed a linear process. Plants able to survive on the raw glacial drift came first, followed by plants that required organic soil material, trees that produced shade, and finally trees that could tolerate shade. The pace and scale of these waves of invasion were affected only by the geographical availability of suitable species. A coniferous forest thrived in the cool conditions left in the immediate wake of the glaciers. This was followed by the entrance of southern mesophytic species that outcompeted conifers in the warming climate. On a geological time scale, this area is still young and the vegetation still in a state of upheaval. If tree species have not yet reached their climatic limits, then forest composition is destined to change. This was the scenario envisioned by Braun when she predicted the eventual submission of the beech-maple region to the western- and mixed-mesophytic associations (Braun 1950).

The boundary between the beech-maple forest region and the western and mixed mesophytic forest regions corresponds with the termination of Wisconsin glaciation.



Therefore, observed differences in vegetation have been attributed to differences in the time available for plant development, rather than differences in climatic or biologic factors (Braun 1950). The observation that beech is very important in larger size classes, but commonly less successful in smaller size classes has been used as evidence of the species migration hypothesis' accuracy. But in Indiana, some researchers concluded that the dynamics of beech-maple and oak-hickory forest types indicate a shift towards beech-maple dominance and away from mixed-mesophytic conditions (Lindsey 1932; Schmelz et al. 1974). They cited the continued dominance of both beech and sugar maple in small size classes and the decline of oaks and hickories declining in all size classes below 24 inches. Because specific tree species are confined to certain parts of the state, some would assume that their position is fixed. Proponents of the species migration theory argue that this situation can, and likely will, change. Over time, some species expand their ranges while others struggle to latch onto ever-decreasing territories. This theory interprets vegetation dynamics as a process in which a species advances or retreats in relation to the hospitality of its constantly changing environment (Braun 1950).

### *Climate Change*

As early as the 1930s, beech's sensitivity to climate change was reported (Cain 1935). Several subsequent studies have dealt indirectly with the subject by exploring reasons for the existence of the so-called "beech border." The term beech-border refers to the western edge of American beech's geographical range. Despite the existence of favorable climatic conditions beyond this point, beech terminates rather abruptly at its western limit. Beech ranges well beyond Indiana to the north, east, and south, but not past a concave boundary that nearly coincides with the state's western border (Lindsey

1932). Beech is probably seldom in a static condition near the edge of its range. There is the possibility that the species is in a continuing state of attempted adjustment to climate fluctuations. If so, a prolonged period of exceptional weather conditions, such as increased temperatures or decreased precipitation, could bring about a decline in beech. Sugar maple, on the other hand, does not change behavior once the beech-border is crossed. With its tolerance of dry conditions, it seems well suited for enduring climate changes (Ward 1956). Harman (1970) analyzed two forest stands situated in an ecological tension zone to test hypotheses relating climatic processes to forest composition. Climatic modification caused by Lake Michigan was indirectly responsible for observed differences in tree composition between the stands. The results of his study affirmed the importance meso-scale climate differences. Hoot Woods is situated very near the southwestern limit of American beech's range.

Friesner (1941) identified temperatures, evaporation rates, and available water supply as the most important controlling factors for a tree's growth. Temperature is thought to control the time of bud activity and, in turn, the initiation of diameter increase. Evaporation rates and precipitation, meanwhile, control the duration of the growing season. Each of these factors is highly variable, changing from season to season and day to day. The combined effect produces radial growth when paired with the unique responses of specific tree species. Friesner contended that no single factor controlled the diameter increase of trees. Rather, he argued that changes to any one factor caused an environmental change and it was this change to which, trees must respond. Friesner showed that by far the greatest proportion of annual growth for beech occurred during the month of June. Beech growth showed a close relationship with rainfall and mild

temperatures for the month of June. In Indiana, late spring and early summer are considered the most favorable periods for diameter tree growth.

Tardif et al. (2001) measured radial growth in sugar maple, beech, and eastern hemlock in an old-growth beech-maple stand in southeastern Quebec using dendroclimatic techniques. The stand was situated near the northern limit of the range of all three tree species. Generally speaking, the species responded well to greater precipitation and poorly to increased temperatures. Each species was positively correlated with precipitation during the early summer months of the year that the annual ring was formed and negatively correlated with temperature during the same months, suggesting that water balance in early summer limits the growth of these species. Growth was also negatively correlated with temperature during the late summer months of the year prior to ring formation. Sugar maple and beech are sensitive to climate and can live more than 300 years, making them well suited for dendroclimatic analysis. All tree species shared a common negative correlation with the July-August temperature of the year prior to ring formation and with the June temperature in the years the growth ring was formed. Sugar maple grew best when a cool July and wet August occurred in the year prior to ring formation or June temperatures were low and precipitation was high for the same year as ring formation. Reduced water stress in the late summer allows sugar maple to accumulate a reserve of carbohydrates. Sugar maple grew worst when too much precipitation occurred in May of the prior year, leading to excessive soil water content. In the latter half of the 20<sup>th</sup> century, sugar maple showed an increasingly negative correlation with mild late-winter conditions.

There were few significant correlations between beech and climate. Low temperatures and good precipitation in the month of June were most important to its success. Tardif et al. (2001) postulated that high temperatures in this summer month may be responsible for increased transpiration and reduced water supply. American beech grows determinately. It develops quickly during the early part of the growing season, but then reaches a point beyond which it will expand no further. Species such as sugar maple, in contrast, grow unabated throughout the entire growing season. Beech consumes twice the amount of water annually that drought resistant species, such as sugar maple, do. Presumably, these characteristics increase the harmfulness of the effects of low precipitation. Beech's most unique feature was a positive correlation with April temperatures. These results might suggest that extreme temperatures or drought over a two-, or more, year period would dramatically impact the health of beech and, by extension, stand composition. However, these growth-climate correlations found by Tardif et al. (2001) were unstable, calling into question their usefulness.

#### *Biological Attributes of Beech & Sugar Maple*

Theories of beech decline that revolve around perceived biological differences between American beech and sugar maple are controversial. They question long-standing beliefs, most notably that beech and sugar maple are equally shade-tolerant codominants (Pell & Mack 1977). Ward (1956) put forth the first suggestions of this sort. He noted the decline of tree species besides beech in stands with many sugar maples and wondered whether natural succession might be the culprit. Beech comes nowhere close to equaling sugar maple in terms of reproduction. In a contest between two otherwise evenly matched opponents, the one with superior numbers is likely to

prevail. Ward questioned whether the reproductive strategy of beech that relies on root sprouts, in conjunction with insufficient pollination, might be to blame for creating genetically alike populations and causing sterility. He also postulated that genetic mutations by sugar maple could enable it to gradually replace beech. Vankat (1975) vehemently refuted the contentions made by Ward. Nevertheless, they represent important insights into the phenomena.

The life history strategies of American beech and sugar maple share several similarities. Both species are very shade tolerant, late successional species common to mesic forests. They can remain in the understories of forests for many years using a series of gaps to reach the canopy. The growth rates of both species significantly increase in canopy gaps (Loehle 1988; Forrester & Runkle 2000; Cowell unpublished). But there are significant differences as well. Sugar maple has a more rapid vertical growth rate, particularly at older ages, which gives it a competitive advantage over beech in larger gaps. Young beeches are well adapted to the understory since their leaves are arranged in a monolayer, which is theoretically a more efficient means for photosynthesis under low light intensities than multilayered leaf arrangements. Some research has attempted to rank beech ahead of sugar maple in terms of shade-tolerance. Forrester and Runkle (2000) argued that beech's horizontal growth enables it to survive up to four times longer than sugar maple. But tested distinctions between American beech and sugar maple based on shade-tolerance are a rarity. Most research assumes that the species are equally tolerant (Loehle 1988). Other biological factors, then, likely account for the recent competitive success of sugar maple.

Sugar maple is recognized as an aggressive reproducer in almost every environment in which it occurs. In Indiana, several studies have reported the dominance of sugar maple reproduction over its main competitor, beech (Potzger & Friesner 1940; Beals & Cope 1964; Jackson & Allen 1968). Although seed crops of sugar maple fluctuate greatly from year to year, their raw numbers are usually staggering. Sugar maple produces enough seeds during most years so that its wind-dispersed seeds saturate the landscape. Large numbers of understory trees act as insurance and allow the species to exploit canopy gaps when they occur (Abrell & Jackson 1977b). Beech has a different life history strategy. Overall rates of germination and seedling survival are low. It does not bear large seed crops annually and much of this is destroyed by animals that prefer it as forage. Root sprouting from large trees is an important source of sapling and understory beech. It is this form of regeneration which accounts for most of the species' reproductive capacity. By relying on the nutrients provided by their parent trees, beech root sprouts can grow quickly and tolerate large amounts of shade. Saplings that germinate and grow from seeds are at a disadvantage in closed canopies because they lack this extra energy source. Beech's long life span and tolerance of shade seem to favor forest stand compositions in which it coexists alongside its more prolific sugar maple counterpart (Abrell & Jackson 1977b). However, this prediction is increasingly challenged by a growing body of evidence that suggests that beech is a waning species in old-growth forest stands.

A high mortality rate among young sugar maple saplings is a commonly observed occurrence. Some research has cited this tendency as reason to believe beech can maintain its codominant status, in spite of its reproductive disadvantage (Williams 1936;

Hett 1971; Vankat 1975; Forrester & Runkle 2000). Most studies that note quickly multiplying sugar maple populations project that the increase will come at the expense of shade-intolerant species, rather than beech. Only a handful of researchers suggest that the reproductive imbalance favors the eventual dominance of sugar maple (Cain 1934; Ward 1956).

Overall mortality rates between the species are roughly equal. Forrester and Runkle (2000) found that beech and sugar maple died at a rate of 2.4 percent a year. But other research suggests that large beech trees are more susceptible to death than large maples (Brewer & Merritt 1978). This finding has severe implications when viewed in the context of the reproductive strategy of beech. Because beech relies on root sprouts for reproduction and root sprouts require large parent trees for nourishment, the species can ill-afford heavy losses of large trees if its population is to be maintained (Esten 1932).

In beech-maple forests, the codominants overwhelmingly control the population from which canopy recruitment occurs (Brewer & Merritt 1978). Evidence of reciprocal replacement patterns between beech and sugar maple has been shown in some studies (Runkle 1981; Forrester & Runkle 2000), but not in others (Poulson & Platt 1996; Kupfer et al. 1997). Reciprocal replacement describes a pattern of reproduction in which the death of one canopy tree tends to release a sapling of another species. Self-replacement describes a pattern of reproduction in which the death of one canopy tree tends to release a sapling of the same species (Kupfer et al. 1997).

In light of this discussion of biological attributes, it is wise to return to the issue of shade. Sugar maple canopies project a deep shade, beneath which few other plants can

grow (Brewer 1980; Zaczek et al. 2002). As the number of sugar maples increase, summer shade in mid- and understories is intensified. Low light conditions continued for several years can cause the slow extinction of improperly adapted species. There is a limit to the amount of shade that even sugar maple itself can endure. With the exception of red maple and American elm, sugar maple comes into leaf much earlier than most shade-intolerant tree species. Basswood, white ash, bitternut hickory, shagbark hickory, and northern red oak begin budding out as much as a month after sugar maple is in full leaf. As these intolerant species gradually die out beneath dense sugar maple canopies, the patches of early-spring light they once afforded are lost. This further reduces light conditions in the subcanopy.

If light is the major factor in determining which species remain and which disappear in old-growth forests, then successful species should tend to possess adaptations for seasonally low light flux, whereas the species which have decreased should tend to lack such adaptations. But based on the decline of many beech populations, it appears that physiological shade tolerance alone is not a successful survival strategy. A more successful tactic might be the avoidance of shade, such as that attempted by the fast-growing tulip poplar. Sugar maple may possess a competitive advantage stemming from a combination of physical attributes. Extreme shade tolerance, tremendous reproductive capability, and a leafing-out strategy that promotes dense shade provide sugar maple with a formidable arsenal of physiological assets. Beech abets sugar maple's strengths by its heavy reliance on root sprouts for reproduction and high mortality among large stems, which paradoxically limit the number of viable stems the species can produce. The high frequency, large area, treefall gaps created by the death of



big beech trees further promote sugar maple as a replacing species. Though by themselves minute, the additive effect of these biological traits is substantial. Over time these subtle traits are expressed forcefully in the changing composition of forest canopies.

### *Gap-phase Dynamics*

A process closely related to the biological traits of tree species is gap-phase dynamics. When a canopy tree falls over or its top is snapped off by wind, a hole, or “gap” commensurate with the tree’s crown size is created on the canopy floor where light, space, and other resources are suddenly available. Fine-scale forest development occurs within these gaps. One or several trees gradually close the canopy opening and come to dominate the forest floor beneath them. A substantial body of literature has developed around the role of small gaps in the dynamics of forested ecosystems. The death of one or a few canopy individuals is thought by some to represent a vital internal disturbance in many remnant forest communities. Gap-phase theories predict that the composition of gaps is linked to the size of openings and the biological attributes of tree species. Large-scale disturbances are relatively uncommon for the beech-maple region. Canopy gaps, meanwhile, affect approximately 1 percent of forest stand area per year. This has led some researchers to argue that treefall gaps are important disturbance agents that determine stand structure and composition (Forrester & Runkle 2000; Turner et al. 2001; Ziegler 2004).

Regeneration in canopy openings is thought to be determined by probabilities of seedling arrival and survival, which are a function the biological attributes of specific tree species. Therefore, most research concerning gap-phase dynamics attempts to relate the

microclimatic conditions encountered in gaps to the perceived preferences of specific tree species. Some of the earliest research on gap-phase dynamics suggested that canopy openings were an important mechanism for the maintenance of shade-intolerant species and species diversity in mature, closed canopy forests (Williamson 1975). New evidence though, has called this position into doubt. In forests with subcanopies or canopies composed of sugar maple and beech, windthrow appears not to maintain species diversity.

Windthrow is a frequent but irregular occurrence. The incidence of canopy gaps fluctuates from year to year. Occasional severe storms that blow down many trees are responsible for the formation of the majority of forest canopy openings. Some studies estimate that windthrow damages 0.2 trees per ha per year in old-growth, beech-maple forests (Brewer & Merritt 1978). On average, large trees, between 50 and 75 cm dbh, are most affected by wind damage. Beech trees larger than 76 cm dbh are particularly susceptible. High densities ensure that the vast majority of potential canopy replacement trees measuring 20-70 feet tall are sugar maple (Brewer & Merritt 1978). The success of sugar maple, and to a lesser extent beech, occurs at the expense of less-tolerant species. Few shade intolerants become established in the understory, canopy openings included (Brewer 1980). This suggests that gaps resulting from the death of one or two trees are insufficient to maintain minor tree species underneath dense canopies. Shade tolerant species, such as sugar maple, seem to dominate mid- and understories regardless of canopy openings (Parker et al. 1985; Cowell et al. unpublished).

Maintenance of canopy diversity in mature forests is ensured by more severe perturbations than gap-phase dynamics can supply. While American beech and sugar

maple survive at comparable rates in and out of gaps, shade-intolerant species require regular and intense disturbances in order to thrive (Cowell et al. unpublished). But from time to time, apparently even shade-tolerant species, such as beech, require catastrophic disturbance events (Brewer & Merritt 1978; Brewer 1980; Poulson & Platt 1996; Stambaugh et al. 2002).

### *Disturbance Agents*

Many studies have shown the importance of disturbance in determining the structure and composition of natural woodlands. Disturbances influence the scale and timing of regeneration opportunities for all tree species. If tolerant species are able to establish dominance in the understory they often preclude regeneration of shade-intolerant taxa, at least until larger gaps are formed in the canopy by disturbance. The role of later successional species in seral processes is influenced by the extent and return interval of disturbance events. Coarse-grained landscapes structured by widespread catastrophic disturbance, like disease, pest infestation, or fire, contrast sharply with fine-grained landscapes structured by localized patterns of canopy disruption and regeneration. Although the importance of disturbance is widely recognized, an understanding of the specific characteristics of disturbances and their interaction with particular environments is sometimes lacking (Parker 1993; Cowell 1995).

Depending on their frequency and intensity, disturbances can accelerate, set back, or absolutely alter successional pathways. Recovery following disturbance is sensitive to the spatial pattern created by the disturbance and the residual species left behind. Residual components are simply the remnants of vegetation from pre-disturbance landscapes. Species with seeds that can survive specific disturbance events, or that can

survive themselves, are well positioned to colonize their new surroundings. When residuals are prevalent following a disturbance, succession is relatively predictable. When the majority of residuals are destroyed, the outcome of succession is unknown. White pine, for example, releases its seeds following a fire, where they can thrive and achieve maximum growth on the newly cleared ground. In areas where fire has been suppressed for many years, few fire-tolerant species remain. In these cases, the reintroduction of fire is unlikely to bring about a restoration of previous conditions because parent trees do not exist in enough numbers to reseed burned areas (Parker 1989; Cronon 1991; Turner et al. 2001; Stambaugh et al. 2002; Cowell & Jackson 2002; Cowell et al. 2006).

In extensively modified areas such as agricultural landscapes, forest fragmentation represents a large scale, external disturbance that may affect dynamics in remnant forests. Because forest edges are characterized by higher levels of light, lower relative humidity, higher wind speeds, higher temperatures, and increased evapotranspiration, reproduction by shade-intolerant species that are excluded from forest interiors is possible. In addition, seed dispersal patterns may be affected as fragmentation increases and a greater proportion of the forest interior is brought into contact with edge species. In agricultural landscapes, the average size of forest remnants is small, ranging from 5 to 15 ha. External disturbances, such as clearing adjacent land, can affect species composition in forest remnants by increasing the exposure of their minuscule interior areas to edge processes (Kupfer et al. 1997). The study area in Hoot Woods is 6.6 ha. But the entire forest is approximately 26 ha, which is large enough to largely avoid any adverse edge effects.

Beals and Cope (1964) concluded that periodic disturbance events would hasten, not slow, declines in American beech populations because its main competitor, sugar maple, gains an overwhelming reproductive advantage via the combination of open space and an abundance of seedlings. They speculated that if beech could grow faster than maples under dense shade that it might be possible for beech to maintain itself under less disturbed conditions. However, evidence from beech-maple stands show fairly definitively that beech is incapable of this (Beals & Cope 1964). Fire suppression is often identified as an important factor in affecting change in species composition. But historical records of the beech-maple forests of Indiana show little indication of the presence or importance of fire (Seischab 1990). And, beech, because of its thin bark, is perhaps more susceptible to fire than even sugar maple (Parker 1989). Disturbance agents presumed to be fatal for beech include pathogens, insects, herbivore predation, drought, and tornadoes.

Although both beech and sugar maple live 250 to 300 years, beech appears to suffer a swifter decline once old-age is reached. The life span of beech at some locations has been linked to its susceptibility to fungus attack. Few species offer an easier entrance into their inner tissues. Beech-bark disease has affected eastern forests since the early 1900s. An insect called the beech scale feeds on beech bark tissue, which is then invaded and killed by fungi of the genus *Nectria*. When finally the sapwood is affected, stems are left with no defense against windthrow. Two *Nectria* species are associated with the disease, *N. coccinea* var. *faginta* which is believed to have been introduced by humans and the native *N. galligena*. Presently, the scale insect has spread westward to northeast Ohio and southward to northwest Virginia. In the northeastern U.S., *Nectria* invasions

followed scale establishment within 5-10 years. Apparently though, the pathogen is yet to reach beech-maple forests located in Indiana (Forrester & Runkle 2000). Beech's susceptibility to invasion by the scale insect and the deadly fungus that follows, would likely hasten its descent in stands where it competes with sugar maple. This presents a particularly troublesome problem because of the species' need for canopy trees and root sprouts to assure its replacement (Williams 1936; Loehle 1988).

Another insect, specifically its larva, is considered to be one of the most serious threats to North American forests. The gypsy moth is an exotic species accidentally introduced to the continent by humans. Shields et al. (2003) investigated the feeding preferences of the gypsy moth for seven tree species. Their results indicated that the insect strongly preferred sweet gum and red oak. Sugar maple and basswood offered the second most popular forage. Beech and black walnut were not favored and tulip poplar was strongly rejected. This pest has just begun to invade the central hardwood region and has yet to reach Indiana or the Hoot Woods. Another animal, the white-tailed deer, has rapidly expanded its population in the Midwestern United States. This native herbivore is a serious pest in some areas and is likely to alter understory plant populations of old-growth forests (Parker 1989). The presence of large deer populations is sometimes cited as a potential source of beech decline because the herbivore contributes to beech regeneration failure by consuming its seeds. Deer prefer this forage to anything offered by sugar maple. Deer also prefer edge habitats and avoid closed areas, especially those that lack a major source of water. The initiator of the Hoot Woods study, Marion Jackson, remarked that in all the years he visited the woods, he observed hardly any

wildlife. In addition, no tree damage consistent with deer predation has ever been observed.

Drought is another disturbance event which may impinge on forest communities from time to time. Rainfall and temperatures are quite variable throughout the beech-maple region and summer droughts happen at least once every 25 to 30 years (Parker et al. 1985). Peterken and Jones (1987) investigated composition and disturbance in an English, beech-maple forest at Lady Park Wood over the course of forty years. A severe drought in 1976 killed many mature beeches and severely weakened those that survived. The canopy continued to disintegrate for 6 to 10 years following the disturbance. Prior to the drought, beech thrived. But after 1976, growth rates slowed dramatically and mortalities ravaged all size classes. Most of the stand's large beech trees were dead or dying seven years after the drought. The authors postulated that the removal of large canopy trees resulting from the disturbance would have lasting impacts on stand composition.

The tornado is a disturbance event which is quite common to the landscape of Indiana. This violent act of nature often creates unbelievable destruction. On average, Indiana is affected by 21 tornadoes per year. Typically, about five of these are severe enough to cause extreme damage and produce human fatalities. The northern half of the state, particularly the northwestern portion, is the most effected by tornadoes. Northern Indiana consists primarily of flat farm-land and few trees which facilitates the formation and intensification of these disturbances. The southern half of the state, in contrast, is hilly and occupied by numerous forested areas. The rougher terrain creates a boundary layer of air flow near the ground which disrupts tornado formation and dissipates weaker

storms. As a result, tornado activity is substantially less in the southern portion of the state (Keyser et al. 1977). Despite its relatively protected southwestern location, a destructive tornado struck Hoot Woods in August of 1980 (Marion T. Jackson, Emeritus Professor – Indiana State University, October 15 2006, letter).

The impact of tornadoes on stand structure and composition has been observed for a handful of Indiana forests. Bailey and MacMillan (1976) conducted a tree census in a wooded valley northeast of Hanover College in Jefferson County, Indiana which was struck by a tornado in April, 1974. Pre-tornado data indicated this was a near mature, second-growth, sugar maple-buckeye community. Post-tornado analysis showed a loss of about one-third of the trees and a change to a sugar maple-white ash-swamp white oak community. The partial destruction of the forest initiated secondary succession in the valley. It is evident that pre-tornado conditions included greater numbers of stems/ha along with lower mean areas and mean distances per tree. The results indicated that sugar maple became strongly established in the wake of the tornado. While buckeye, a moderately fast growing and shade tolerant tree that prefers moist well-drained soil, was reduced greatly.

Potzger (1942) examined stand dynamics in Cox Woods, an old-growth beech-maple remnant in south-central Indiana. A portion of the stand sampled was leveled by a tornado in 1887 and since then left to natural reestablishment. Potzger reported that the crown cover was controlled by sugar maple and American beech. In the areas disturbed by the tornado, an oak-hickory-sugar maple forest prevailed. Beech suffered the greatest reduction in importance in the disturbed areas. Jackson (1968) found that intolerant species, such as sassafras and black cherry, and hackberry represented a large percentage



of medium-sized stems in an area of Hemmer Woods disturbed by a tornado. In Warren's Woods, Brewer and Merritt (1978) observed the composition of a 0.5 ha section of canopy that was removed by a tornado in 1975. They reported that sugar maple and beech were the probable replacement species in the area. The authors noted the potential of tornadoes to contribute to species richness by providing an interlude prior to the flush of sugar maple growth that is favorable to less shade-tolerant species.

Brewer (1980) discovered that recurrent disturbance preserved diversity among herbaceous plants in Warren's Woods. If periodic disturbance is an important factor in maintaining species diversity, then the abundance of specific species should change with time following a catastrophic event. When tornadoes are severe enough to remove large portions of the canopy, they can help retain shade-intolerant species. But tornadoes also seem to accelerate the takeover of dense species, such as sugar maple. For Hoot Woods, it is clear that the 1980 tornado significantly impacted stand composition and structure. The removal of crown cover may have raised evapotranspiration rates, increased soil aeration, and reduced soil moisture. These microclimatic variations do not favor beech.

### Problem Statement

This study furthers multiple decades of effort by several generations of investigators. In June of 2005, a tree-by-tree comparison was made for a 6.6 ha (16.3-acre) portion of Hoot Woods, an old growth beech-maple stand. Hoot Woods was first censused in 1965 (Abrell & Jackson 1977a) and has been inventoried every ten years hence. This study investigates changes in stand composition and structure within Hoot Woods over the course of forty years. It attempts to demonstrate which factors affect

change, the scale at which they operate, and how these patterns may apply to other similar landscapes. The examination of Hoot Woods extends knowledge about permanent plot studies, vegetation dynamics, and the status of Midwestern forests, as well as the theories of succession, coexistence, and disturbance regimes.

Temporal patterns of vegetation change, or pathways, describe changes in stand composition and structure (Bakker et al. 1996). For this study, successional pathways were examined using the following questions. Have stand density and basal area changed significantly? Have individual tree species changed in importance within the stand? Have changes occurred at a steady rate and in one direction? Or have changes oscillated in direction and fluctuated in intensity from decade to decade?

The agents, circumstances, and actions responsible for successional patterns, or causes, describe why pathways exist (Bakker et al. 1996). Successional causes were investigated using the following questions. How did ingrowth and mortality contribute to the observed vegetation change? What do the size-class distributions of individual tree species say about the dynamics of those species in relation to the stand's development? What are the spatial patterns of tree survivors, ingrowths, and mortalities throughout the study? Have gap-phase dynamics played an important role in species behavior and success?

Pathways and causes interact to bring about successional change (Bakker et al. 1996). These interactions were inferred through answers to the following questions. How do changes in the Hoot Woods' species composition and distribution compare to trends within similar stands? What factors, besides competition, could have affected the observed changes? Which theory provides the most logical explanation of beech decline?

## CHAPTER TWO

### STUDY AREA

Hoot Woods is situated in Owen County, Indiana, approximately three miles northwest of the town of Freedom at 39.2° N latitude, 89.9° W longitude (Figure 2.1). Ecologically, the stand rests in a tension zone between the beech-maple forest to the east, northeast, and southeast and an arm of the oak-hickory forest to the west (Petty & Lindsey 1961).

#### Indiana Landscape Conditions

When Europeans first set foot on the North American continent, the eastern third of what is today the United States was covered by the Eastern deciduous forest. Approximately 99.5% of this pre-settlement timber was logged and cleared (Diggins & Kershner 2005). Due to its strength, plasticity, ease of use, and widespread availability wood was an extremely important component of settler life: it was used to heat homes, cook meals, run steam engines, make tools, build farm machinery, and construct barns, corncribs, homes, churches, and schools. Ironically, wood was the vital resource that allowed farmers to partition the landscape's fertile soils for agricultural use (Cronon 1991).

The beech-maple region occurs on some of the most productive soils in North America. Because this terrain is also relatively flat, beech-maple forests were rapidly cleared and converted to croplands. As time progressed, farming operations became

# Hoot Woods

*Landscape Features*

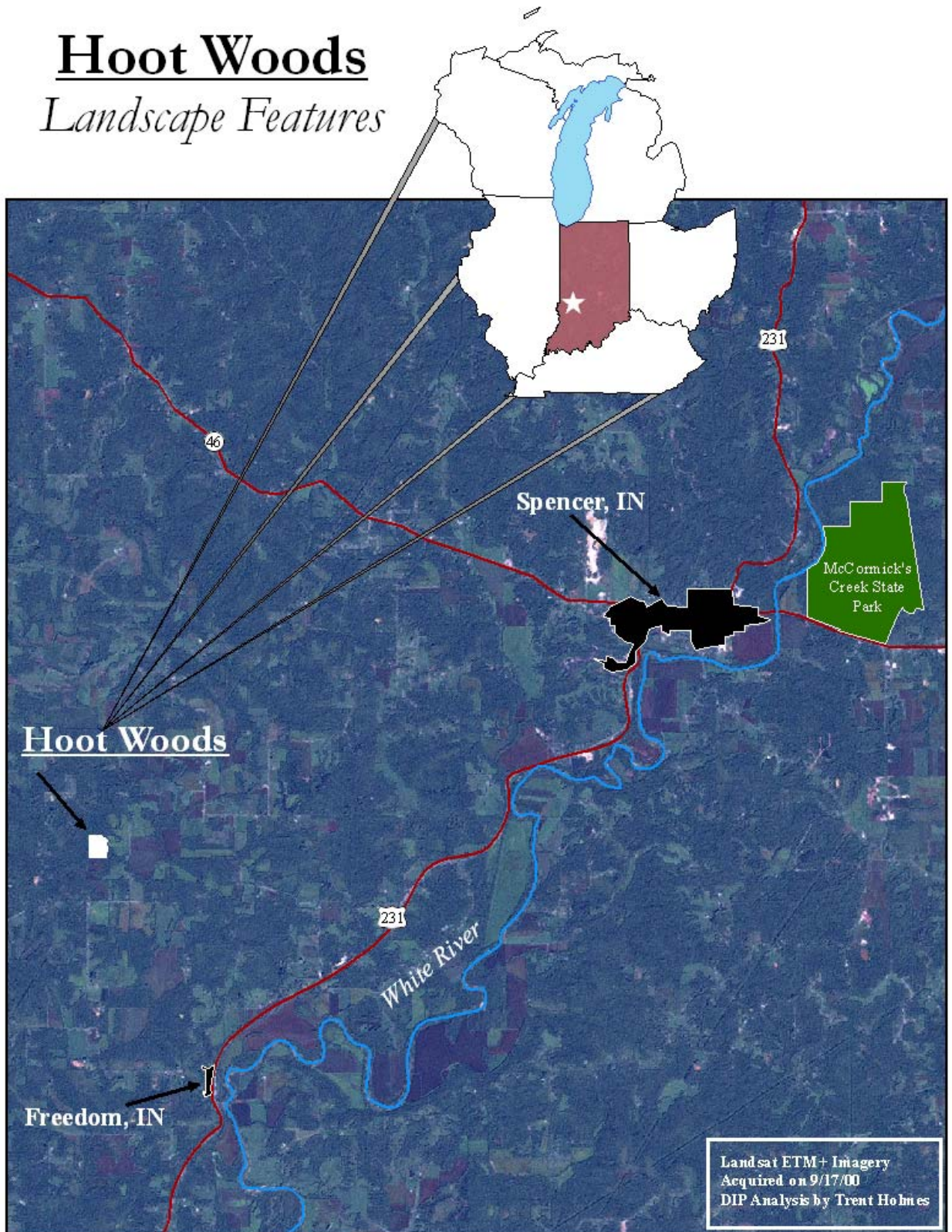


Figure 2.1 – Landsat ETM+ Image of Hoot Woods & Surrounding Landscape

larger and more centrally operated in an effort to maximize returns on investments and boost grain production. Intensive cash-grain production replaced smaller operations (Medley et al. 2003), and most old-growth woodlots that had been protected on family farms were subsequently destroyed.

In Indiana, early settlers nearly cleared the state of its “forest primeval.” Indiana’s landscape was approximately 87% forested in 1816 (Spetich et al. 1997). Throughout the nineteenth century, its timber reserves were such that white oaks harvested from the state were renowned for their quality world-wide. But by 1905, the state’s supply of oaks and hickories had been all but exhausted (Potzger & Friesner 1942). Five years later, most of the lowland forests were gone. At the turn of the twentieth century, the once contiguous broadleaf forest of Indiana had been reduced to a patchwork of secondary forests and old-growth remnants scattered throughout an expansive agricultural landscape (Potzger 1935; Medley et al. 2003). Forest acreage reached its low point in the 1930s, but rebounded slightly to an estimated 19.3% (1.78 million ha) of Indiana’s total land area by 1986 (Spetich et al. 1997).

Indiana’s modern-day landscape is an agricultural matrix. The state ranks 48<sup>th</sup> in the U.S. in the proportion of original plant communities that remain intact (Santelmann 2004). Steep slopes with shallow soils tended to be considered unsuitable sites for successful farming (Potzger 1935). As a result, the majority of timbered areas that remained untouched were situated in these less favorable places (Diggins & Kershner 2005).

Indiana’s tracts of old-growth forests are so few in number that a concerted effort has been made to inventory them all so that they can be studied and preserved. In the

mid-1960s, this interest was heightened by the initiation of the Indiana Natural Areas Survey, an effort that sought to identify areas that had escaped major anthropogenic disturbance (Jackson 1968). In 1969, Lindsey and Schmelz identified 58 relatively undisturbed old-growth stands in Indiana. They categorized the forests as either oak-hickory, beech-maple, lowland-depressional, or mixed woods. More recently, Spetich et al. (1997) summarized the condition of Indiana's old-growth forests. They reduced the number of old-growth sites to 33. These remnants comprise approximately 607 ha and most occur within an agricultural matrix. Nineteen old-growth forests, including Hoot Woods, are held in public trust in Indiana. These stands occupy a total of just 362 ha. Eight sites greater than or equal to 4 ha are privately owned, totaling 215 ha.

### Physical Setting

A general knowledge of Indiana's physical landscape is beneficial to understanding the distribution of tree species across the state (Figure 2.2). Topographically, the state is a plain sloping slightly southwest with high elevations in the central portion and low elevations in the north and extreme southwest. Streams meander and the land slopes in every direction from the elevated region. Approximately  $\frac{5}{6}$  of Indiana was once covered by Illinoian-age glaciers, while Wisconsin glaciation affected only the northern half of the state (Lindsey 1932). The Illinoian sheet extended southward in two immense sections, producing a triangle-shaped driftless area in the center of the state with its apex in the northern part of Monroe County and its sides running through Clark and Posey Counties. Much of what is the Boonville Hills, Mitchell Plateau, Crawford Upland and Norman Upland fall below this southern limit of



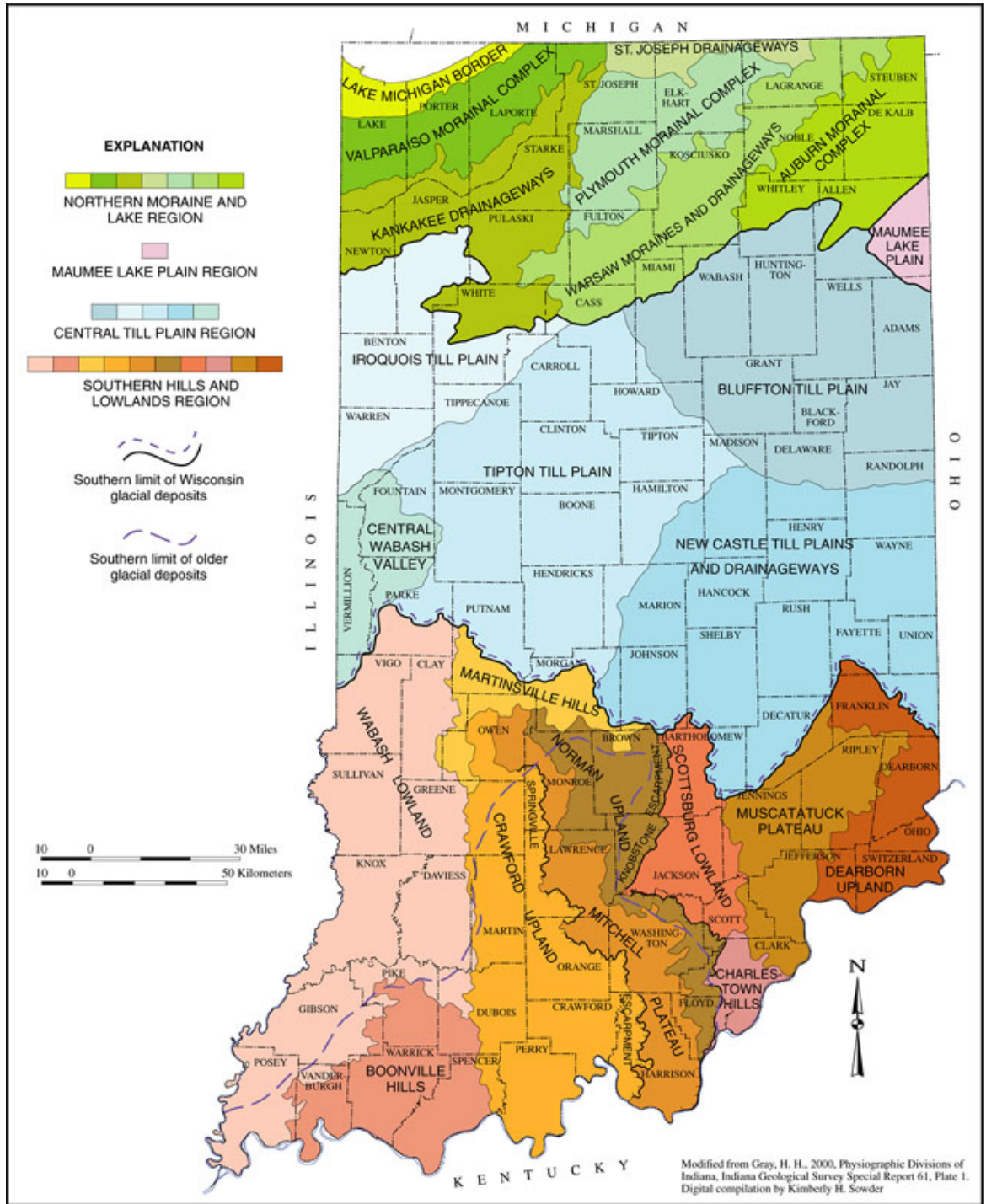


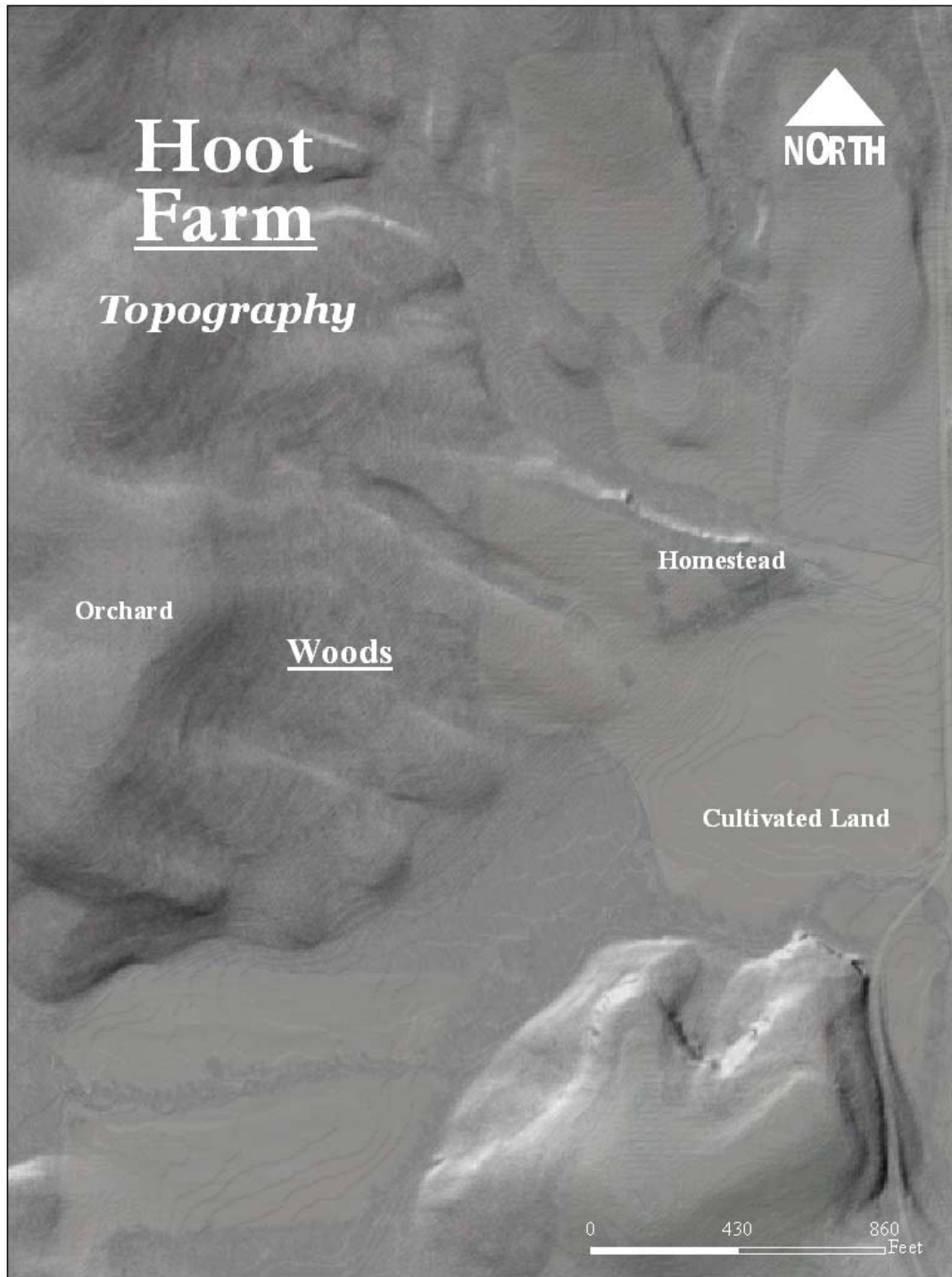
Figure 2.2 – Map of Physiographic Divisions of Indiana (Indiana Geological Survey 2000)

older glacial deposits. The northern portion of the state is relatively flat and characterized by drift deposits, morainic basins and glacial lakes. Landuse is primarily agricultural with small forest patches interspersed. Lake Michigan once extended into the northwestern counties of Indiana; as a result, this region of the state is covered in drift sand. The western counties contain the eastern limit of the midwestern prairies and the western limit of American beech's geographical range. Most of the counties situated along the Ohio River and in the southern interior are topographically diverse and contain larger forested areas. Hoot Woods is on the eastern edge of the Crawford Upland and was affected by Illinoian glaciation and limited subsequent erosion (Petty & Lindsey 1961).

### Site Description

Hoot Woods is a high-canopied beech-maple stand that occupies 25.9 ha (64 acres) of an east-facing slope (Figure 2.3). A small intermittent stream dissects the area. Hoot Woods' soil is composed primarily of a melanized podsol derived from Illinoian glacial deposits. This soil type is thick and loose, containing significant levels of potassium and phosphorus. A texture analysis of the soil was conducted in 1961. It revealed that the tract's composition averaged 68% silt, 28% clay, and 4% gravel-sand, with pH values ranging from 5.0 to 5.5 (Abrell & Jackson 1977a). With the exception of a handful of trees that were harvested from the northern end of the stand, little direct anthropogenic disturbance has occurred in Hoot Woods. The most notable natural disturbance occurred in August 1980, when a tornado blew down a significant portion of the stand. In the absence of human impacts, processes of competitive development,





**Figure 2.3 – Hillshade Image Produced from DEMs, ISDS (2005)**

windthrow, gap replacement, decay, and natural disturbance have been allowed to operate naturally (Petty & Lindsey 1961; Abrell & Jackson 1977a).

### Site History

Like other old-growth forests of Indiana, Hoot Woods is a small, isolated patch surrounded by non-forested land (Figure 2.1). Also like most others, Hoot Woods was originally preserved as part of a family farm. The property was purchased as an original homestead in the mid-1860s by a German immigrant named Michael Hout (Family Search 2006). The surname “Hout” was altered to “Hoot” by immigration officials and the anglicized version stuck. Following Michael Hoot’s death in the late 19<sup>th</sup> century, ownership of the farm passed to two of his sons. These brothers owned Hoot Farm as undivided shares. While one son never married, the other, named George, wed and produced eight children. These siblings are the generation of Hoots that Marion T. Jackson met and knew.

George’s brother died first and left his  $\frac{1}{2}$  share of the farm to his two favorite nieces, Alice and Dorothy Hoot. When George Hoot passed away in 1945, his  $\frac{1}{2}$  share of the farm was split eight ways between his children. When combined with the  $\frac{1}{4}$  ownerships left to them by their uncle, Alice and Dorothy each possessed a  $\frac{5}{16}$  ownership in the farm. This unequal division of the property created tension among the Hoot heirs (Marion T. Jackson, Emeritus Professor – Indiana State University, October 23 2006, e-mail).

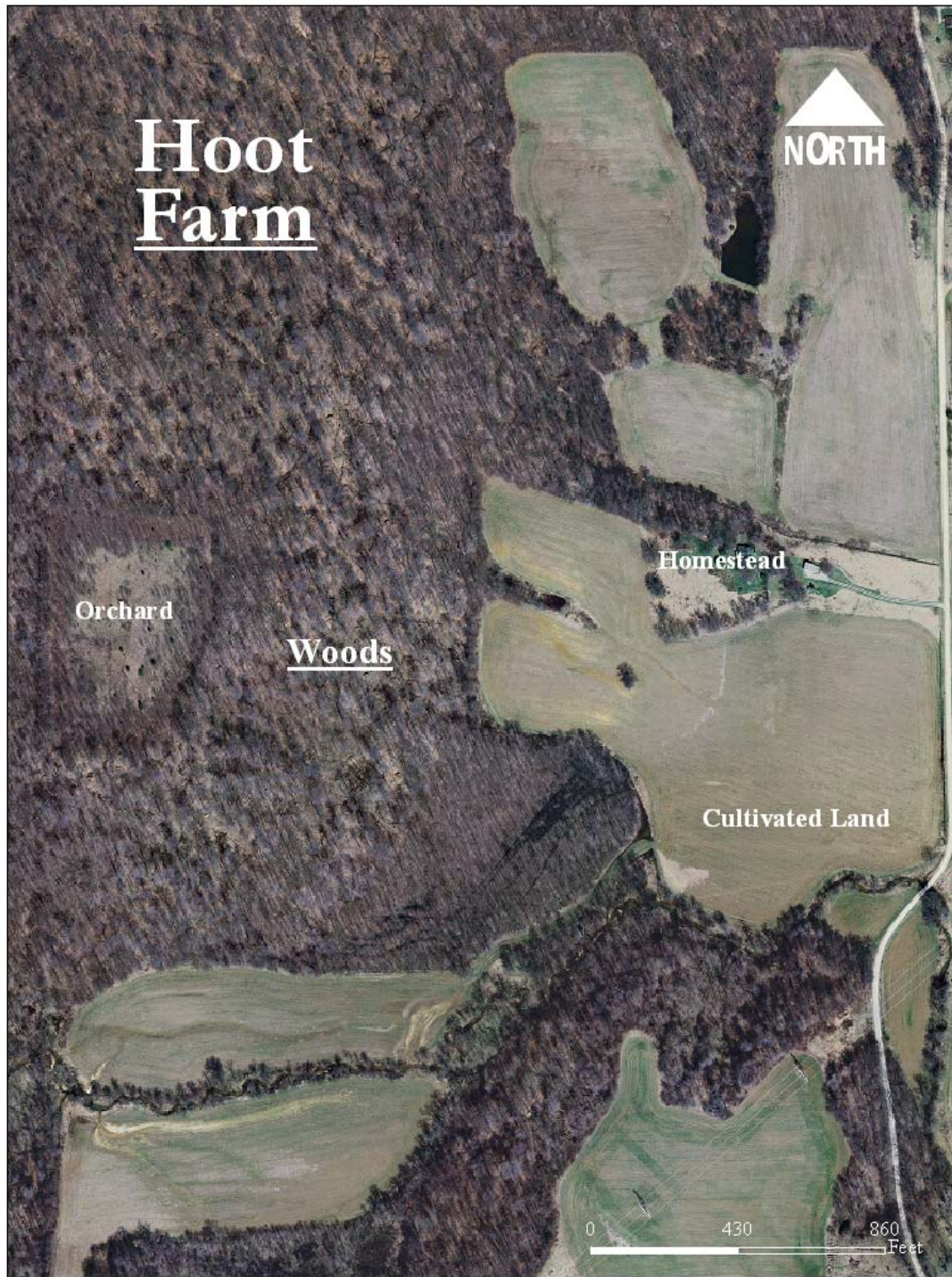
In the mid-1960s, following well more than a century of possession by the Hoot family, private individuals sought to buy the homestead and cultivated portions of the

Farm (Figure 2.4). Ecologist Marion Jackson became aware of this, and lobbied his institution, Indiana State University, to purchase the old-growth woods. But Robert Hoot, the youngest and only son of George Hoot, would not agree to the sale. When a deal could not be struck between the University and all of the heirs of the Hoot estate, Jackson instead arranged for the property to be protected by The Nature Conservancy via a conservation easement in 1980, thus ensuring Hoot Woods' continued existence (Marion T. Jackson, Emeritus Professor – Indiana State University, October 15 2006, letter).

At present, Hoot Woods “exists in a landscape of privately owned forest lands.” The stand lies 42,325 meters from the nearest old-growth forest, but is separated from the nearest non-old-growth forest patch by only 200 meters (Spetich et al. 1997). Throughout the Hoot family's ownership, a majority of the 64.7 ha (160 acre) farm was dedicated to crops and support buildings (Figure 2.5). A fruit orchard, planted at the top of the farm's largest hill, occupied a small portion of the land. The remainder of the property was left in its wooded state, with few logs harvested.

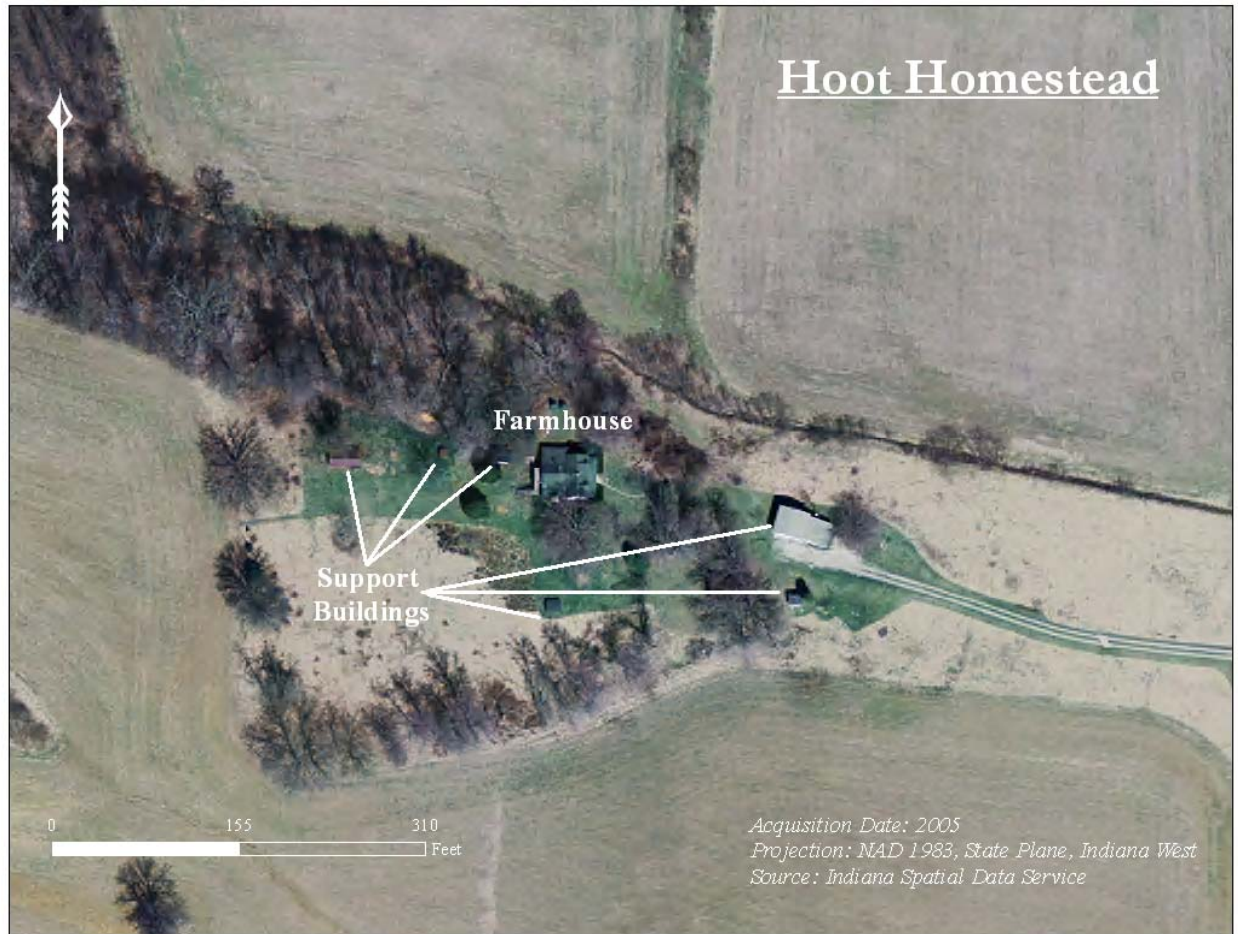
### Sampling History

As part of the Indiana Natural Areas Survey effort, Petty and Lindsey (1961) inventoried 6.9 ha (17 acres) of Hoot Woods and accounted for every tree measuring 10 cm (4 in.) or greater in diameter at breast height (dbh). At that time, twenty-two tree species and 1,263 individual trees were present. Hoot Woods was dominated by beech in this inventory, with a density of 78.8 stems per ha (32 stems/acre). Sugar maple had a codominant status, with 56.7 stems per ha (23 stems/acre). Tulip poplar ranked third, and other shade intolerant species, such as sassafras and wild black cherry, were present.



**Figure 2.4 – High-resolution Aerial Image of Hoot Farm, ISDS (2005)**





**Figure 2.5 – High-resolution Aerial Image of Hoot Homestead, ISDS (2005)**

Based on these observations, Petty and Lindsey concluded that the previously underemphasized natural process of gap replacement had been important in producing the composition of Hoot Woods. Petty and Lindsey’s investigation was not designed as part of a permanent plot analysis, and they did not map any of the stand.

Williamson (1975) collected spatial data for a 1.1 ha portion of Hoot Woods and related that information to canopy gaps created by windthrown trees (Figure 2.6). He mapped trees 5.1 cm (2 in.) dbh or greater and recorded the location of individual tree stems on a 50×100 m grid for the purposes of conducting a nested quadrat analysis.

According to Williamson, Hoot Woods is composed of a mosaic of species of different seral stages. He considered ash, tulip poplar, sassafras, red and black oaks, walnut, and elm early seral tree species, while white oak, sugar maple, and beech were categorized as late seral species. The former group takes advantage of opportunities when light resources are plentiful, while the latter group competes better when light is scarce.

Williamson (1975) hypothesized that early seral tree species would regenerate in light gaps from tree-falls and be found clumped around these gaps. He theorized that the degree of clumping would be proportional to the size of the light gaps. His analysis indicated that tulip poplar and ash were clumped near light gaps, while beech and sugar maple were not. Trees of different seral stages possess different characteristics related to reproduction, and Williamson argued that shade tolerance, wood strength, and age of first seed production increase with species of increasing seral stages. He inferred that early seral species sacrifice wood strength in order to grow quickly and reach the canopy. These factors suggest that early seral species spring up around light gaps in the canopy, becoming isolated patches within the beech-maple matrix.

Marion Jackson (Figure 2.7) initiated a long-term study of Hoot Woods in 1965, and this inventory has been repeated at ten year intervals to allow direct comparisons of the stand's composition and structure. In 1965, a complete census was made for a 4.4 ha (10.9 acres) portion of Hoot Woods by Marion Jackson and Indiana State University student Phillip R. Allen. The results of that survey were not published, but the detailed records maintained by Professor Jackson.

The study area was again censused in 1975, by Marion Jackson and student Brian Abrell. Abrell and Jackson (1977a) discovered that beech had declined 11.2% in density



**Figure 2.6 – Photo of a Tip-up Mound Created by a Wind-thrown Beech Tree (Mark Cowell 2005)**

and 7.2% in importance. Meanwhile, sugar maple increased in density by 8.9% and importance by 10% over a ten-year period. Hoot Woods' four other leading tree species varied little in importance percentage during the decade-long time interval. Based on such information, the authors concluded that Hoot Woods was a forest stand approaching climax conditions. Decreasing levels of beech coupled with increasing levels of sugar maple led them to hypothesize that these changes were possibly the result of a long-term wave of succession in beech and maple dominance.





**Figure 2.7 – Photo of Dr. Marion T. Jackson Measuring a Tulip Poplar Tree (Jim Hayes 2005)**

In a separate analysis, Abrell and Jackson (1977b) assessed mortality rates of Hoot Woods' tree species. Trees ranging from 15.2 to 25.4 cm (6 - 10 in) dbh were most affected by disturbance. They accounted for sixty percent of all mortality over the ten years. They concluded that the spatial distribution of mortality from 1965 to 1975 was typical of a stand affected by tree-falls and other natural disturbances. Tree accessions tended to be clustered at particular sites rather than evenly distributed. The authors observed biomass increasing in Hoot Woods, and postulated that "barring increased levels of disturbance, this trend is expected to continue, but at a diminishing rate in future decades." They attributed the recent decline in beech to an unusually high incidence of windthrow and tornadoes that occurred in southwestern Indiana from 1965 to 1975. Being rather brittle, beech is more susceptible to storm damage than many other hardwood species. Abrell and Jackson (1977b) concluded that numerous resurveys of



particular sites would be required to clarify hypothesized relationships between the codominants.

Hoot Woods was censused again under the supervision of Marion Jackson in 1985 (with Rebecca Strait & Brian Abrell) and 1995 (with Brenda Morgan & Brian Abrell), although the results were not published. Fieldwork for the 2005 survey was conducted by Marion Jackson, Mark Cowell, Brenda Morgan, Brian Abrell and the author of this thesis, Trent Holmes.

## CHAPTER THREE

### METHODS

Forest ecosystem dynamics result from adaptations made by individual species to repeating patterns of environmental change (Loucks 1970). In order to understand these dynamics, some studies employ analyses of tree locations on a given site over extended periods of time. This method of research is commonly referred to as permanent plot analysis and can be used to infer the processes that influence stand dynamics (Bakker et al. 1996; Chen 2004; North 2004). That information can in turn be used to better manage forest resources. This study is concerned with the dynamics of a single stand and, therefore, avoids the shortcomings of the more commonly used approach of chronosequences. Chronosequences are space-for-time substitutes that attempt to predict the conditions that will be present in one vegetative site based on a set of different aged sites. This type of analysis is readily collected in a short time period. Unfortunately, chronosequences are unreliable predictors of successional change because they assume homogeneity of site locations and disturbance history. The foresight and long-term effort required to conduct a permanent plot study is uncommon, and makes this Hoot Woods dataset particularly valuable.

#### Permanent Plots

Permanent plots are a means of tracking a plant community's demography over time. Each time a permanent plot is surveyed, it represents a snapshot in that

community's history. When numerous surveys are conducted over an extended period of time, researchers can begin to compare characteristics from one survey to another and draw inferences concerning successional change. Permanent plot studies are a source of compelling evidence that may reveal mechanisms that lie beneath the functioning of forested ecosystems (McCune & Cottam 1985; McCune & Menges 1986; Bakker et al. 1996).

The difficulties associated with making exact determinations of forest stand succession patterns based on tree-by-tree analysis over extended time periods are tremendous. Permanent plot studies require prolonged attention in the form of surveys conducted at regular time intervals. This task often involves difficult, time-consuming, and sometimes expensive work. Relocating individual trees after a great deal of time has elapsed is not a simple process. And because human and tree lifespans do not coincide, an individual researcher cannot live long enough to witness the entire process of succession or coexistence within a forest community. But the rewards are great for those willing to persevere. The information generated from permanent plot studies can be employed to verify predictions made by model-based research. Ecosystem properties are continuously changing. Theories that attempt to explain and predict change are created, in part, from observations made during permanent plot studies. Perhaps most importantly, permanent plots enable the description of species replacement patterns during succession. The exact sequence of events in forest stand succession is critically important. Once its order is known, external causes of succession can be inferred and hypotheses concerning internal causes can be generated (Abrell & Jackson 1977; Bakker et al. 1996).

## Data Collection

In June of 2005, the Hoot Woods study area was completely censused to determine its contemporary composition, structure, and spatial patterning. All trees  $\geq 10$  cm dbh were cataloged. In the 1965 census, the researchers divided a 4.4 ha (10.9 acre) section into 64 square quadrats, each 26.2 m (86 feet) on a side. The location, diameter, and species of each individual stem were mapped and recorded on McBee punch cards. The total area of the stand survey was brought to 6.6 ha (16.3 acres) with the mapping of an additional 2.2 ha (5.4 acres) during the 1975 resurvey (Abrell & Jackson 1977a). The card entries for this census included the species symbol, plot number, plot coordinates, 1965 dbh, diameter and volume changes, and a mortality or accession code if applicable.

For the 2005 analysis, a series of graduated symbol maps of preexisting trees was created for each of Hoot Woods' plots. Symbols were sized in accord with the dbh values of individual trees and labeled according to their tree identification number and species code. In addition, each map indicated the relative location of center posts, numbered aluminum tubes left behind by the study's initiators. Living tree stems from the 1995 census were relocated and ingrowths were mapped into the plots. The center posts, when locatable, were used to measure the coordinates of each ingrowth ( $\geq 10$  cm dbh). At other times it was more expedient to measure the distance of ingrowths to nearby trees with known x-y coordinates. Their approximate positions were hand drawn onto the graduated symbol maps and later translated into correct coordinates using GIS procedures. The data from 1965 covers only 64 of the 96 plots in the study; in 2005 all 96 plots were resurveyed.

## Stand Analysis

### *Composition*

Density, relative density, basal area, relative basal area, frequency, relative frequency and importance values are statistical measures used to estimate the influence of specific tree species within particular stands (Spetich et al. 1997). These statistics were calculated for each census, producing five sets of statistics, from which to compare changes in stand composition. Of the handful of permanent plot studies conducted in the Midwest, few have utilized more than two complete censuses (McCune & Menges 1986).

Density refers to the number of individual stems occurring in a specified area. It is calculated by dividing a stand's total number of trees by the area of the stand. Relative density is computed for an individual species to indicate its proportion of the entire stand density; it is derived by simply dividing the observed number of occurrences of a particular species by the total number of trees within the stand. Dominance is commonly measured as basal area. Its standard equation is:  $\pi (dbh/2)^2$ . The basal area of each tree species was totaled and divided by the area of the study area. It is typically expressed in  $m^2/ha$ . Relative basal area is the proportion of total stand basal area accounted for by specific tree species (McCune & Menges 1986). Frequency refers to the number of quadrats containing at least one living stem of a given species. Frequency is derived by dividing the number of quadrats that each species appears in by the total number of quadrats analyzed. Relative frequency, meanwhile, is calculated by dividing the frequency of a particular species by the sum frequency of all species. The importance value (I.V.) is often used in permanent plot analyses, and is a single value index that measures the significance of a given species within a community (Curtis & McIntosh

1951). In order to calculate importance values for Hoot Woods, the values for each species' relative density, relative basal area, and relative frequency were summed and divided by three.

The above metrics facilitate a detailed evaluation of stand changes. Percentage change in compositional statistics between 1965-1975, 1975-1985, 1985-1995, and 1995-2005 were calculated. These figures allow the direction and intensity of compositional changes to be observed. Fluctuations in the values of each variable were evaluated for both the entire forty years and the individual ten-year period. Percent change is calculated using the formula  $[(A-B)/A * 100]$ , where "A" denotes to the value of a variable in one census and "B" denotes its value in the succeeding census (Helms & Jackson 1977).

### *Structure*

Stand structure is assessed by plotting stem density according to 10 cm size classes. Once graphed, they can be compared at successive time intervals. Abrell and Jackson (1977a) suggested that size class distribution curves integrate stand changes from ingrowth, mortality, and individuals moving from smaller to larger size classes. They are also used to deduce if a specific tree species is self-replacing. Size class distributions are often an indicator of past disturbance and stages of recovery.

Structure curves typically exhibit one of three forms: negative exponential, multimodal, or unimodal (Ziegler 1995). Negative exponential curves are characterized by a large number of tree stems in small diameter categories, with progressively fewer trees in larger size classes. Tree species with negative exponential curve structures are considered to be actively and successfully reproducing. Multimodal curves differ from

negative exponential curves in that they display one or more peaks in the size distribution classes. Tree species possessing this type of structure curve are characterized by pulse reproduction. Unimodal distributions typically resemble the shape of a bell curve, with stems clustered in the middle to large size classes. This situation signifies an even-aged cohort that is failing to regenerate. Modal curves are common for species that are decreasing in stand dominance (Cowell & Jackson 2002). For this study, structure curves were generated for all tree species except those with extremely low stem counts.

### *Spatial Pattern*

Evaluation of tree ingrowth and mortality were made on a tree-by-tree basis. Mortality rates among canopy trees are an important component of forest dynamics, providing information for assessing the impacts of environmental stresses on forest stands. The locations of individual stems were recorded in the field using x-y coordinates. These coordinates were used to plot the distribution of living stems, ingrowth, and mortality, with analysis conducted on the five most important tree species: sugar maple, American Beech, tulip poplar, black cherry, and slippery elm. A series of thematic maps was created in ArcMap 9.1 and projected in Universal Transverse Mercator (UTM), Zone 16. The maps present spatial pattern changes for each species throughout the study's forty-year time span. They combine size and location attributes to display ingrowths, mortalities, and surviving stems on the same map.

Field data directly measuring the size and location of canopy gaps has not been collected over the course of the Hoot Woods permanent plot study. However, methods exist for estimating forest canopy gaps. Runkle (1990) monitored canopy gaps in an old-growth, beech-maple forest for 12 years. He suggested that the size of canopy gaps can

be estimated using the equation  $[EG = 149 + 0.040(\text{Basal Area})]$ . The abbreviation “EG” refers to the area of the expanded gap, or simply, “gap area.” This gap area solution can then be used to calculate “gap radius” via the equation  $[GR = \sqrt{(\text{Gap Area}/\pi)}]$ .

This project utilized Runkle’s empirical formula within a GIS to estimate canopy gap sizes in Hoot Woods. The location of each gap maker was shifted three meters northward to account for the solar sun angle at the Hoot Woods’ latitude. Tree stems measuring greater than 45 cm dbh were considered “gap makers.” Next, the equations for expanded gap and gap radius were used to compute a buffer distance for each gap maker. A file containing the attributes of the gap makers was then buffered according to these values. Finally, overlapping polygons created by the buffer were dissolved to create a single coverage. When overlaid with ingrowth point data, the tree species correlated with regeneration in and around canopy gaps became apparent.

It should be noted that some research has found canopy gaps in the beech-maple region to be shaped like ellipses rather than circles (Forrester & Runkle 2000). Other studies of actual canopy gaps have indicated that openings are often created by more than one tree (Stambaugh et al. 2002). Despite its limitations, the process used here for estimating canopy gaps appears to provide an adequate basis for evaluating theories of gap-phase dynamics. A bar graph summarizing the number of stems of each tree species occurring in or within 3 m of the gaps accompanies each map. When viewed together, they provide insight into the species composition of canopy light gaps inside Hoot Woods. The shared objective of these compositional, structural, and spatial metrics is to reveal the successional pathways, causes, and mechanisms which have occurred in Hoot Woods over a forty-year period.



## Presentation of Results

The display of data is an important element of permanent plot studies. Because the information gleaned from tables and figures can be used by subsequent generations of researchers to continue permanent plot analyses, it is a good practice to include detailed quantitative results. Values for overall stand density and basal area values are occasionally left out of published accounts (McCune & Menges 1986). Because there are no means to convert relative percentages back into their absolute values, this information is lost. In addition, many permanent plot studies are published with rare species grouped together into a singular “other” or “minor” category. It is important that these “other” tree species be given their own categories. Though they may have little impact on community-level composition and dynamics, data on these trees will likely be an invaluable resource for other investigations. Flowering dogwood, for instance, rarely occurs in significant numbers in beech-maple forests, but is believed to be particularly susceptible to air pollution. Therefore, its absence within a given stand may indicate poor environmental conditions (McCune & Menges 1986). In order to facilitate comparison to the findings of past, present, and future research, the results of this study are fully reported.

## CHAPTER FOUR

### RESULTS

Hoot Woods changed in composition, structure, and spatial pattern between 1965 and 2005. At the study's outset, American beech was clearly dominant, but has since continually diminished. Sugar maple, meanwhile, has steadily increased its presence, and now exceeds beech. The 1980 tornado led overall stand density to decrease in the short term, producing mortality mainly among large beech trees. Stand basal area increased and the ongoing trends among the codominants grew more exaggerated during the remainder of the study period.

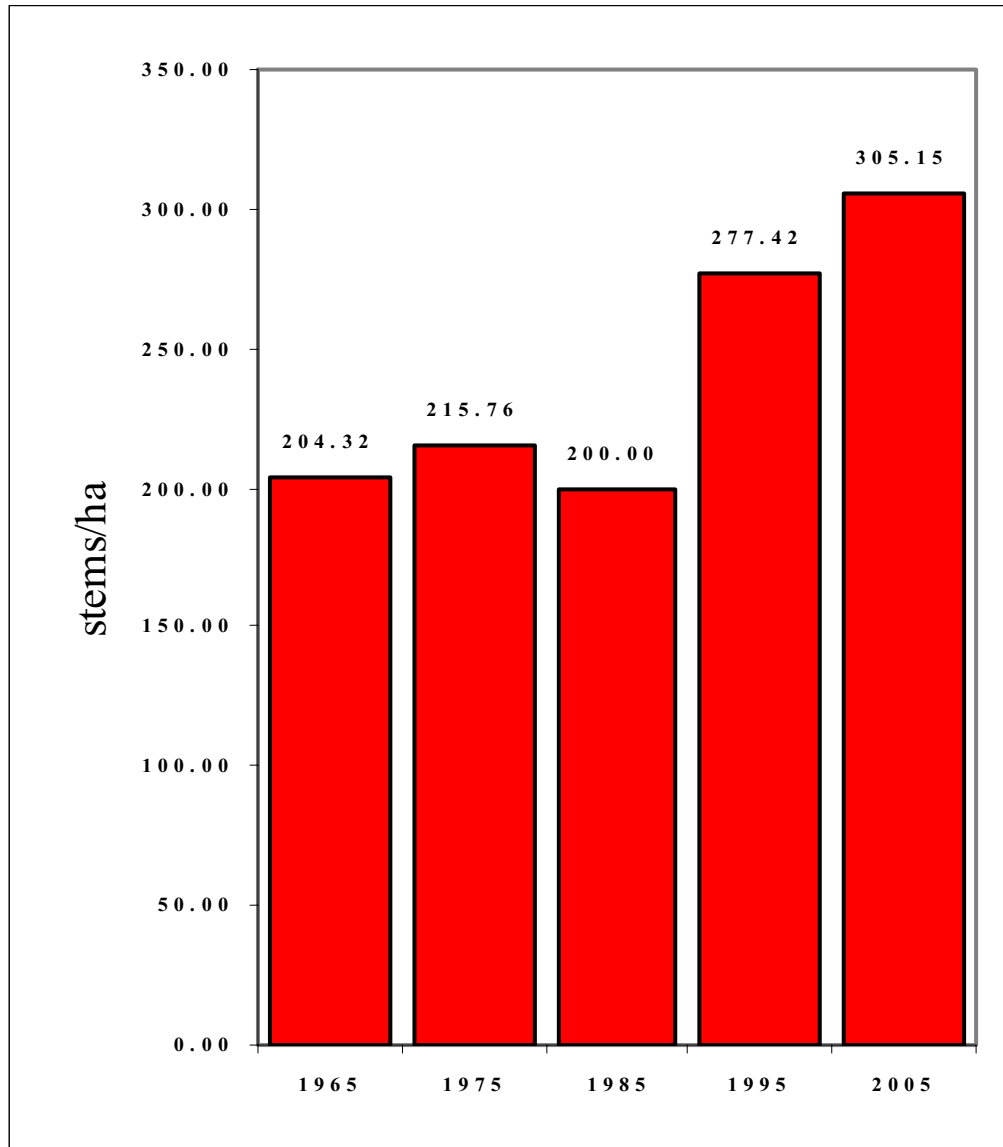
#### Stand Analysis

Overall, density increased by nearly 100 stems/ha over the 40 years of the study (Figure 4.1). In 1965, density was 204.3 stems/ha, which rose to 215.8 by the next census, dropped to 200.0 in 1985 as the effects of the tornado were felt, rebounded to 277.4 in 1995 aided by an influx of young trees, and then increased to 305.2 during the most recent census. Stand basal area oscillated in a similar fashion (Figure 4.2). Basal area increased between 1985 and 2005 but has not yet recovered to its pre-tornado high point. The stand fluctuated between 27.6, 30.0, 24.7, 26.0, and 26.6 basal area m<sup>2</sup>/ha for the respective census years.

#### Species Analysis

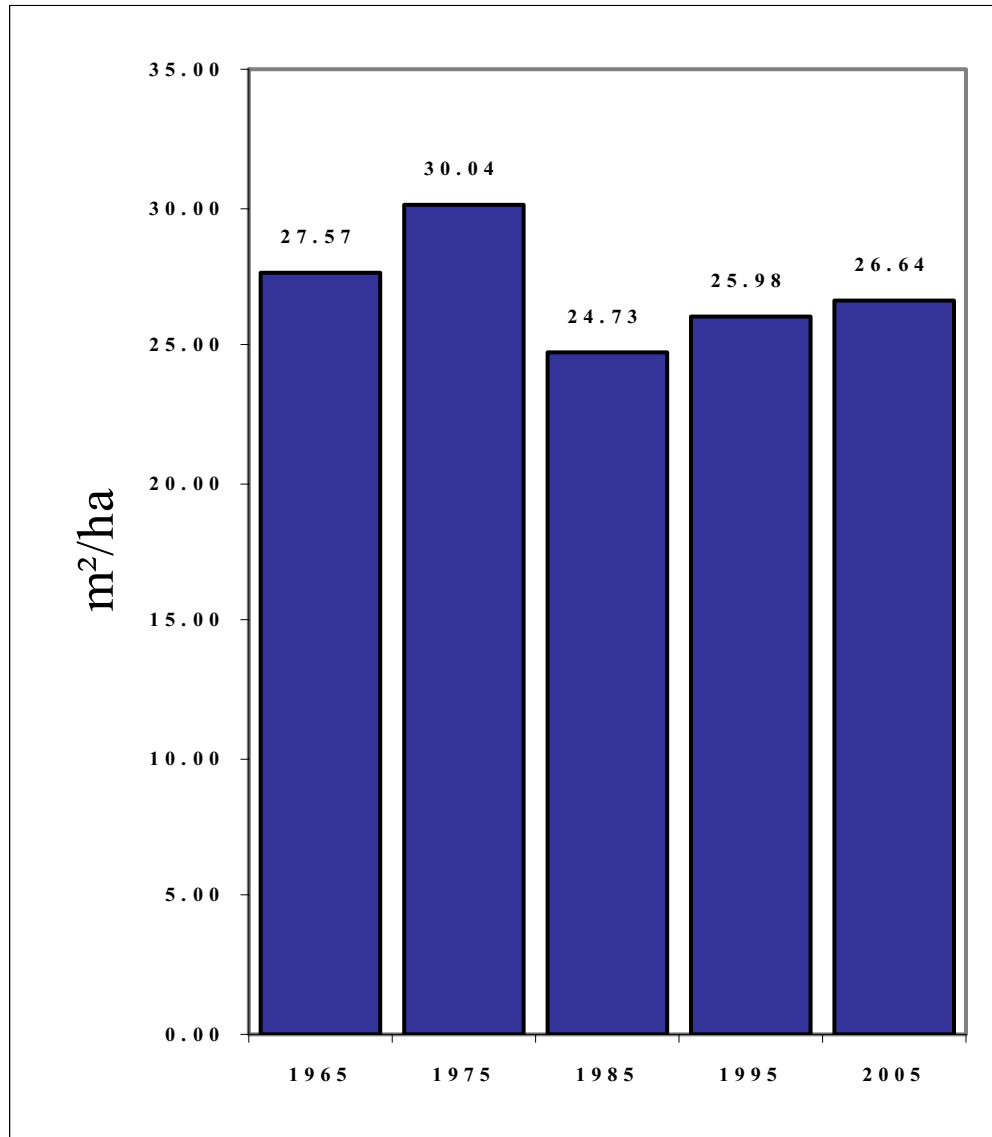
Compositionally, beech declined steadily in density, basal area, frequency, and

importance over the course of the study period. Its importance dipped from a high of 40.5% in 1965 to a relatively low 22.6% in 2005 (Table 4.1). During the period prior to the tornado, beech declined in density from 76.1 to 70.5 stems/ha and in basal area from 15.0 to 14.7 m<sup>2</sup>/ha (Tables 4.2 & 4.3). From 1975 to 1985 (following the tornado), beech



**Figure 4.1 – Stand Density 1965-2005, Hoot Woods, Indiana**

declined in density to 51.8 stems/ha and 10.5 m<sup>2</sup>/ha in basal area. In the remaining two periods it dropped to 47.7 and 42.8 stems/ha in density and 9.9 and 8.7 m<sup>2</sup>/ha in basal area. Following a 1985 drop-off, ingrowth rates for beech increased to 3.2/ha, and 4.4/ha for the remaining census years (Tables 4.4, 4.5, 4.6, & 4.7). Its absolute frequency of



**Figure 4.2 – Stand Basal Area 1965-2005, Hoot Woods, Indiana**

Table 4.1 – Importance Values 1965-2005, Hoot Woods, Indiana

Importance Values					
Species	1965	1975	1985	1995	2005
Box Elder	0.00%	0.00%	0.00%	0.00%	0.07%
Black Maple	0.00%	0.11%	0.09%	0.08%	0.08%
Red Maple	0.00%	0.26%	0.20%	0.25%	0.28%
Sugar Maple	28.97%	30.67%	36.16%	35.05%	37.78%
Redbud	0.00%	0.00%	0.00%	0.07%	0.00%
Ironwood	0.13%	0.27%	0.09%	0.15%	0.42%
Bitternut Hickory	0.45%	0.63%	0.57%	0.41%	0.25%
Dogwood	0.13%	0.41%	0.98%	1.06%	0.09%
Pignut Hickory	0.26%	0.17%	0.09%	0.07%	0.07%
Shagbark Hickory	0.42%	1.03%	1.15%	1.34%	1.34%
Hackberry	1.33%	0.87%	0.89%	0.62%	0.61%
White Ash	3.24%	1.94%	2.10%	1.92%	1.55%
American Beech	40.49%	36.80%	31.84%	26.13%	22.64%
Green Ash	2.91%	2.80%	2.86%	2.47%	2.30%
Black Walnut	0.88%	0.79%	0.56%	0.33%	0.33%
Tulip Poplar	12.30%	11.46%	12.68%	12.75%	13.12%
Black Gum	0.43%	0.57%	0.54%	0.55%	0.69%
Hop Hornbeam	0.13%	0.16%	0.09%	0.22%	0.52%
Black Cherry	1.51%	2.09%	1.84%	4.33%	4.33%
White Oak	0.18%	1.14%	0.15%	0.14%	0.15%
Chinkapin Oak	0.69%	0.73%	0.86%	0.47%	0.48%
Northern Red Oak	0.66%	1.21%	1.19%	0.96%	0.75%
Sassafras	2.57%	2.93%	1.71%	1.79%	2.88%
Basswood	0.00%	0.00%	0.09%	0.07%	0.00%
American Elm	0.77%	0.80%	1.08%	2.04%	2.54%
Slippery Elm	1.55%	2.16%	2.18%	6.72%	6.74%

88.3% declined to 71.4% by 2005 (Table 4.8). Structurally, beech in 2005 displays a unimodal distribution typical of a decreasing species (Figure 4.3). The majority of Hoot Woods' beech population is comprised of mid-sized trees. Spatially, beech is still relatively well-distributed throughout the stand. Figure 4.4 indicates the locations of numerous of large beech trees that died during the 1980 tornado. Beech mortality rates

Table 4.2 – Species Density 1965-2005, Hoot Woods, Indiana

Species Density						
stems/ha						
Species	1965	1975	1985	1995	2005	65 - '05
Box Elder	0.000	0.000	0.000	0.000	0.152	NA
Black Maple	0.000	0.303	0.152	0.152	0.152	NA
Red Maple	0.000	0.455	0.303	0.455	0.606	NA
Sugar Maple	78.636	93.939	105.909	140.606	167.879	53.16%
Redbud	0.000	0.000	0.000	0.152	0.000	NA
Ironwood	0.227	0.606	0.152	0.303	0.909	75.00%
Bitternut Hickory	0.682	0.909	0.758	0.606	0.303	-125.00%
Dogwood	0.227	0.758	1.667	2.424	0.303	25.00%
Pignut Hickory	0.455	0.303	0.152	0.152	0.152	-200.00%
Hackberry	0.682	1.818	1.818	3.030	3.182	78.57%
Shagbark Hickory	2.273	1.515	1.364	1.212	1.061	-114.29%
White Ash	4.773	2.879	2.424	2.273	1.667	-186.36%
American Beech	76.136	70.455	51.818	47.727	42.879	-77.56%
Green Ash	4.318	4.091	3.182	3.030	2.727	-58.33%
Black Walnut	1.364	1.212	0.758	0.455	0.455	-200.00%
Tulip Poplar	18.182	16.667	15.000	19.091	19.091	4.76%
Black Gum	0.682	0.909	0.758	1.061	1.364	50.00%
Hop Hornbeam	0.227	0.303	0.152	0.455	0.909	75.00%
Black Cherry	3.182	3.636	2.727	18.485	19.697	83.85%
White Oak	0.227	1.061	0.152	0.152	0.152	-50.00%
Chinkapin Oak	0.909	0.758	0.758	0.606	0.606	-50.00%
Northern Red Oak	0.909	1.364	1.061	0.909	0.758	-20.00%
Sassafras	5.455	6.212	2.727	3.485	8.333	34.55%
Basswood	0.000	0.000	0.152	0.152	0.000	NA
American Elm	1.364	1.515	1.970	5.152	6.970	80.43%
Slippery Elm	3.409	4.091	4.091	25.303	24.848	86.28%

Table 4.3 – Basal Area 1965-2005, Hoot Woods, Indiana

Basal Area						
m <sup>2</sup> /ha						
Species	1965	1975	1985	1995	2005	65 - '05
Box Elder	0.000	0.000	0.000	0.000	0.002	NA
Black Maple	0.000	0.009	0.005	0.007	0.011	NA
Red Maple	0.000	0.019	0.016	0.031	0.046	NA
Sugar Maple	5.300	5.942	5.613	6.721	7.846	32.45%
Redbud	0.000	0.000	0.000	0.002	0.000	NA
Ironwood	0.003	0.006	0.001	0.003	0.014	81.86%
Bitternut Hickory	0.066	0.133	0.100	0.099	0.089	25.58%
Dogwood	0.002	0.007	0.017	0.028	0.003	36.79%
Pignut Hickory	0.009	0.006	0.003	0.003	0.003	-188.89%
Hackberry	0.041	0.165	0.167	0.183	0.217	81.24%
Shagbark Hickory	0.141	0.110	0.122	0.086	0.107	-32.24%
White Ash	0.726	0.586	0.619	0.706	0.641	-13.30%
American Beech	15.019	14.681	10.520	9.901	8.744	-71.78%
Green Ash	0.732	0.831	0.854	0.901	0.946	22.55%
Black Walnut	0.107	0.132	0.095	0.089	0.104	-3.68%
Tulip Poplar	4.022	4.339	4.613	5.111	5.585	28.00%
Black Gum	0.048	0.081	0.075	0.085	0.103	52.91%
Hop Hornbeam	0.003	0.003	0.002	0.005	0.173	98.47%
Black Cherry	0.313	0.563	0.434	0.495	0.514	39.05%
White Oak	0.049	0.673	0.048	0.057	0.067	26.48%
Chinkapin Oak	0.231	0.349	0.360	0.188	0.207	-11.66%
Northern Red Oak	0.135	0.438	0.432	0.419	0.329	58.89%
Sassafras	0.371	0.503	0.292	0.251	0.308	-20.68%
Basswood	0.000	0.000	0.001	0.002	0.000	NA
American Elm	0.088	0.106	0.097	0.161	0.109	19.14%
Slippery Elm	0.165	0.353	0.243	0.449	0.473	65.03%

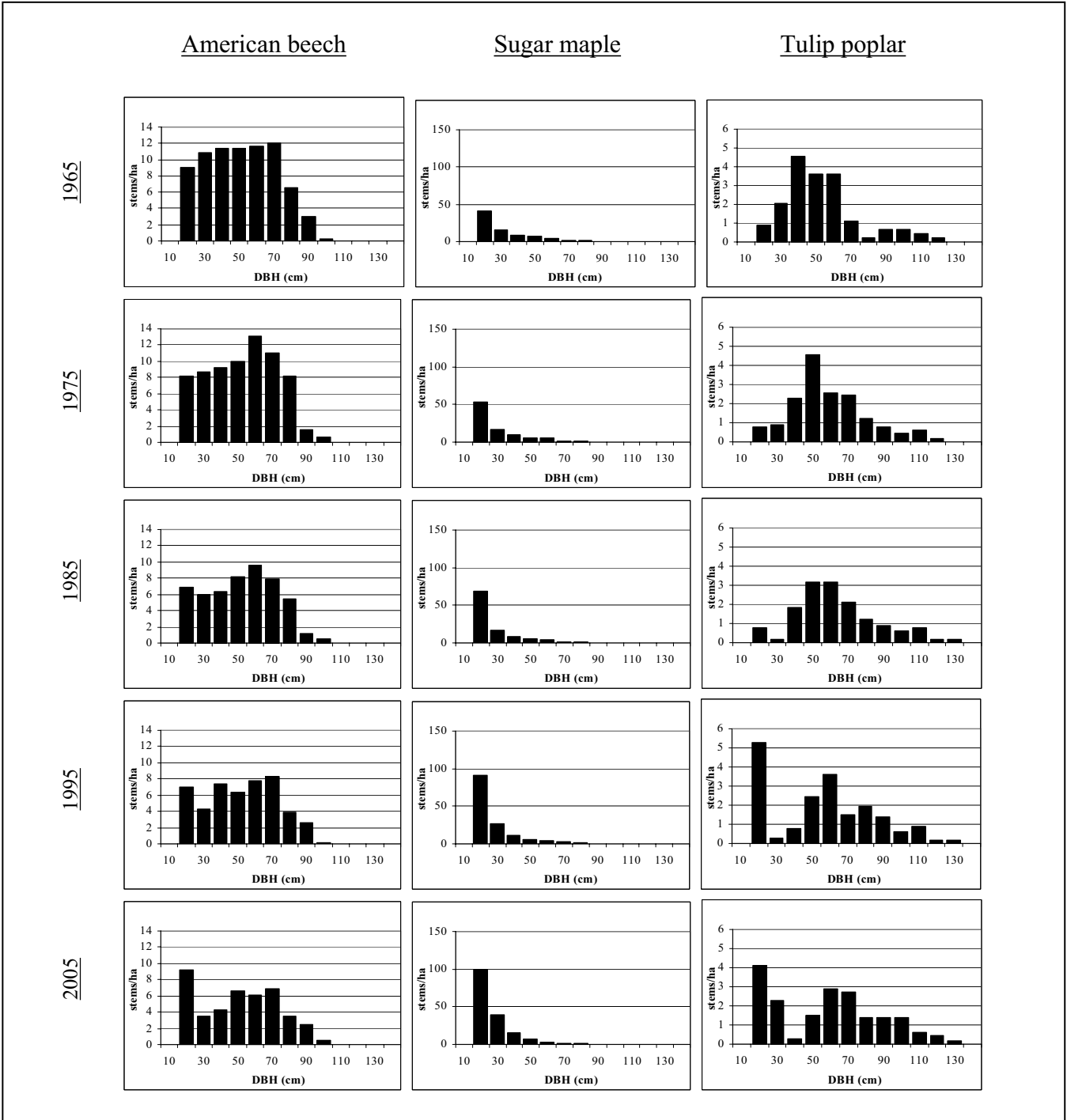


Figure 4.3 – Size Distributions for American beech, Sugar maple, & Tulip poplar



Table 4.4 – Ingrowth in 1975

INGROWTHS		
1975 Census		
Species	Ingrowths	Density per ha
Box Elder	0	0.00
Black Maple	2	0.30
Red Maple	3	0.45
Sugar Maple	297	45.00
Redbud	0	0.00
Ironwood	3	0.45
Bitternut Hickory	4	0.61
Dogwood	5	0.76
Pignut Hickory	0	0.00
Hackberry	9	1.36
Shagbark Hickory	1	0.15
White Ash	2	0.30
American Beech	168	25.45
Green Ash	8	1.21
Black Walnut	3	0.45
Tulip Poplar	38	5.76
Black Gum	3	0.45
Hop Hornbeam	1	0.15
Black Cherry	12	1.82
White Oak	6	0.91
Chinkapin Oak	1	0.15
Northern Red Oak	5	0.76
Sassafras	22	3.33
Basewood	0	0.00
American Elm	6	0.91
Slippery Elm	18	2.73

Table 4.5 – Ingrowth in 1985

INGROWTHS		
1985 Census		
Species	Ingrowths	Density per ha
Box Elder	0	0.00
Black Maple	0	0.00
Red Maple	0	0.00
Sugar Maple	214	32.42
Redbud	0	0.00
Ironwood	0	0.00
Bitternut Hickory	0	0.00
Dogwood	7	1.06
Pignut Hickory	0	0.00
Hackberry	1	0.15
Shagbark Hickory	0	0.00
White Ash	1	0.15
American Beech	17	2.58
Green Ash	0	0.00
Black Walnut	0	0.00
Tulip Poplar	3	0.45
Black Gum	0	0.00
Hop Hornbeam	0	0.00
Black Cherry	2	0.30
White Oak	0	0.00
Chinkapin Oak	0	0.00
Northern Red Oak	0	0.00
Sassafras	3	0.45
Basewood	1	0.15
American Elm	9	1.36
Slippery Elm	17	2.58

Table 4.6 – Ingrowth in 1995

INGROWTHS		
1995 Census		
Species	Ingrowths	Density per ha
Box Elder	0	0.00
Black Maple	0	0.00
Red Maple	2	0.30
Sugar Maple	303	45.91
Redbud	1	0.15
Ironwood	2	0.30
Bitternut Hickory	0	0.00
Dogwood	6	0.91
Pignut Hickory	0	0.00
Hackberry	9	1.36
Shagbark Hickory	0	0.00
White Ash	1	0.15
American Beech	21	3.18
Green Ash	0	0.00
Black Walnut	0	0.00
Tulip Poplar	31	4.70
Black Gum	2	0.30
Hop Hornbeam	3	0.45
Black Cherry	113	17.12
White Oak	0	0.00
Chinkapin Oak	0	0.00
Northern Red Oak	0	0.00
Sassafras	11	1.67
Basewood	0	0.00
American Elm	23	3.48
Slippery Elm	147	22.27

Table 4.7 – Ingrowth in 2005

INGROWTHS		
2005 Census		
Species	Ingrowths	Density per ha
Box Elder	1	0.15
Black Maple	0	0.00
Red Maple	1	0.15
Sugar Maple	321	48.64
Redbud	0	0.00
Ironwood	4	0.61
Bitternut Hickory	0	0.00
Dogwood	2	0.30
Pignut Hickory	0	0.00
Hackberry	6	0.91
Shagbark Hickory	0	0.00
White Ash	0	0.00
American Beech	29	4.39
Green Ash	0	0.00
Black Walnut	0	0.00
Tulip Poplar	16	2.42
Black Gum	3	0.45
Hop Hornbeam	4	0.61
Black Cherry	31	4.70
White Oak	0	0.00
Chinkapin Oak	0	0.00
Northern Red Oak	0	0.00
Sassafras	40	6.06
Basewood	0	0.00
American Elm	28	4.24
Slippery Elm	45	6.82

exceeded sugar maple in almost all size classes for every census (Tables 4.8, 4.9, 4.10, & 4.11).

Like all other species, beech had an abnormally high mortality rate (30.1%) for 1980 due to the tornado disturbance. But for beech, mortality was particularly high in the largest size classes. In the 50-59.9 cm dbh class, the mortality rate was 31.4 %. For the 60-69.9, 70-79.9, and 80+ classes, mortality rates were 38.4%, 46.3%, and 50%, respectively. Though not as dramatic, the same pattern held true for the 1995 and 2005 censuses, which were characterized by deaths of several trees larger than 50 cm dbh.

In contrast to American beech, the density, basal area, frequency, and importance of sugar maple increased substantially over the course of the study period. Over the forty year course of the study, sugar maple increased by 53.2% and 32.5% in density and basal area, respectively (Tables 4.2 & 4.3). The rate of sugar maple ingrowth grew from 13.9/ha in 1975 to 32.4, 45.9, and 48.6/ha in 1985, 1995, and 2005 (Tables 4.4, 4.5, 4.6, & 4.7). Frequency rates underscore the ubiquity of sugar maple (Table 4.12). At the start of the study, it appeared in 88% of the plots and by 2005 that number had risen to 97%. Sugar maple increased steadily in importance from 1965-1985, before dipping by 1% in 1995, and then continuing its upward ascent during the last census (Table 4.1). Its representation has increased while beech has inversely declined (Figures 4.5 & 4.6). Sugar maple displays a negative exponential distribution for each census year, signifying a self-replacing species (Figure 4.3). Sugar maple survivors, ingrowths, and mortalities were spatially well distributed throughout the stand per census year (Figure 4.7). In every census year, the majority of sugar maple deaths occurred in the 10-19.9 cm dbh size class. A significant number of deaths also occurred in the 20-29.9 class with rates

# *Hoot Woods*

## *Spatial Distribution of Survivors, Ingrowth & Mortalities*

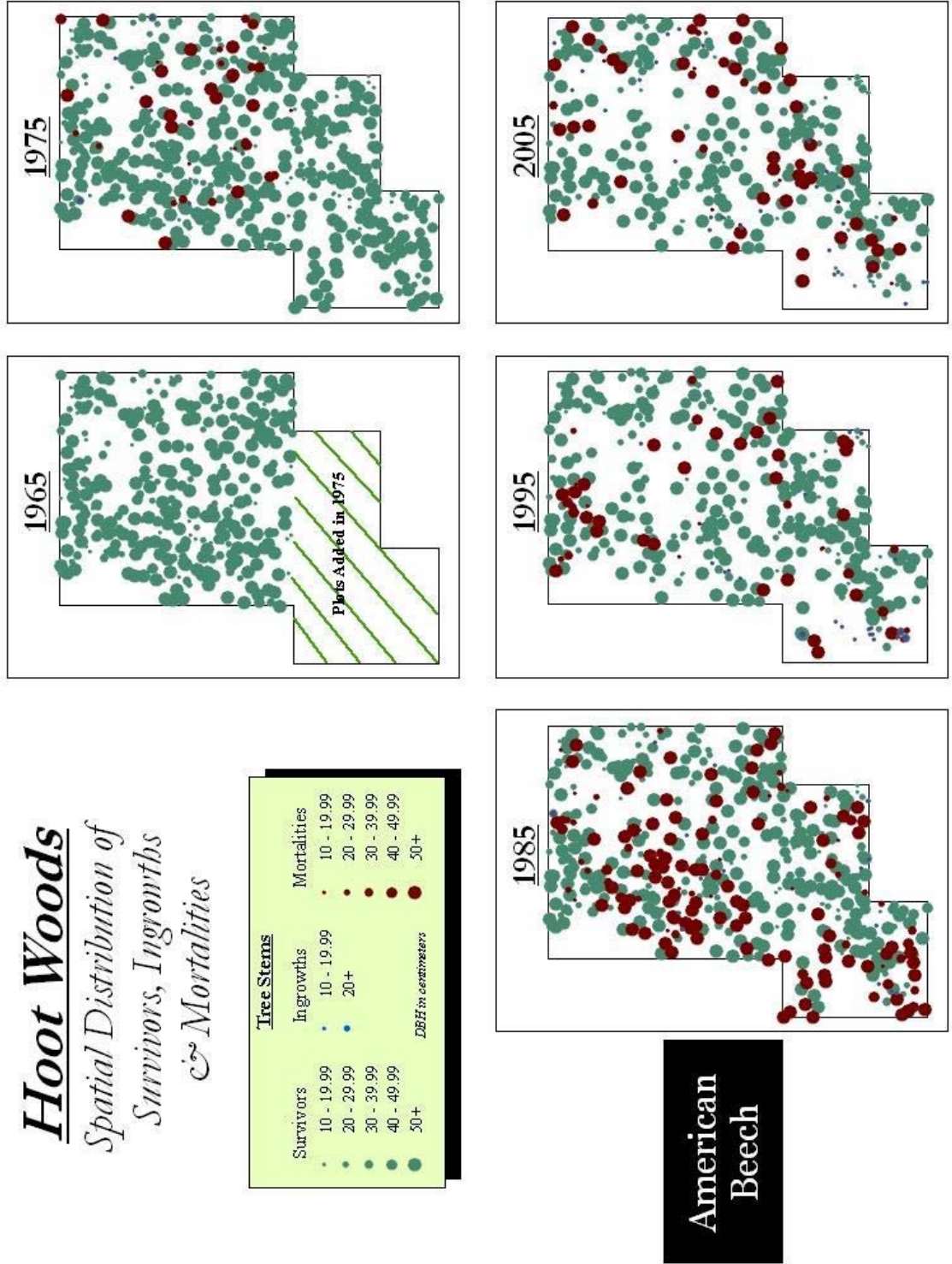
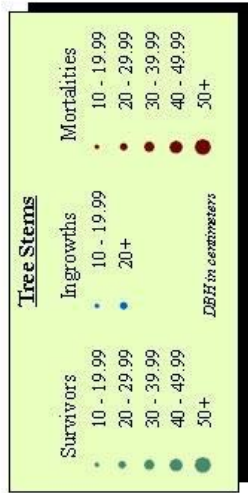


Figure 4.4 – Map of American Beech Tree Stem Locations, Hoot Woods, Indiana

Table 4.8 – Mortality in 1975, Hoot Woods, Indiana

Species		1975 Census										Size Classes (m dbh)																			
		DS	LS	OMR	DPH	TBA	ABA	AA	%A	B	BB	%B	C	CC	%C	D	DD	%D	E	EE	%E	F	FF	%F	G	GG	%G	H	HH	%H	
Box Elder	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Black Maple	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Red Maple	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Sugar Maple	23	346	6.65%	5.23	0.3259	0.0142	15	178	8.43%	2	67	2.99%	1	39	2.56%	2	33	5.08%	2	16	12.50%	1	9	11.1%	0	4	0	0	0		
Redbud	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Ironwood	0	1	0.00%	0.00	0.0000	0.0000	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Bitternut Hickory	1	3	33.33%	0.23	0.0018	0.0018	1	100.00%	0	1	100.00%	0	1	100.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Dogwood	1	1	0.00%	0.23	0.0019	0.0019	1	100.00%	0	0	100.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Pignut Hickory	0	2	0.00%	0.00	0.0000	0.0000	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Hackberry	0	10	0.00%	0.00	0.0000	0.0000	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Shagbark Hickory	1	3	33.33%	0.23	0.0025	0.0025	1	6	16.67%	0	2	0	1	33.33%	0	3	10.00%	0	2	0	0	0	0	0	0	0	0	0	0		
White Ash	4	21	19.05%	0.91	0.0238	0.0059	3	6	50.00%	1	3	33.33%	0	3	0	3	0	3	0	2	1.96%	8	53	15.05%	3	29	10.34%	3	14	21.43%	
American Beech	38	335	11.34%	8.64	1.7553	0.0462	5	40	12.50%	6	48	12.50%	7	50	14.00%	5	50	10.00%	1	51	10.00%	0	0	0	0	0	0	0	0	0	
Green Ash	0	19	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Black Walnut	1	6	16.67%	0.23	0.0180	0.0180	0	1	0	2	0	2	1	4	25.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Tulip Poplar	8	80	10.00%	1.82	0.1822	0.0228	2	4	50.00%	2	9	22.22%	2	20	10.00%	1	16	6.25%	1	16	6.25%	0	5	0	1	0	0	0	0	0	
Black Gum	0	3	0.00%	0.00	0.0000	0.0000	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hop Hornbeam	0	1	0.00%	0.00	0.0000	0.0000	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Black Cherry	2	14	14.29%	0.45	0.0054	0.0027	2	4	50.00%	0	5	0	1	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
White Oak	0	1	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chinkapin Oak	0	4	0.00%	0.00	0.0000	0.0000	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Northern Red Oak	0	4	0.00%	0.00	0.0000	0.0000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sassafras	5	24	20.83%	1.14	0.0277	0.0055	4	5	80.00%	1	10	10.00%	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Basswood	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Elm	2	6	33.33%	0.45	0.0140	0.0070	1	3	33.33%	1	2	50.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slippery Elm	6	15	40.00%	1.36	0.0326	0.0054	4	10	40.00%	2	3	66.67%	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

DS (# of Dead Stems in Current Census); LS (# of Living Stems in Previous Census); OMR (Overall Mortality Rate); DPH (Density per ha); TBA (Total Basal Area of Dead Stems); ABA (Average Basal Area of Dead Stems); A (Dead Stems in 10-19.9 cm dbh Size-class); AA (Living Stems in 10-19.9 cm dbh Size-class); %A (Size-class 'A' Mortality Rate); B (Dead Stems in 20-29.9 cm dbh Size-class); BB (Living Stems in 20-29.9 cm dbh Size-class); %B (Size-class 'B' Mortality Rate); C (Dead Stems in 30-39.9 cm dbh Size-class); CC (Living Stems in 30-39.9 cm dbh Size-class); %C (Size-class 'C' Mortality Rate); D (Dead Stems in 40-49.9 cm dbh Size-class); DD (Living Stems in 40-49.9 cm dbh Size-class); %D (Size-class 'D' Mortality Rate); E (Dead Stems in 50-59.9 cm dbh Size-class); EE (Living Stems in 50-59.9 cm dbh Size-class); %E (Size-class 'E' Mortality Rate); F (Dead Stems in 60-69.9 cm dbh Size-class); FF (Living Stems in 60-69.9 cm dbh Size-class); %F (Size-class 'F' Mortality Rate); G (Dead Stems in 70-79.9 cm dbh Size-class); GG (Living Stems in 70-79.9 cm dbh Size-class); %G (Size-class 'G' Mortality Rate); H (Dead Stems in 80+ cm dbh Size-class); HH (Living Stems in 80+ cm dbh Size-class); %H (Size-class 'H' Mortality Rate)



Table 4.9 – Mortality in 1985, Hoot Woods, Indiana

Species		1985 Census											Size Classes (cm dbh)																			
		DS	LS	OMR	DPH	TBA	ABA	A	AA	%A	B	BB	%B	C	CC	%C	D	DD	%D	E	EE	%E	F	FF	%F	G	GG	%G	H	HH	%H	
Box Elder	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Black Maple	1	2	50.00%	0.15	0.0123	0.0123	1	2	50.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Red Maple	1	3	33.33%	0.15	0.0208	0.0208	0	1	50.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Sugar Maple	135	620	21.77%	20.45	3.2919	0.0244	68	350	19.43%	29	115	25.22%	15	61	24.59%	8	40	20.00%	8	33	24.24%	4	10	40.00%	2	9	22.22%	1	2	50.00%		
Redbud	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Ironwood	3	4	75.00%	0.45	0.0070	0.0023	3	4	75.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Bitternut Hickory	1	6	16.67%	0.15	0.1382	0.1382	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dogwood	1	5	20.00%	0.15	0.0037	0.0037	1	5	20.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Pignut Hickory	1	2	50.00%	0.15	0.0063	0.0063	1	2	50.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hackberry	1	12	8.33%	0.15	0.0306	0.0306	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Shagbark Hickory	1	10	10.00%	0.15	0.0027	0.0027	1	5	20.00%	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
White Ash	4	19	21.05%	0.61	0.1269	0.0317	2	4	50.00%	1	2	50.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
American Beech	140	465	30.11%	21.21	10.5359	0.0753	15	54	27.78%	16	57	28.07%	11	61	18.03%	11	66	16.67%	27	86	16.67%	28	73	38.36%	25	54	46.30%	7	14	50.00%		
Green Ash	6	27	22.22%	0.31	0.2559	0.0426	0	0	0	4	4	100.00%	0	4	100.00%	0	4	100.00%	1	6	16.67%	1	6	16.67%	0	6	0	0	0	0	0	
Black Walnut	3	8	37.50%	0.45	0.1012	0.0337	0	1	100.00%	1	4	25.00%	1	4	25.00%	1	1	100.00%	0	1	100.00%	0	0	0	0	0	0	0	0	0	0	0
Tulip Poplar	14	110	12.73%	2.12	0.5529	0.0395	3	5	60.00%	3	6	50.00%	1	15	6.67%	1	30	3.33%	4	17	23.53%	1	16	6.25%	0	8	0	0	0	0	0	
Black Gum	1	6	16.67%	0.15	0.0294	0.0294	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hop Hornbeam	1	2	50.00%	0.15	0.0018	0.0018	1	2	50.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black Cherry	8	24	33.33%	1.21	0.4007	0.0501	2	5	40.00%	3	5	60.00%	1	4	25.00%	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
White Oak	6	7	85.71%	0.31	1.8944	0.3157	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chinkapin Oak	0	5	0.00%	0.00	0.0000	0.0000	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Northern Red Oak	2	9	22.22%	0.30	0.1140	0.0570	0	0	0	0	0	0	1	1	100.00%	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sassafras	26	41	63.41%	3.94	0.5209	0.0200	7	8	87.50%	9	13	69.23%	7	12	58.33%	2	7	28.57%	1	1	100.00%	0	0	0	0	0	0	0	0	0	0	0
Basswood	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Elm	6	10	60.00%	0.31	0.0780	0.0130	3	12	25.00%	2	0	0	1	1	100.00%	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slippery Elm	17	27	62.96%	2.58	0.4300	0.0253	8	11	72.73%	4	6	66.67%	1	1	100.00%	3	6	50.00%	1	2	50.00%	0	1	0	0	0	0	0	0	0	0	0

DS (# of Dead Stems in Current Census); LS (# of Living Stems in Previous Census); OMR (Overall Mortality Rate); DPH (Density per ha); TBA (Total Basal Area of Dead Stems); ABA (Average Basal Area of Dead Stems); A (Dead Stems in 10-19.9 cm dbh Size-class); AA (Living Stems in 10-19.9 cm dbh Size-class); %A (Size-class 'A' Mortality Rate); B (Dead Stems in 20-29.9 cm dbh Size-class); BB (Living Stems in 20-29.9 cm dbh Size-class); %B (Size-class 'B' Mortality Rate); C (Dead Stems in 30-39.9 cm dbh Size-class); CC (Living Stems in 30-39.9 cm dbh Size-class); %C (Size-class 'C' Mortality Rate); D (Dead Stems in 40-49.9 cm dbh Size-class); DD (Living Stems in 40-49.9 cm dbh Size-class); %D (Size-class 'D' Mortality Rate); E (Dead Stems in 50-59.9 cm dbh Size-class); EE (Living Stems in 50-59.9 cm dbh Size-class); %E (Size-class 'E' Mortality Rate); F (Dead Stems in 60-69.9 cm dbh Size-class); FF (Living Stems in 60-69.9 cm dbh Size-class); %F (Size-class 'F' Mortality Rate); G (Dead Stems in 70-79.9 cm dbh Size-class); GG (Living Stems in 70-79.9 cm dbh Size-class); %G (Size-class 'G' Mortality Rate); H (Dead Stems in 80+ cm dbh Size-class); HH (Living Stems in 80+ cm dbh Size-class); %H (Size-class 'H' Mortality Rate)

Table 4.10 – Mortality in 1995, Hoot Woods, Indiana

Species		1995 Census										Size Classes (cm dbh)																			
		DS	LS	OMR	DPH	TBA	ABA	AA	A	AA	B	BB	%B	C	CC	%C	D	DD	%D	E	EE	%E	F	FF	%F	G	GG	%G	H	HH	%H
Box Elder	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black Maple	0	1	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Red Maple	1	2	50.00%	0.15	0.0060	0.0060	1	1	100.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sugar Maple	74	639	10.59%	11.21	1.3209	0.0260	44	449	9.80%	13	115	11.30%	2	52	3.85%	4	34	11.76%	6	30	20.00%	2	10	20.00%	2	7	28.57%	1	2	50.00%	
Redbud	0	0	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ironwood	1	1	100.00%	0.15	0.0018	0.0018	1	1	100.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bitternut Hickory	1	5	20.00%	0.15	0.0343	0.0343	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dogwood	1	11	9.09%	0.15	0.0019	0.0019	1	11	9.09%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pignut Hickory	0	1	0.00%	0.00	0.0000	0.0000	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hackberry	1	12	8.33%	0.15	0.0504	0.0504	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Shagbark Hickory	1	3	11.11%	0.15	0.0784	0.0784	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
White Ash	2	16	12.50%	0.30	0.0755	0.0777	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Beech	48	342	14.04%	7.27	3.5818	0.0746	6	45	13.32%	4	39	10.26%	5	42	11.90%	6	54	11.11%	9	63	14.29%	6	52	11.54%	7	36	19.44%	5	11	45.45%	
Green Ash	1	21	4.76%	0.15	0.0858	0.0858	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black Walnut	2	5	40.00%	0.30	0.0303	0.0151	1	1	100.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tulip Poplar	4	99	4.04%	0.61	0.1651	0.0413	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black Gum	0	5	0.00%	0.00	0.0000	0.0000	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hop Hornbeam	1	1	100.00%	0.15	0.0032	0.0032	1	1	100.00%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black Cherry	9	18	50.00%	1.36	0.6237	0.0700	2	4	50.00%	2	3	66.67%	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
White Oak	0	1	0.00%	0.00	0.0000	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chinkapin Oak	1	5	20.00%	0.15	0.5393	0.5393	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Northern Red Oak	1	7	14.29%	0.15	0.2227	0.2227	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sassafras	6	18	33.33%	0.91	0.2245	0.0374	1	2	50.00%	1	2	50.00%	3	7	42.86%	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Basswood	0	1	0.00%	0.00	0.0000	0.0000	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Elm	2	13	15.38%	0.30	0.0071	0.0035	2	29	6.90%	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slippery Elm	7	27	25.93%	1.06	0.2839	0.0406	4	20	20.00%	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

DS (# of Dead Stems in Current Census); LS (# of Living Stems in Previous Census); OMR (Overall Mortality Rate); DPH (Density per ha); TBA (Total Basal Area of Dead Stems); ABA (Average Basal Area of Dead Stems); A (Dead Stems in 10-19.9 cm dbh Size-class); AA (Living Stems in 10-19.9 cm dbh Size-class); A' Mortality Rate); B (Dead Stems in 20-29.9 cm dbh Size-class); BB (Living Stems in 20-29.9 cm dbh Size-class); %B (Size-class 'B' Mortality Rate); C (Dead Stems in 30-39.9 cm dbh Size-class); CC (Living Stems in 30-39.9 cm dbh Size-class); %C (Size-class 'C' Mortality Rate); D (Dead Stems in 40-49.9 cm dbh Size-class); DD (Living Stems in 40-49.9 cm dbh Size-class); %D (Size-class 'D' Mortality Rate); E (Dead Stems in 50-59.9 cm dbh Size-class); EE (Living Stems in 50-59.9 cm dbh Size-class); %E (Size-class 'E' Mortality Rate); F (Dead Stems in 60-69.9 cm dbh Size-class); FF (Living Stems in 60-69.9 cm dbh Size-class); %F (Size-class 'F' Mortality Rate); G (Dead Stems in 70-79.9 cm dbh Size-class); GG (Living Stems in 70-79.9 cm dbh Size-class); %G (Size-class 'G' Mortality Rate); H (Dead Stems in 80+ cm dbh Size-class); HH (Living Stems in 80+ cm dbh Size-class); %H (Size-class 'H' Mortality Rate)

Table 4.11 – Mortality in 2005, Hoot Woods, Indiana

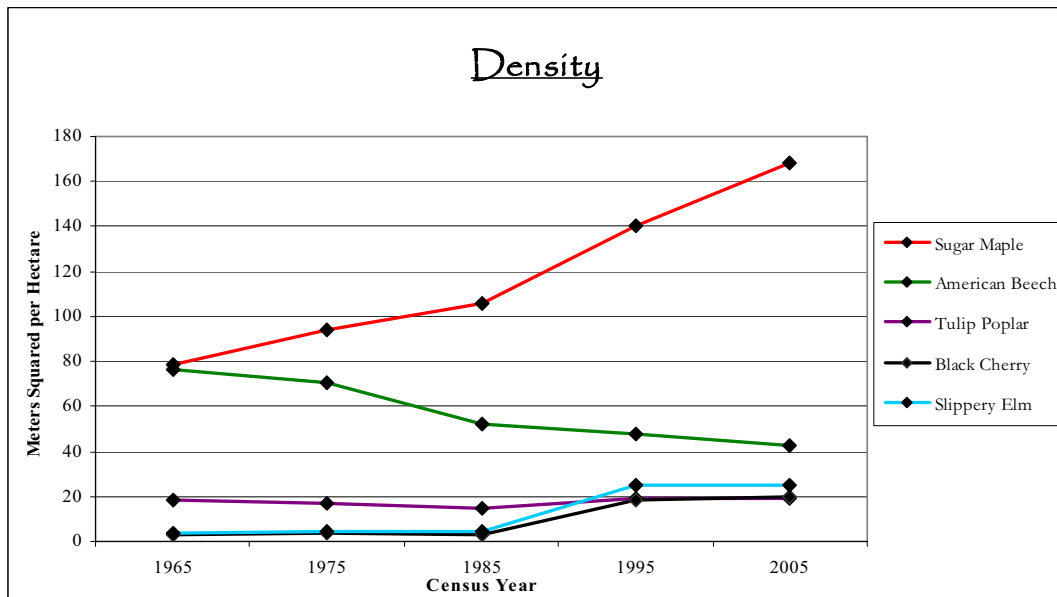
Species		2005 Census											Size Classes (cm dbh)																	
		DS	LS	OMR	DPH	TBA	ABA	AA	AA	%A	B	BB	%B	C	CC	%C	D	DD	%D	E	EE	%E	F	FF	%F	G	GG	%G	H	HH
Box Elder	0	0	0.00%	0.00	0.0000	0.00000	0	0		0	0		0	0		0	0		0	0		0	0		0	0		0	0	
Black Maple	0	1	0.00%	0.00	0.0000	0.00000	0	0		0	1		0	0		0	0		0	0		0	0		0	0		0	0	
Red Maple	0	3	0.00%	0.00	0.0000	0.00000	0	0		0	2		0	0		0	0		0	0		0	0		0	0		0	0	
Sugar Maple	141	928	15.19%	21.36	2.7087	0.0182	89	597	14.9%	16	177	9.04%	11	71	15.49%	6	34	17.65%	11	28	39.29%	5	14	35.7%	2	5	40.00%	1	2	50.00%
Redbud	1	1	100.00%	0.15	0.0047	0.0047	1	1	100.00%	0	0		0	0		0	0		0	0		0	0		0	0		0	0	
Ironwood	0	2	0.00%	0.00	0.0000	0.00000	0	2		0	0		0	0		0	0		0	0		0	0		0	0		0	0	
Bitternut Hickory	2	4	50.00%	0.30	0.0346	0.073	1	1	100.00%	0	0		1	1	100.00%	0	1		0	0		0	1		0	0		0	0	
Dogwood	16	16	100.00%	2.42	0.0562	0.0035	16	16	100.00%	0	0		0	0		0	0		0	0		0	0		0	0		0	0	
Pignut Hickory	0	1	0.00%	0.00	0.0000	0.00000	0	1		0	0		0	0		0	0		0	0		0	0		0	0		0	0	
Hackberry	5	20	25.00%	0.76	0.0511	0.0102	4	13	30.77%	1	3	33.33%	0	1		0	0		0	2		0	1		0	0		0	0	
Shagbark Hickory	1	8	12.50%	0.15	0.0072	0.0072	0	2		1	4	25.00%	0	1		0	0		0	1		0	0		0	0		0	0	
White Ash	4	15	26.67%	0.61	0.2330	0.0582	1	2	50.00%	0	1		0	0		1	3	33.33%	0	0		0	2		2	6	33.33%	0	1	
American Beech	61	315	19.37%	9.24	4.9174	0.0806	7	46	15.22%	2	28	7.14%	7	49	14.29%	6	42	14.29%	12	51	23.53%	11	55	20.00%	9	26	34.62%	7	18	38.89%
Green Ash	2	20	10.00%	0.30	0.2574	0.1287	0	0		0	0		0	0		1	4	25.00%	0	2		0	6		1	5	20.00%	0	0	
Black Walnut	0	3	0.00%	0.00	0.0000	0.00000	0	0		0	0		0	0		0	2		0	1		0	0		0	0		0	0	
Tulip Poplar	16	126	12.70%	2.42	0.5486	0.0343	10	35	28.57%	0	2		1	5	20.00%	2	16	12.50%	1	24	4.17%	1	10	10.00%	0	13		1	12	8.33%
Black Gum	1	7	14.29%	0.15	0.0028	0.0028	1	5	20.00%	0	0		0	0		0	1		0	1		0	0		0	0		0	0	
Hop Hornbeam	1	3	33.33%	0.15	0.0049	0.0049	1	3	33.33%	0	0		0	0		0	0		0	0		0	0		0	0		0	0	
Black Cherry	23	122	18.85%	3.48	0.5085	0.0221	18	109	16.57%	0	5		1	2	50.00%	2	4	50.00%	0	0		2	2	100.00%	0	0		0	0	
White Oak	0	1	0.00%	0.00	0.0000	0.00000	0	0		0	0		0	0		0	0		0	0		0	1		0	0		0	0	
Chinkapin Oak	0	4	0.00%	0.00	0.0000	0.00000	0	0		0	1		0	0		0	0		0	0		0	0		0	0		0	0	
Northern Red Oak	1	6	16.67%	0.15	0.4935	0.4935	0	0		0	0		0	0		0	0		0	3		0	0		0	1		1	100.00%	
Sassafras	8	23	34.78%	1.21	0.1730	0.0216	4	12	33.33%	0	0		2	5	40.00%	2	5	40.00%	0	1		0	0		0	0		0	0	
Basswood	0	1	0.00%	0.00	0.0051	0.00000	0	1		0	0		0	0		0	0		0	0		0	0		0	0		0	0	
American Elm	16	34	47.06%	2.42	0.2498	0.0156	13	30	43.33%	1	2	50.00%	0	0		0	0		2	2	100.00%	0	0		0	0		0	0	
Slippery Elm	48	167	28.74%	7.27	0.4038	0.0084	41	158	25.95%	3	5	60.00%	2	2	100.00%	1	1	100.00%	1	1	100.00%	0	0		0	0		0	0	

DS (# of Dead Stems in Current Census); LS (# of Living Stems in Previous Census); OMR (Overall Mortality Rate); DPH (Density per ha); TBA (Total Basal Area of Dead Stems); ABA (Average Basal Area of Dead Stems); A (Dead Stems in 10-19.9 cm dbh Size-class); AA (Living Stems in 10-19.9 cm dbh Size-class); AA' (Mortality Rate); B (Dead Stems in 20-29.9 cm dbh Size-class); BB (Living Stems in 20-29.9 cm dbh Size-class); %B (Size-class 'B' Mortality Rate); C (Dead Stems in 30-39.9 cm dbh Size-class); CC (Living Stems in 30-39.9 cm dbh Size-class); %C (Size-class 'C' Mortality Rate); D (Dead Stems in 40-49.9 cm dbh Size-class); DD (Living Stems in 40-49.9 cm dbh Size-class); %D (Size-class 'D' Mortality Rate); E (Dead Stems in 50-59.9 cm dbh Size-class); EE (Living Stems in 50-59.9 cm dbh Size-class); %E (Size-class 'E' Mortality Rate); F (Dead Stems in 60-69.9 cm dbh Size-class); FF (Living Stems in 60-69.9 cm dbh Size-class); %F (Size-class 'F' Mortality Rate); G (Dead Stems in 70-79.9 cm dbh Size-class); GG (Living Stems in 70-79.9 cm dbh Size-class); %G (Size-class 'G' Mortality Rate); H (Dead Stems in 80+ cm dbh Size-class); HH (Living Stems in 80+ cm dbh Size-class); %H (Size-class 'H' Mortality Rate)



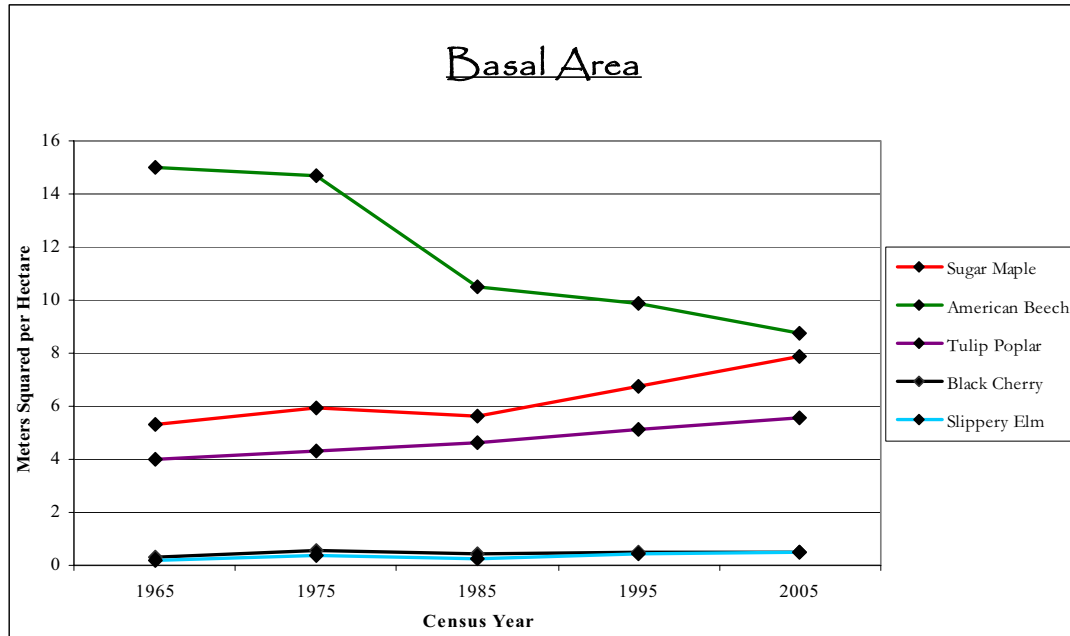
**Table 4.12 – Absolute & Relative Frequency 1965-2005, Hoot Woods, Indiana**

Frequency										
Species	1965 Census		1975 Census		1985 Census		1995 Census		2005 Census	
	FRQY	R-FRQY	FRQY	R-FRQY	FRQY	R-FRQY	FRQY	R-FRQY	FRQY	R-FRQY
Box Elder	0.00%	0.00%	0.0%	0.00%	0.0%	0.00%	0.0%	0.00%	0.5%	0.15%
Black Maple	0.00%	0.00%	0.5%	0.17%	0.5%	0.19%	0.5%	0.16%	0.5%	0.15%
Red Maple	0.00%	0.00%	1.6%	0.51%	1.0%	0.37%	1.6%	0.47%	1.6%	0.46%
Sugar Maple	86.72%	29.21%	88.0%	28.69%	92.2%	32.84%	94.3%	28.59%	97.9%	28.88%
Redbud	0.00%	0.00%	0.0%	0.00%	0.0%	0.00%	0.5%	0.16%	0.0%	0.00%
Ironwood	0.78%	0.26%	1.6%	0.51%	0.5%	0.19%	1.0%	0.32%	3.1%	0.92%
Hackberry	2.34%	0.79%	3.1%	1.02%	2.6%	0.93%	2.1%	0.63%	1.0%	0.31%
Dogwood	0.78%	0.26%	2.6%	0.85%	5.7%	2.04%	7.3%	2.21%	0.5%	0.15%
Pignut Hickory	1.56%	0.53%	1.0%	0.34%	0.5%	0.19%	0.5%	0.16%	0.5%	0.15%
Bitternut Hickory	2.34%	0.79%	5.2%	1.70%	5.2%	1.86%	7.3%	2.21%	7.3%	2.15%
Shagbark Hickory	7.03%	2.37%	4.7%	1.53%	4.2%	1.48%	3.6%	1.11%	3.6%	1.08%
White Ash	14.06%	4.74%	7.8%	2.55%	7.3%	2.60%	7.3%	2.21%	5.7%	1.69%
American Beech	88.28%	29.74%	88.5%	28.86%	76.0%	27.09%	76.0%	23.06%	71.4%	21.04%
Green Ash	11.72%	3.95%	11.5%	3.74%	9.9%	3.53%	9.4%	2.84%	8.3%	2.46%
Black Walnut	4.69%	1.58%	4.2%	1.36%	2.6%	0.93%	1.6%	0.47%	1.6%	0.46%
Tulip Poplar	39.84%	13.42%	37.5%	12.22%	33.3%	11.87%	38.5%	11.69%	41.1%	12.14%
Black Gum	2.34%	0.79%	3.1%	1.02%	2.6%	0.93%	3.1%	0.95%	4.2%	1.23%
Hop Hornbeam	0.78%	0.26%	1.0%	0.34%	0.5%	0.19%	1.6%	0.47%	2.1%	0.61%
Black Cherry	5.47%	1.84%	8.3%	2.72%	6.8%	2.41%	14.6%	4.42%	15.6%	4.61%
White Oak	0.78%	0.26%	2.1%	0.68%	0.5%	0.19%	0.5%	0.16%	0.5%	0.15%
Chinkapin Oak	2.34%	0.79%	2.1%	0.68%	2.1%	0.74%	1.6%	0.47%	1.6%	0.46%
Northern Red Oak	3.13%	1.05%	4.7%	1.53%	3.6%	1.30%	3.1%	0.95%	2.6%	0.77%
Sassafras	10.94%	3.68%	13.0%	4.24%	7.3%	2.60%	10.4%	3.16%	16.1%	4.76%
Basswood	0.00%	0.00%	0.0%	0.00%	0.5%	0.19%	0.5%	0.16%	0.0%	0.00%
American Elm	3.91%	1.32%	4.2%	1.36%	5.2%	1.86%	12.0%	3.63%	16.7%	4.92%
Slippery Elm	7.03%	2.37%	10.4%	3.40%	9.9%	3.53%	30.7%	9.32%	34.9%	10.29%



**Figure 4.5 – Changes in Density of Five Important Species, Hoot Woods, Indiana**





**Figure 4.6 – Changes in Basal Area of Five Important Species, Hoot Woods, Indiana**

ranging from 3.0% to 25.2% (Tables 4.8, 4.9, 4.10, & 4.10).

Tulip poplar is the third most important tree species in Hoot Woods, and has remained consistent in abundance, dominance, frequency, and importance throughout the study (Tables 4.1, 4.2, 4.3, & 4.12 & Figures 4.5 & 4.6). Ingrowth figures oscillated between censuses, from 0.7 in 1975, to 0.5, 4.7, and 2.4 in 1985, 1995, and 2005 (Tables 4.4, 4.5, 4.6, 4.7). Tulip poplar performed steadily in terms of stand importance, alternately rising and falling by a half or full percentage point from decade to decade (Table 4.1) The spatial distribution of tulip poplar survivors changed relatively little from census to census (Figure 4.9). Structurally, tulip poplar reproduction differed by census year (Figure 4.3). The structure curves for 1965, 1975, and 1985 are multimodal, indicating a species characterized by pulse reproduction. But for 1995 and 2005, the distribution is seemingly negative exponential. Based on its size diagrams, tulip poplar

# ***Hoot Woods***

## *Spatial Distribution of Survivors, Ingrowths & Mortalities*

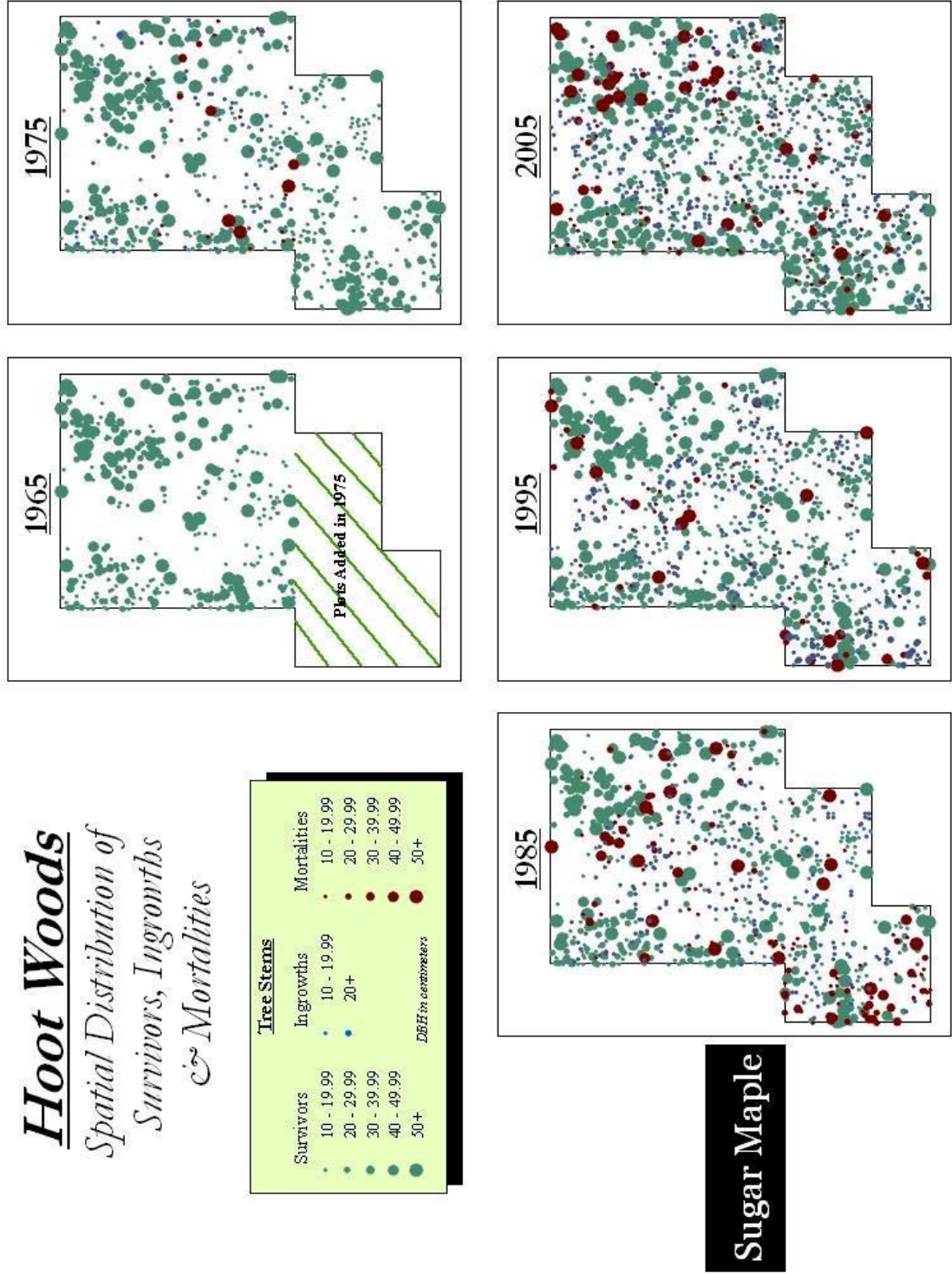
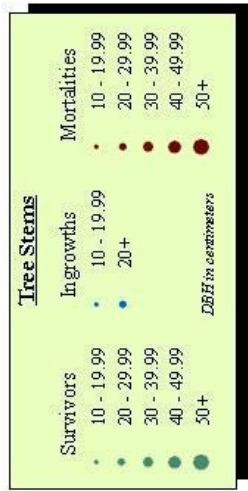


Figure 4.7 – Map of Sugar Maple Tree Stem Locations, Hoot Woods, Indiana

appears to be a species capable of maintaining itself at present levels.

### Tornado Disturbance

The 1980 tornado disturbance had a major impact on stand composition, structure, and spatial pattern. Compositionally, the period from 1975 to 1985 shows the greatest changes in composition (Tables 4.2 & 4.3). All tree species declined in density between 1975 and 1985 except for sugar maple, dogwood, basswood, and American elm. All species declined in basal area except dogwood, hackberry, shagbark hickory, white ash, green ash, tulip poplar, chinquapin oak, and basswood. Very few slippery elm or black cherry stems were recorded during the earliest censuses, but both species surged in the final two censuses. Slippery elm reproduction surged during the second half of the study (Figures 4.8). It is difficult to predict if its size structures represent an emerging trend or an anomaly because few stems exist in the large size classes. The majority of slippery elm ingrowths occurred in the center of the stand in 1995 to 2005 (Figure 4.10). Black cherry ingrowths were clustered in the southwestern portion of the stand, presumably a delayed effect from the 1980 tornado (Figure 4.11). The ascension of slippery elm and black cherry culminated in 2005 importance values of 6.7% and 4.3% (Table 4.1). Similarly, American elm became more frequent throughout the stand in the years following the tornado (Table 4.12).

### Minor Species

Hackberry and sassafras are notable for their consistent reproduction and importance levels (Table 4.1 & Figures 4.8 & 4.13). Sassafras maintained frequency

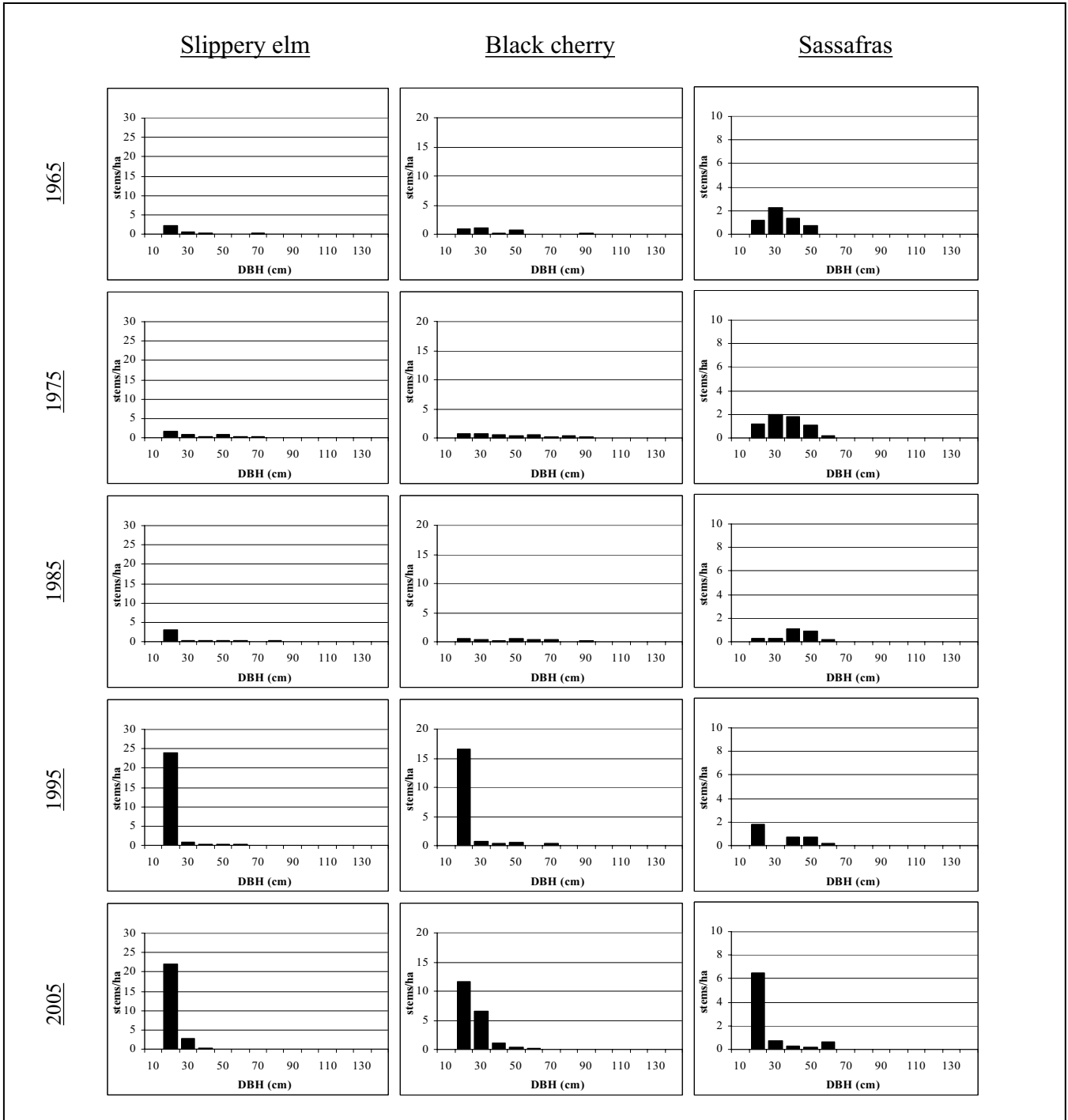


Figure 4.8 – Size Distributions for Slippery elm, Black cherry, & Sassafras

# *Hoot Woods*

## *Spatial Distribution of Survivors, Ingrowth & Mortalities*

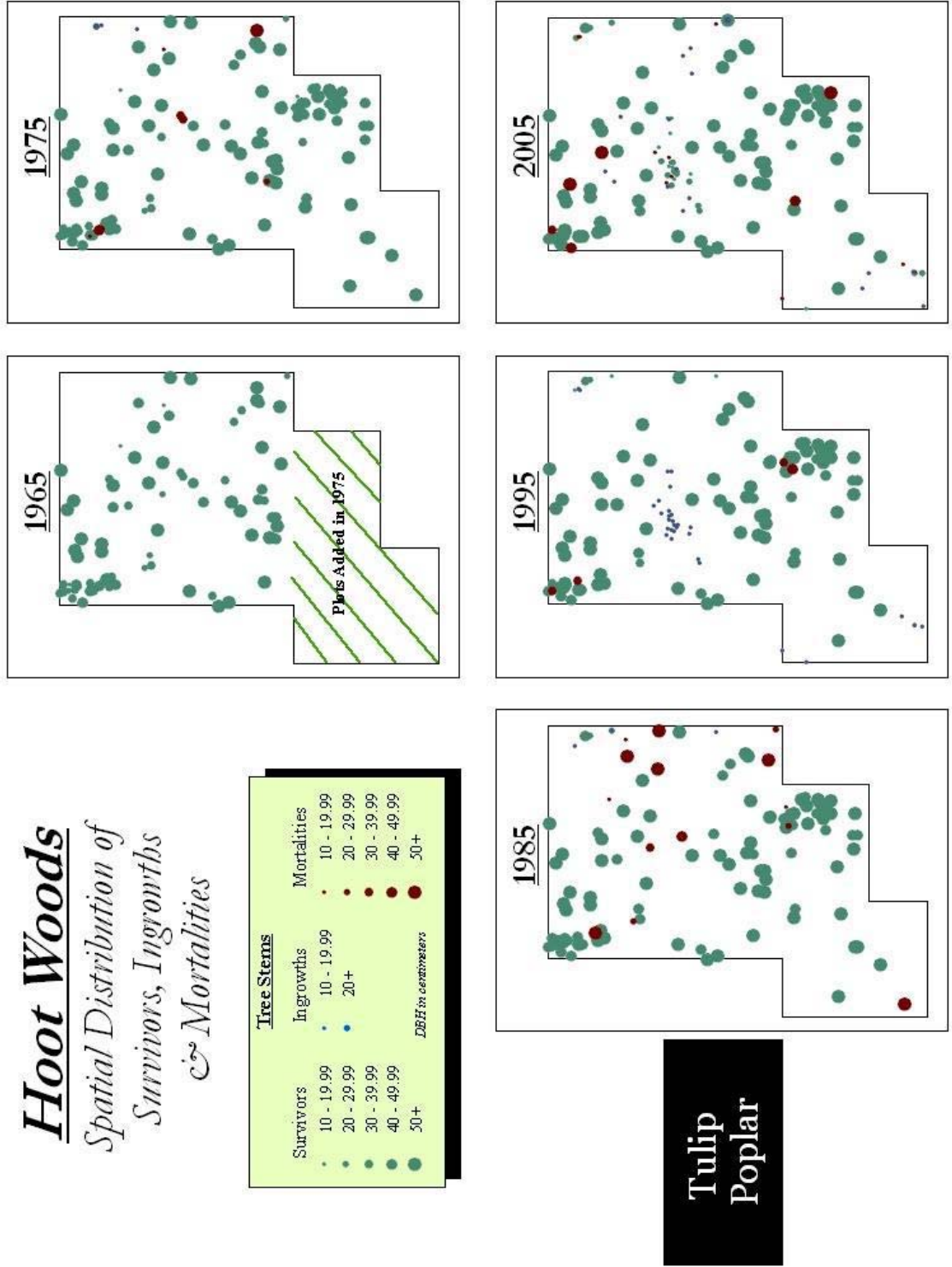
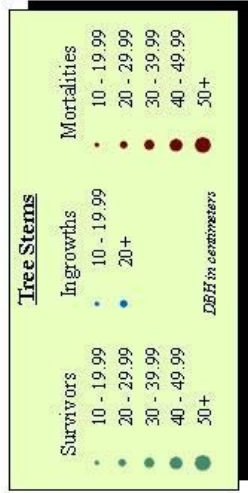


Figure 4.9 – Map of Tulip Poplar Tree Stem Locations, Hoot Woods, Indiana

# *Hoot Woods*

## *Spatial Distribution of Survivors, Ingrowth & Mortalities*

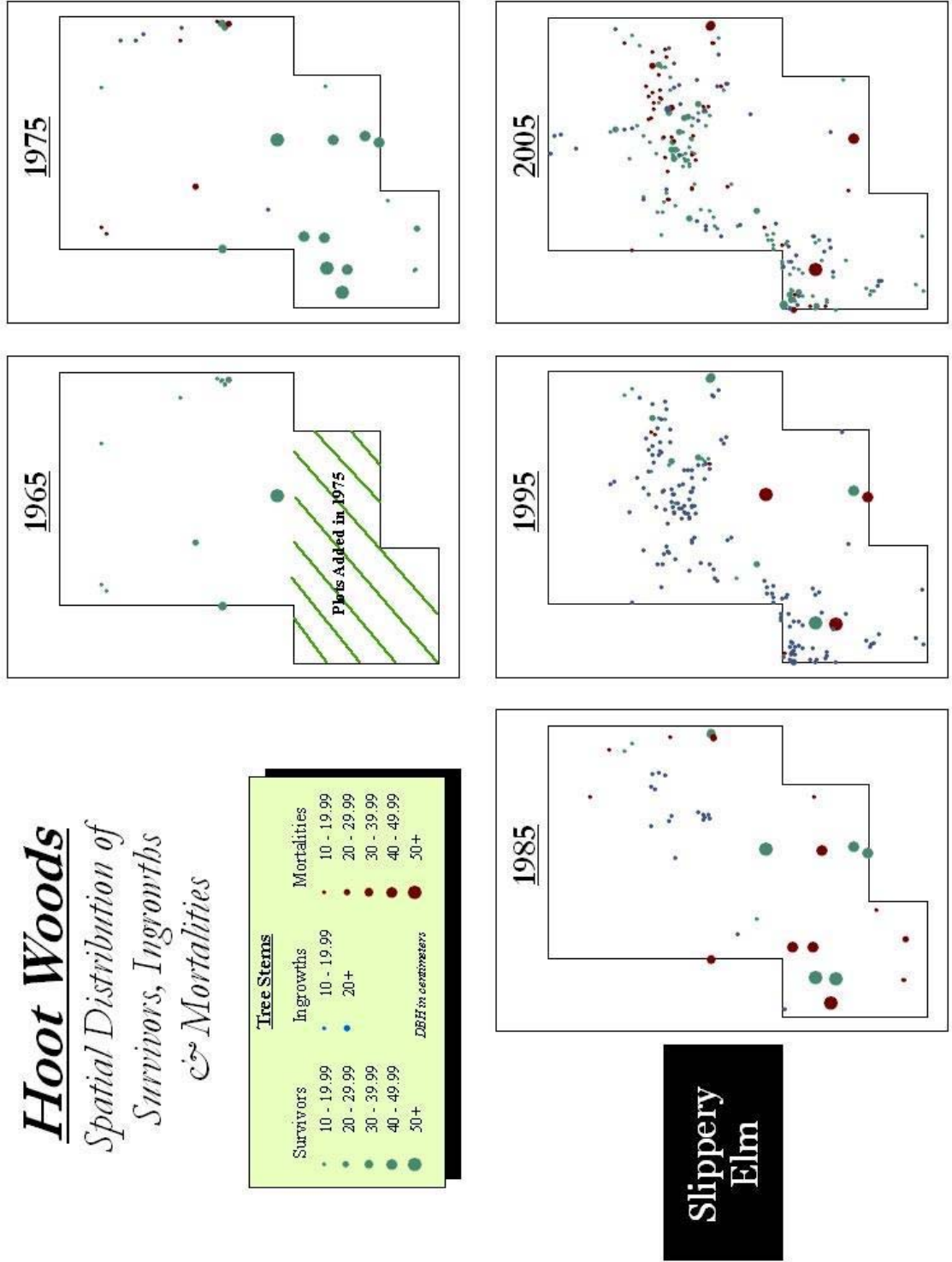
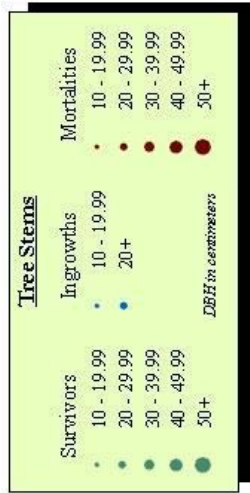


Figure 4.10 – Map of Slippery Elm Tree Stem Locations, Hoot Woods, Indiana

# *Hoot Woods*

## *Spatial Distribution of Survivors, Ingrowth & Mortalities*

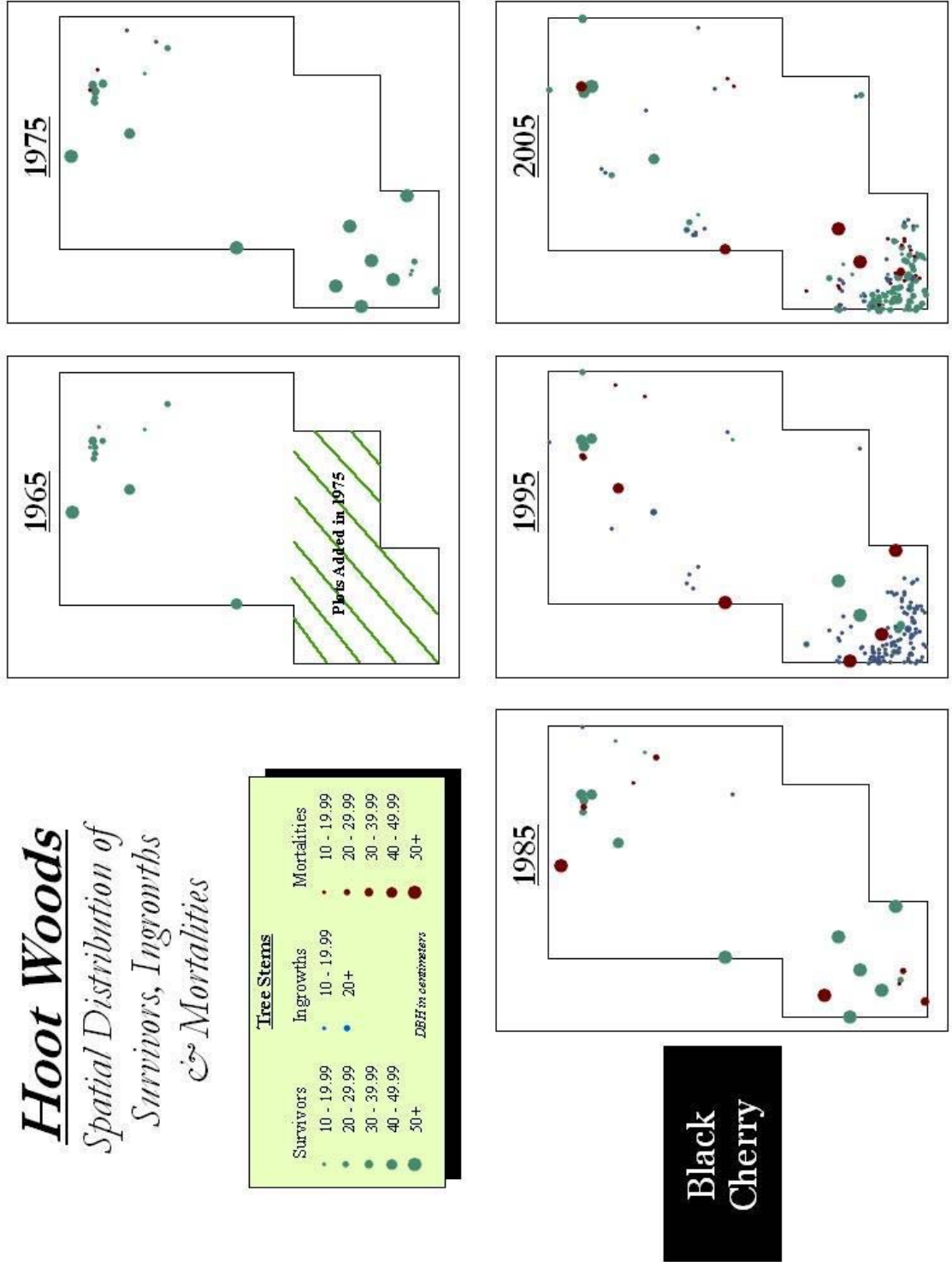
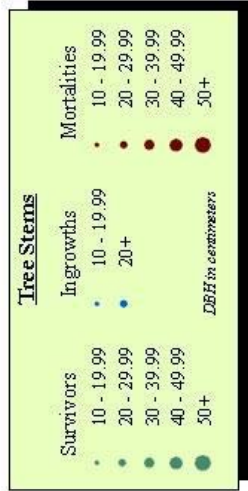


Figure 4.11 – Map of Black Cherry Tree Stem Locations, Hoot Woods, Indiana

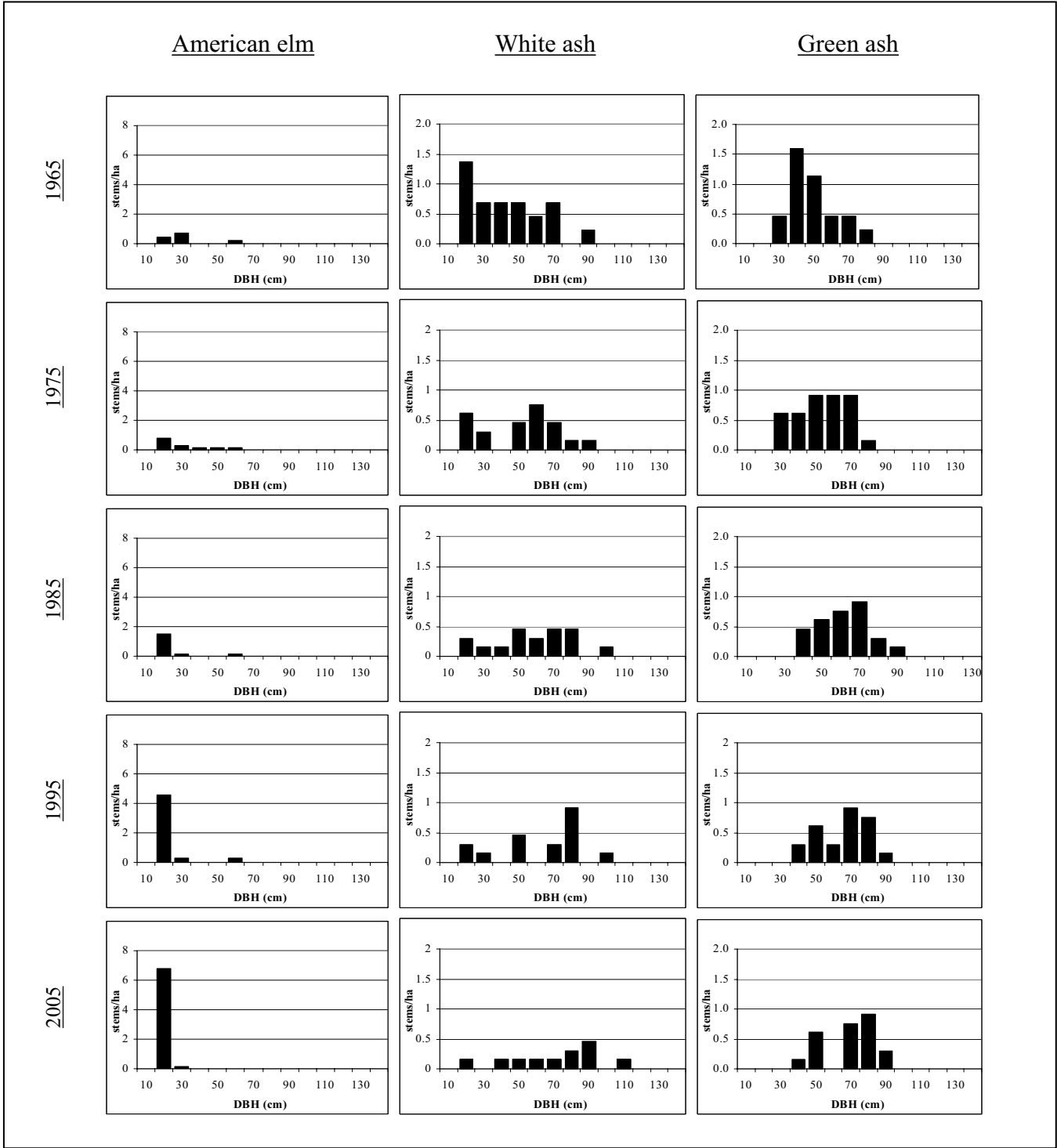


Figure 4.12 – Size Distributions for American elm and White & Green ash



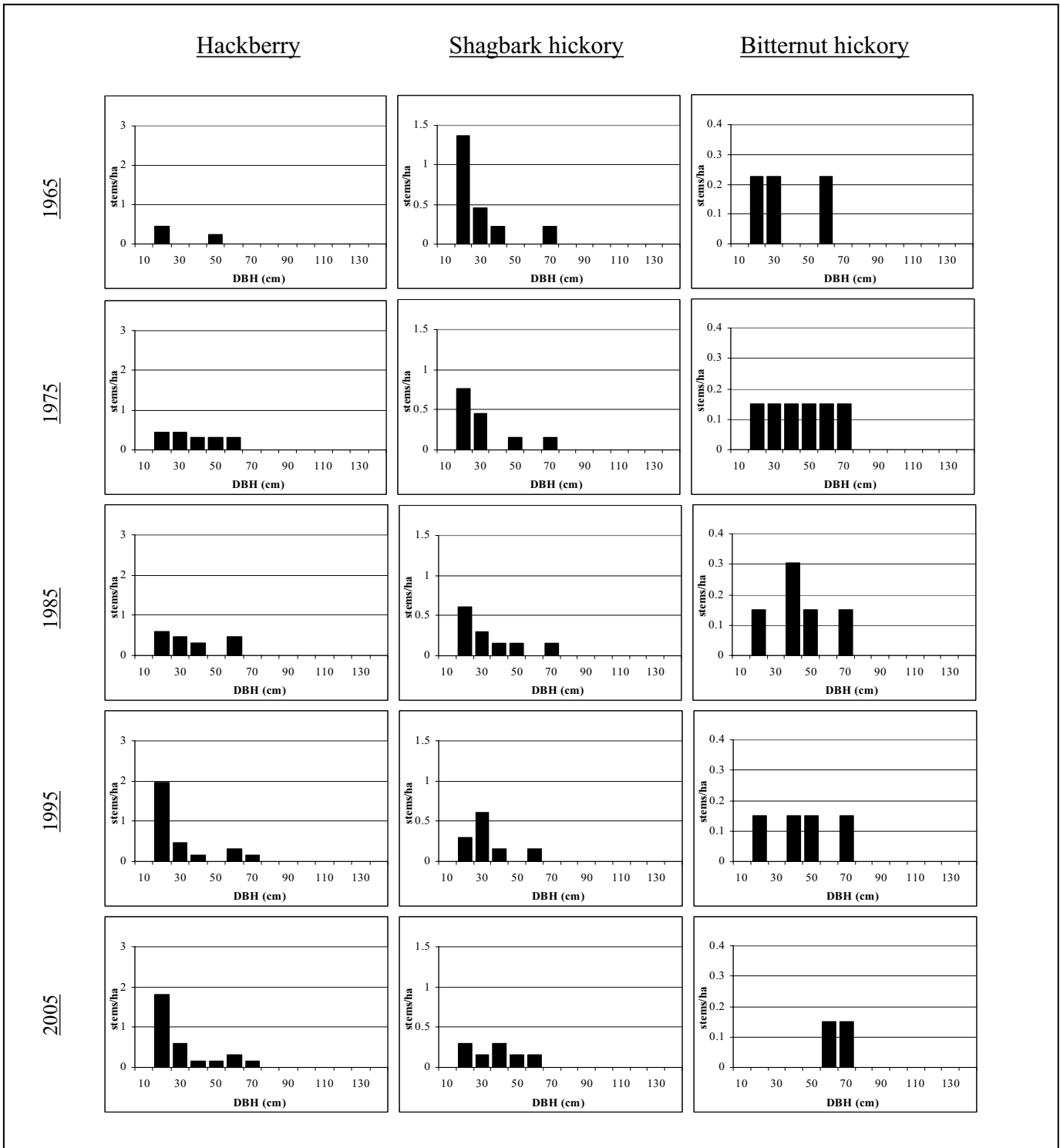


Figure 4.13 – Size Distributions for Hackberry and Shagbark & Bitternut hickory

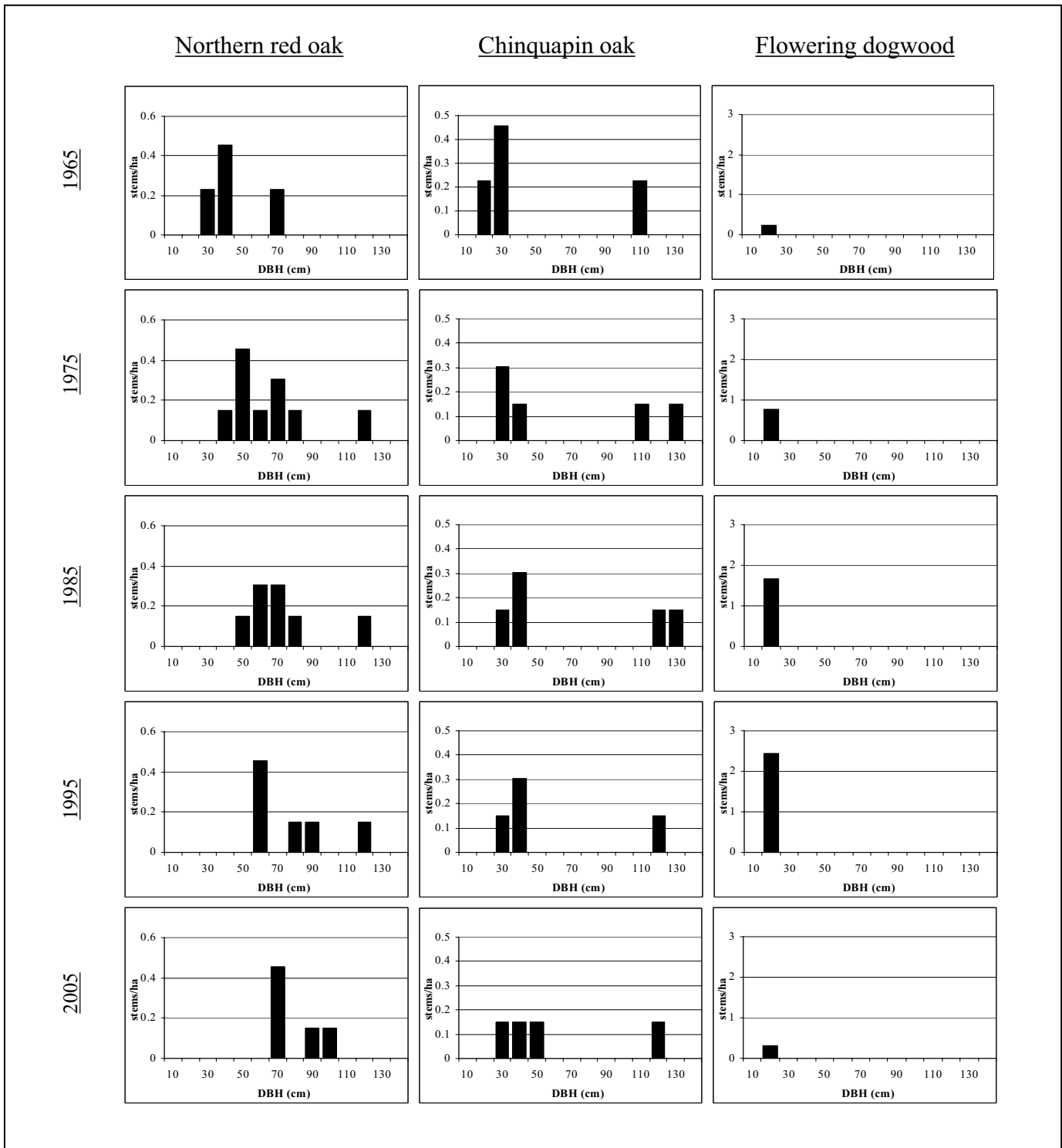


Figure 4.14 – Size Distributions for Northern red & Chinquapin oak and Dogwood

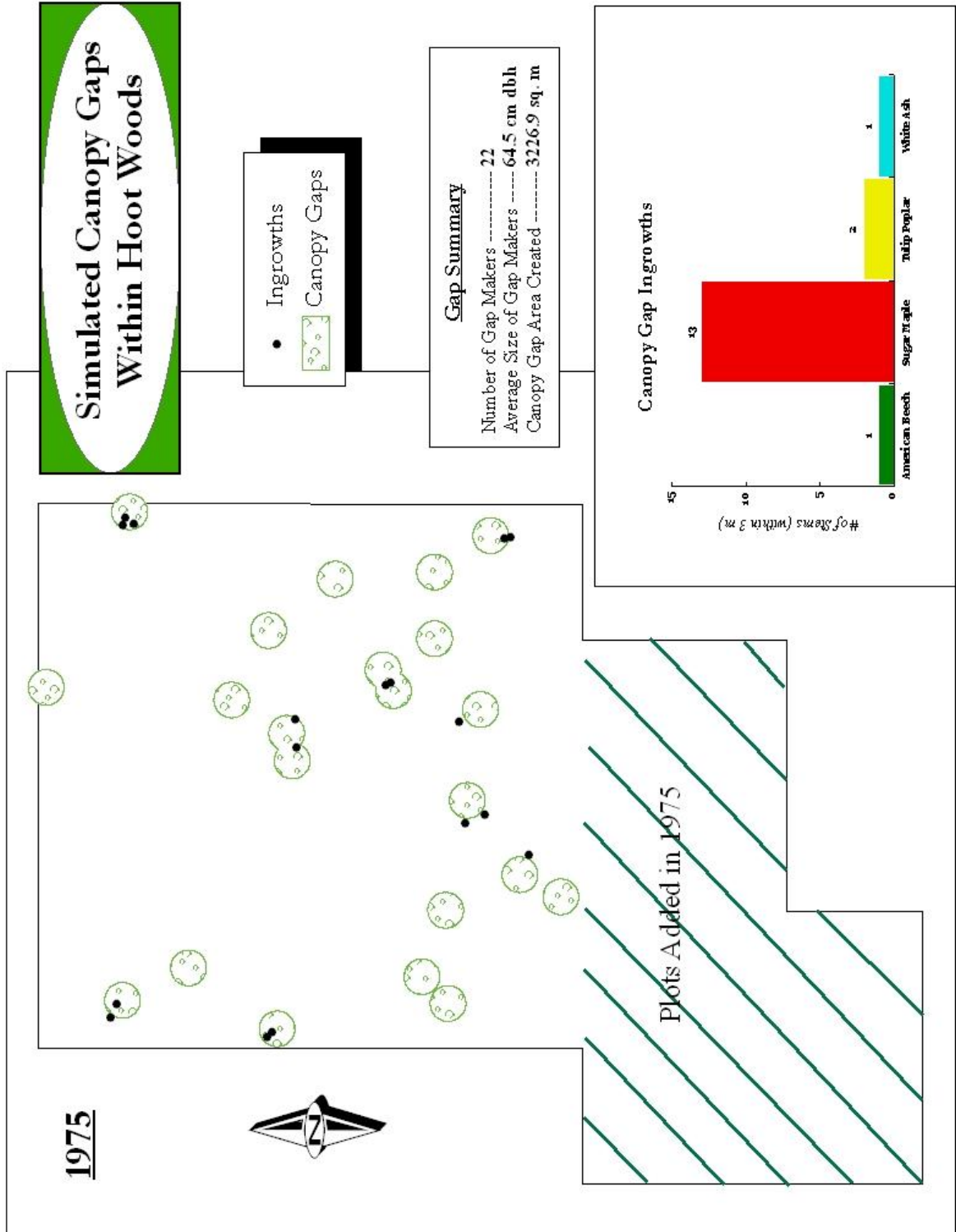


Figure 4.15 – Map of Estimated Canopy Gaps in 1975, Hoot Woods, Indiana

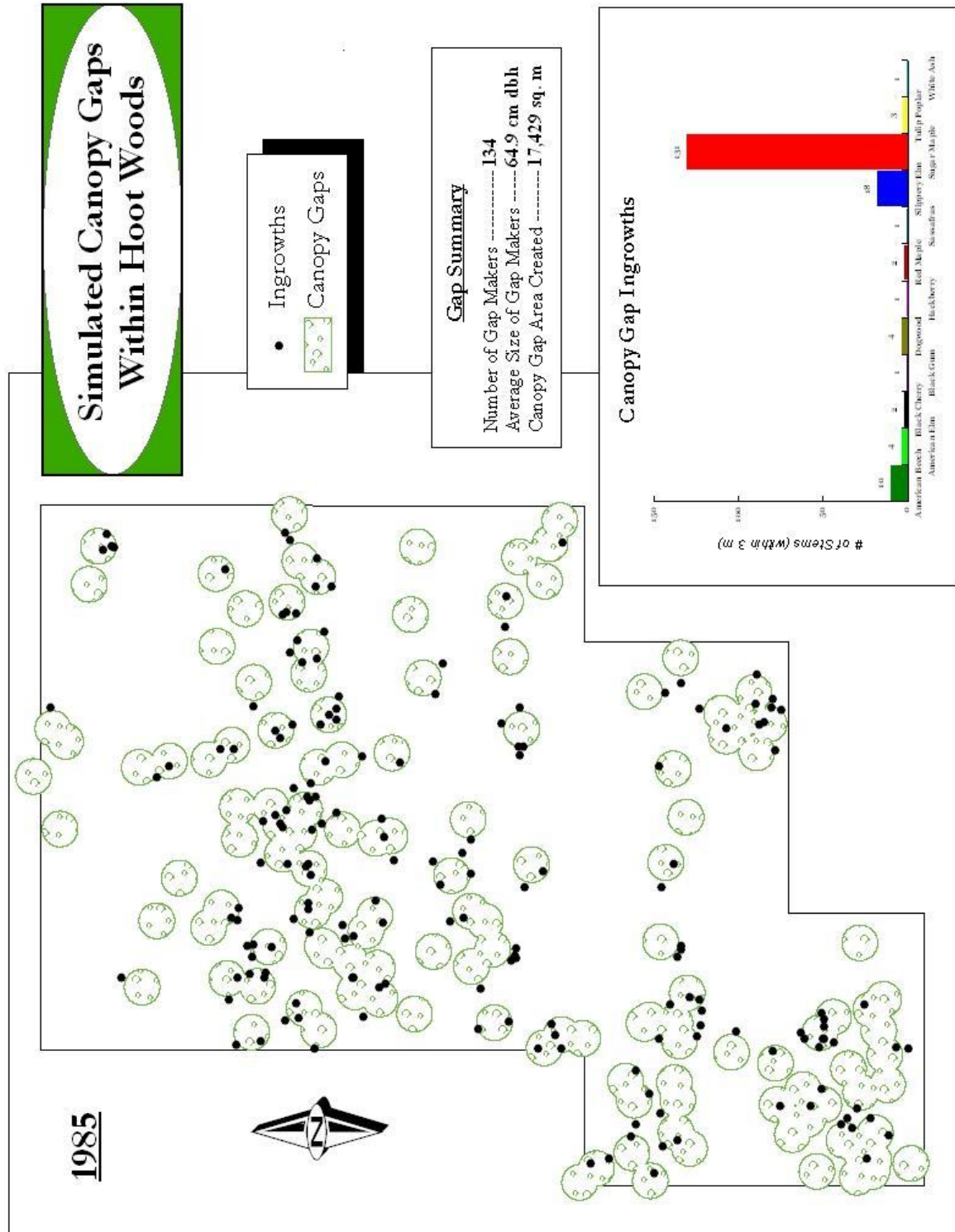


Figure 4.16 – Map of Estimated Canopy Gaps in 1985, Hoot Woods, Indiana



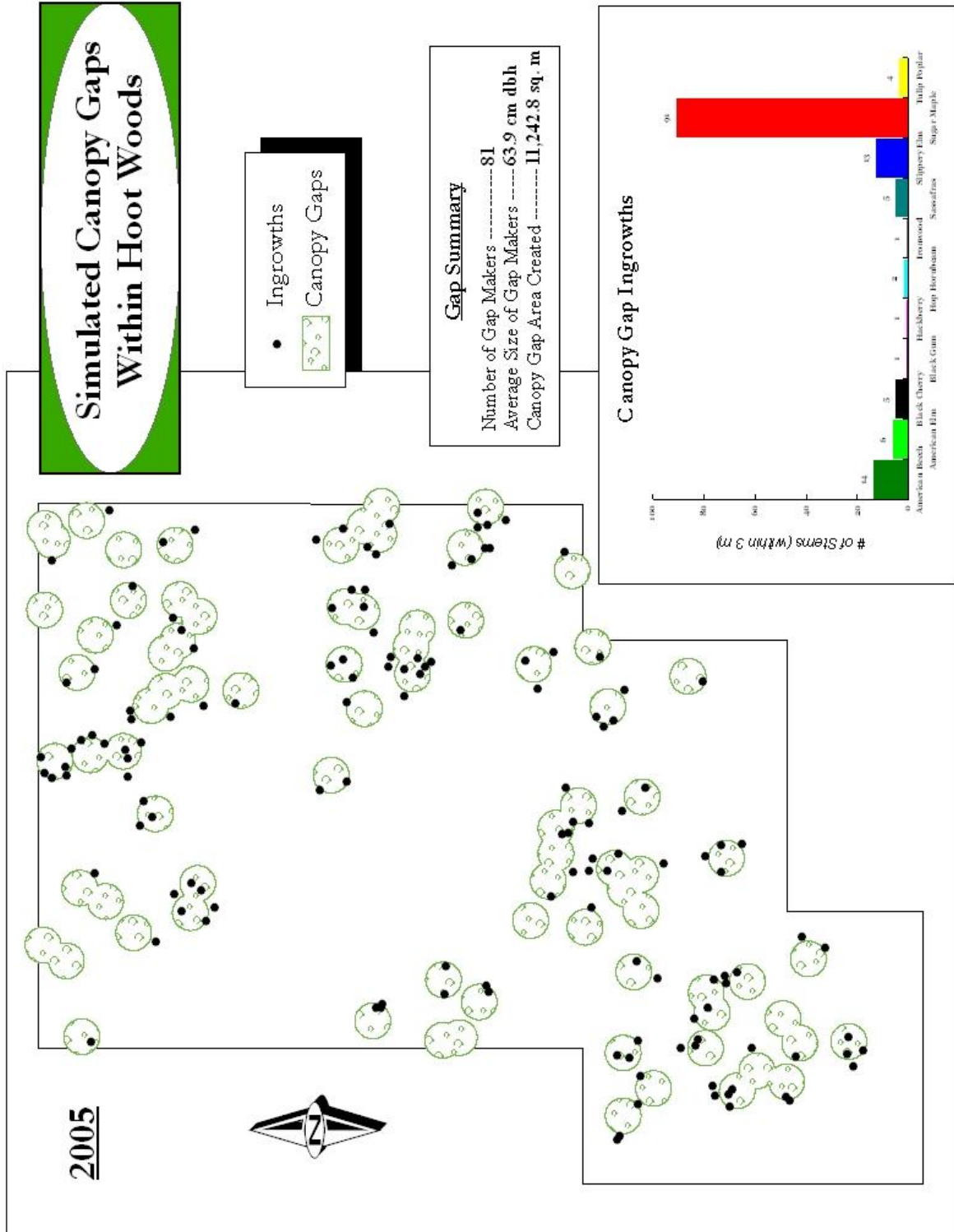


Figure 4.18 – Map of Estimated Canopy Gaps in 2005, Hoot Woods, Indiana

levels around 9% until the last census, when it increased to 16.1%. Other minor species are notable for recent or steady declines. As a group, hickories performed the most poorly (Figure 4.13). Bitternut, pignut, and shagbark declined in density to 0.3, 0.1, and 1.1 stems/ha (Table 4.2). Pignut and shagbark hickory declined in basal area until the last census, when both rose slightly (Table 4.12). Bitternut hickory increased in basal area over the course of the study, owing to a significant increase during the first decade interval. But it has declined ever since (Table 4.3). White and green ash also progressively declined over the course of the study (Figures 4.12). Importance values for white, chinquapin, and northern red oak remained quite low throughout the study (Table 4.1). White oak declined in density and basal area from 1975 to 1985, due to the death of several large individuals caused by the tornado (Tables 4.2 & 4.3). The majority of remaining oak trees are in the large size classes, which suggests that these species are relicts of recruitment that occurred in the distant past (Figure 4.14). Once the few remaining standard bearers give way, oaks may recede permanently from Hoot Woods. Dogwood is characterized by an overall small number of stems and a size structure that suggests either a declining or static population (Figure 4.14). An emergence or resurgence in the canopy representation of any of these species appears unlikely.

#### Local Environmental Conditions

Gap-phase dynamics and local climate played no appreciable role in the decline of beech. Figures 4.15, 4.16, 4.17, and 4.18 illustrate the spatial relationship between canopy gaps and ingrowths. Unlike the scenario envisioned by Williamson (1975), sugar maple is the species that capitalizes on the extra light resources afforded by canopy gaps.

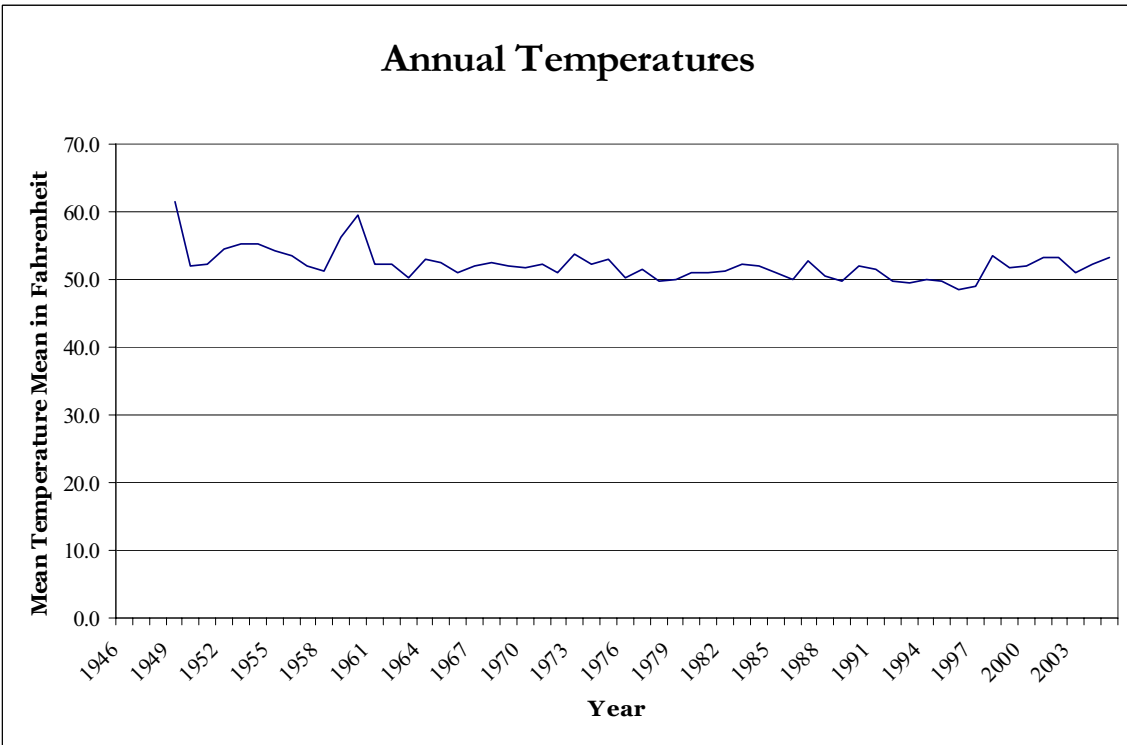
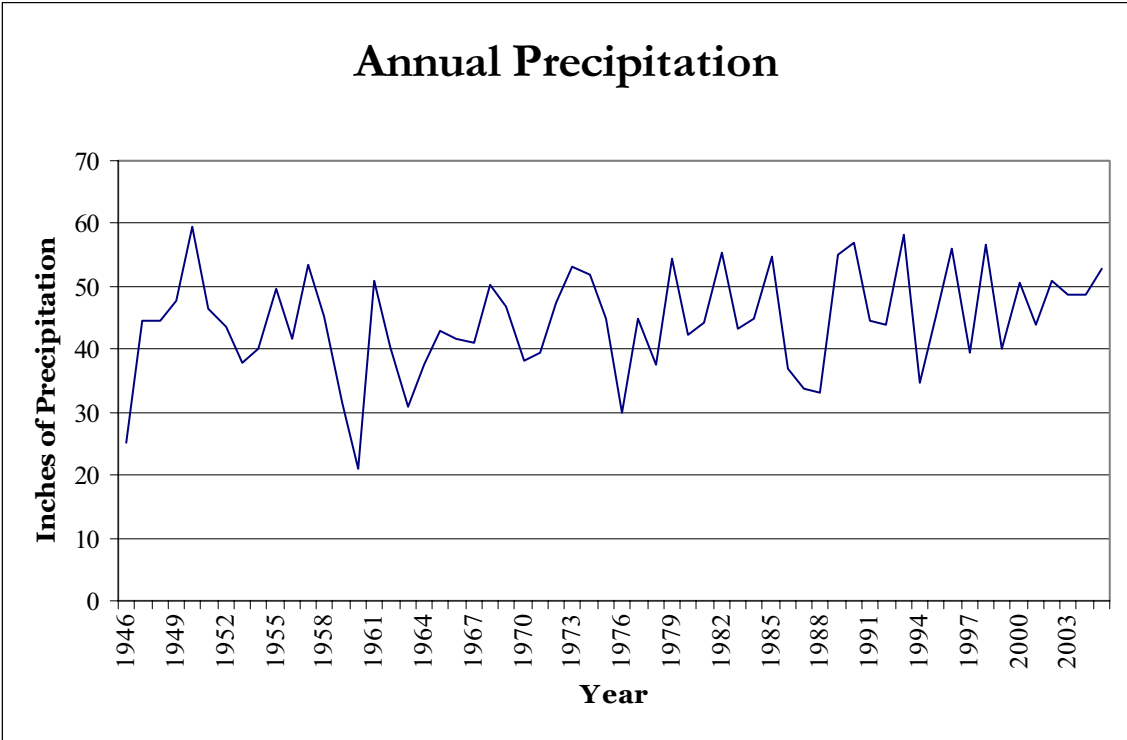


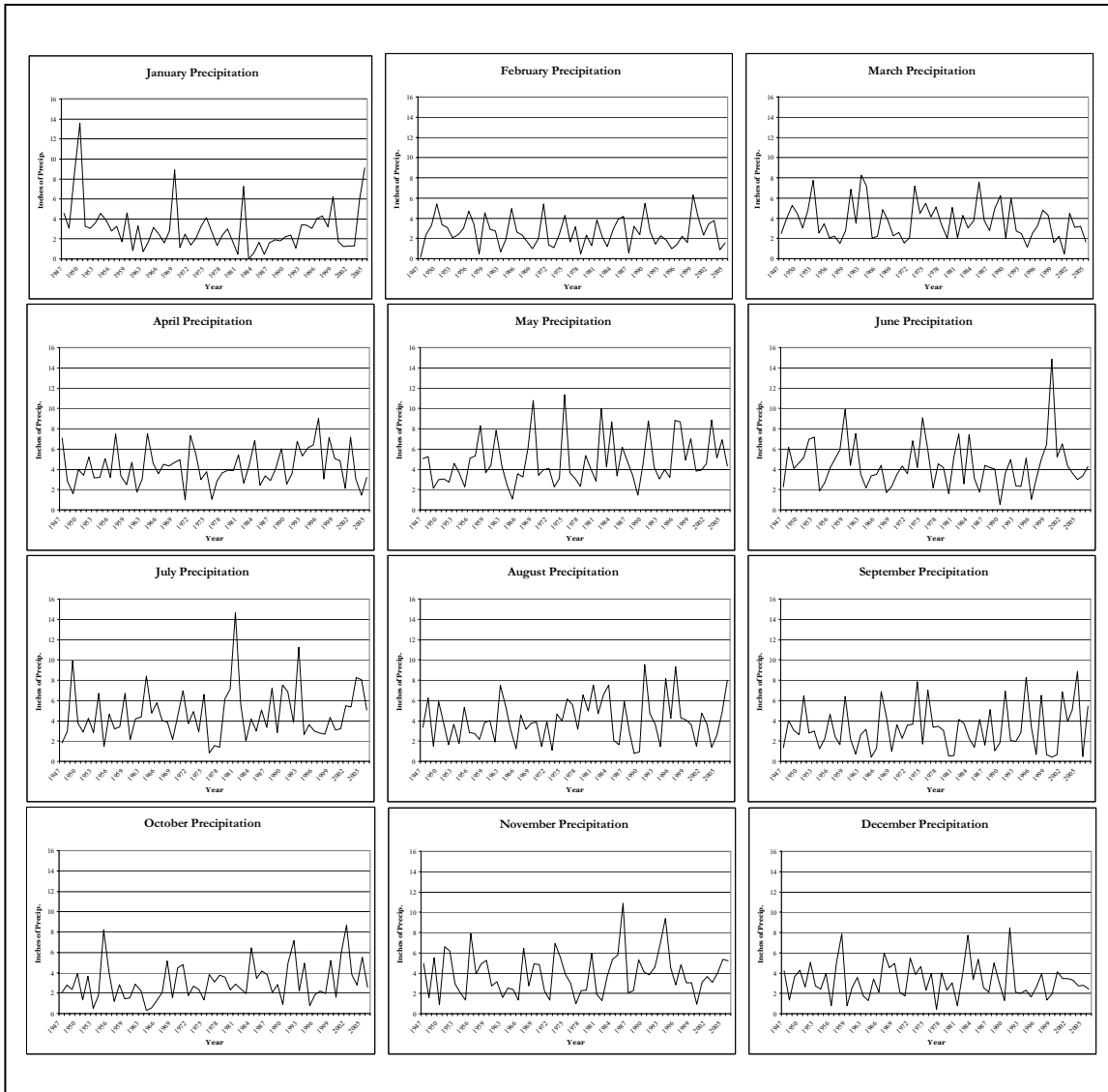
Figure 4.19 - Annual Precipitation & Temperature 1946-2005, Spencer, Indiana



Seventeen ingrowths occurred within simulated canopy gaps for 1975. Thirteen were sugar maple and one was beech. Early seral tree species that Williamson believed would reproduce in light gaps, such as tulip poplar and white ash, fared poorly. Tulip poplar had two ingrowths, while white ash had only one (Figure 4.15). Canopy gap area increased steeply to 17,429 m<sup>2</sup> in 1985 as a result of the 1980 tornado. This time, sugar maple accounted for 131 ingrowths. Slippery elm and the codominant beech trailed far behind with 18 and 10 stems respectively. Once again, white ash was represented by only a single tree. Other shade intolerant species, such as sassafras, fared poorly (Figure 4.16). Canopy gap area and total number of ingrowths declined in 1995, but the pattern of sugar maple dominance continued. Black cherry and slippery elm ingrowths increased during this census. Tulip poplar made its finest showing in the canopy gaps with 11 stems for 1995. American beech was fairly well represented with 12 stems (Figure 4.17). In 2005, sugar maple was once again the most prevalent species, with 91 stems recorded. Beech made the second strongest showing with 14 stems (Figure 4.18).

Few tulip poplar ingrowths occurred in canopy gaps. For 1975, 1985, 1995, and 2005, the percentage of ingrowths occurring in gaps was 66.6, 100, 35.5, and 25.0, respectively. The high percentages for 1975 and 1985 are misleading because the overall number of ingrowths in both those years was paltry. When the number of ingrowths increased in 1995, the proportion dropped. Over the course of the study, 37.7% of the 53 tulip poplar ingrowths occurred in canopy gaps. Perhaps this is an indication that tulip poplar is a versatile competitor, suited to capitalizing on both gap-phase and major windthrow disturbance.

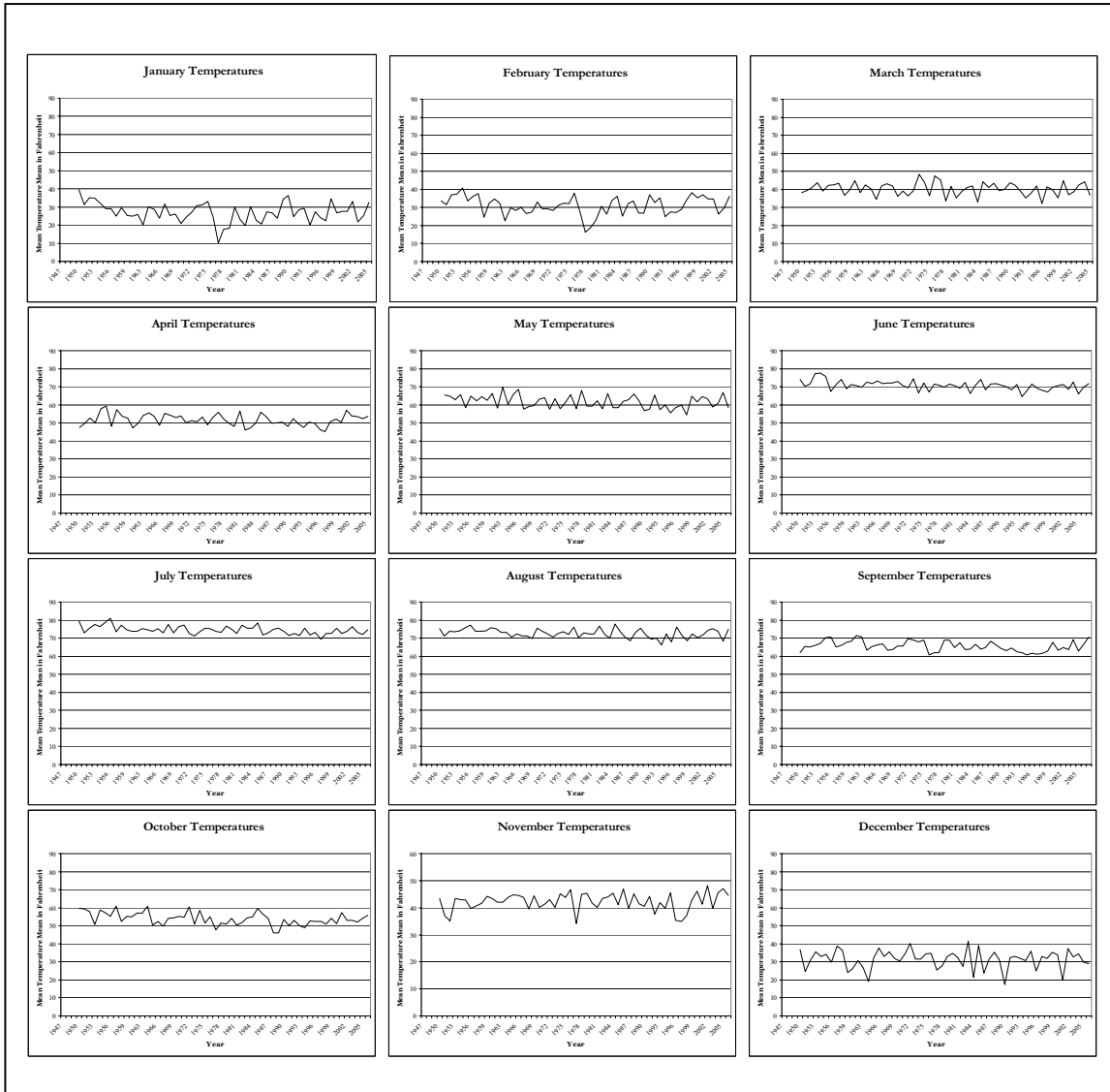
To evaluate environmental change theories, atmospheric information was acquired from the National Climatic Data Center. Three weather stations have been in operation since 1946 at Spencer, Indiana, the town situated a few miles northeast of Hoot



**Figure 4.20 – Monthly Precipitation 1946-2005, Spencer, Indiana**

Woods. The first two stations ran for a combined 3½ years and collected data only on precipitation. In June of 1949, the present, and more modern monitoring station came online. Station three collects more detailed information, including temperature records.

Unfortunately, because of either a mechanical failure with the station or an error in record keeping, 13 entries were missing from the climate dataset. Five of these errors involved an existing, but incomplete record. In June of 1956, no value for monthly precipitation



**Figure 4.30 – Monthly Temperatures 1946-2005, Spencer, Indiana**

was available. In November of 1953 and 1956, August of 1957, and June of 1966 no value for mean temperature mean was available. In the eight other instances of missing data, the complete record was absent. In October, November, and December of 1959,

January, February, March, April, and May of 1960, and July of 1986 this situation was the case. These omissions were dealt with in one of two fashions. For the former type of mistake, a replacement value was estimated by averaging the precipitation or temperature values of the month prior and subsequent to the missing data value. For the latter group of errors, no recourse was sought. These records are simply missing and presumed lost. While these qualifiers should be taken into account when interpreting Figures 4.19, 4.20, and 4.21, the effect is small given the extent of the data set. Out of 708 records, only 13 (1.8%) were incomplete.

Hoot Woods is situated very near the western limit of the species' geographical range and drought is thought to be particularly harmful to it. Previous literature has suggested that the growth of beech is associated with precipitation and temperature values for specific months of the year. Warm April temperatures and moist and moderate conditions in June and July favor beech (Friesner 1941; Tardif et al. 2001). But the climatic indicators for these months indicate no trends that would have hindered the success of beech (Figures 4.20 & 4.21). The annual averages for precipitation and temperature, likewise, reveal no clear change (Figure 4.19). If any trend at all can be said to exist, it is that the climate has become slightly cooler and moister.

### Summary

1. Stand density increased by nearly 100 stems/ha between 1965 and 2005. Stand basal area increased between 1985 and 2005 but has yet to reach to its 1975 high point.

2. The density, basal area, frequency, and importance of American beech has declined steadily over the course of the study period.
3. The density, basal area, frequency, and importance of sugar maple has increased rapidly over the course of the study period.
4. Tulip poplar has performed remarkably consistently according to all metrics of performance and appears likely to maintain its position as the stand's third most important species.
5. The 1980 tornado disturbance had a major impact on stand composition, structure, and spatial pattern. The disturbance eliminated a disproportionate number of large beech trees, enhanced the success of sugar maple, and increased the density of two minor tree species, slippery elm and black cherry.
6. Edaphic and physiographic controls, species migration, climate change, gap-phase dynamics, and several types of disturbance appear to have played no significant role in the decline of beech.

## CHAPTER FIVE

### DISCUSSION

Characteristics of old-growth forests are usually considered to be controlled by the integration of physiography, climate, and anthropogenic and natural disturbances. The precise causes and mechanisms that influence successional pathways are hard to identify (Bakker et al. 1996; Zhang et al. 2000). The long-term data collected for Hoot Woods suggest that present conditions result mainly from the interaction of natural disturbance and the biological attributes of specific tree species.

#### Succession & Climate Change

The successional theories advocated by Clements (1916) and Cowles (1899; 1901) appear to have only moderate utility in this investigation. Sugar maple is the prototypical late-seral species that succession theories predict as the dominant in older plant communities. But the cycles envisioned by Cowles poorly explain vegetation dynamics in Hoot Woods. Both Cowles and Clements expect vegetation change to occur gradually via slow species adaptations to climate or landform. Rather than slow transformations and stability, Hoot Woods' recent history is characterized by significant change.

Similarly, coexistence theories fail to explain present stand conditions (Vankat 1975; Pell & Mack 1977, Poulson & Platt 1997). Coexistence theories assume stability and contend that environmental heterogeneity promotes species coexistence rather than

competitive exclusion (Bakker et al. 1996). Poulson and Platt (1996) observed little change in composition in Warren's Woods and concluded that allogenic coexistence best explained the old-growth, beech-maple stand's dynamics. But successional pathways observed in Hoot Woods offer no suggestion, whatsoever, of coexistence.

Although beech and maple are a classical association, the species have responded very differently to the same environmental variables over the study period. The individualistic concept of plant communities developed by Gleason (1926) better withstands scrutiny. Gleason interpreted plant species as independent entities reacting uniquely to environmental variables. Recent observations of American beech and sugar maple in Hoot Woods, particularly in response to the 1980 tornado, can only be understood in the context of the stand's ecological and geographical history.

It is difficult to correlate the geographic boundaries of a specific tree species' range with climatic conditions. Limiting factors in one part of a species' range are often irrelevant in other portions. Ward (1958) lamented this predicament when he warned that the exact relationships between beech trees and climate in his Wisconsin study could only be revealed by macro- and microclimatic studies within individual forest stands. He described sugar maple reproduction in the southern portion of his study region as "decidedly superior" to beech. Sugar maple was present in all stands that beech occurred in and averaged higher importance values. In northern stands, sugar maple was present in all the same stands as beech, but its level of importance was less. Ward postulated that climate could account for the differences reported between study areas. In northern areas with more severe climatic regimes, beech often reproduces by sprouting and is more susceptible to ice damage. General climate trends for the nearby town of Spencer, IN

show no obvious reason to suggest that climate is driving the compositional change in Hoot Woods. But it warrants more detailed analysis, such as the micro- and macro-scale investigations suggested by Ward.

Braun's (1950) hypothesis that the southern beech-maple forest is undergoing long-term succession toward a western or mixed mesophytic forest is also not supported by the dynamics seen in Hoot Woods. The site was subjected to Illinoian glaciation and highly modified by the more recent Wisconsin ice sheets that cleared most of the beech-maple region of its native vegetation. If, at the very outset of succession towards the beech-maple association, the area was not devoid of vegetative life, then the species migration hypothesis carries less weight. Furthermore, the beech-maple association's existence on a disparate array of topography and soils is indication that edaphic and physiographic controls can be safely dismissed as important controllers of stand dynamics in Hoot Woods.

#### Allogenic Factors

Due to characteristics of the stand, a number of allogenic factors can be eliminated out of hand as possible reasons for American beech's decline. Although situated in an agricultural matrix, anthropogenic alteration of adjacent lands is an unlikely source of present stand conditions. According to stand records, most of the disturbance agents thought to be detrimental to beech have never affected Hoot Woods. Neither GLO land notes nor the oral history of the woods gives any indication that fire has been a major determinant of stand structure or composition during the past century. Pests such as gypsy moths are not to blame for the decline in beech either. There is no evidence of



the insect's existence within the stand and research indicates that it prefers several tree species, including sugar maple, ahead of beech. Likewise, deer are not the cause of beech's fallen status. No significant levels of tree predation by these herbivores have been observed in the forest. Beech-bark disease has yet to reach the stand. But when this event eventually transpires, the effects on the diminishing beech population will likely be devastating. A highly destructive tornado struck the stand in August of 1980. This high-intensity disturbance allowed a handful of minor species to succeed. Rather than promote species diversity though, the tornado helped consolidate sugar maple's stand control.

#### Autogenic Factors

In old-growth forests, future changes in species composition are often best indicated by the success of species' regeneration in the understory. The need for light is often a preeminent control of stand dynamics. Species tolerance to suppression and shade, competitive success in canopy openings, and response to variations in the physical environment are expressed by size-class data (Schmelz et al. 1974; Pell & Mack 1977). Beech and sugar maple have long been considered near equals in terms of their tolerance of low light conditions, but examination of size-class distributions for Hoot Woods reinforces the impression that the recent success of sugar maple in Hoot Woods was made at the expense of beech. Sugar maple dwarfs beech in number of stems in the small size classes.

Canopy gaps were estimated for the purposes of understanding the regeneration and recruitment of tree species occurring in the openings, particularly sugar maple versus relatively shade intolerant species. The average canopy gap initiation rate for

undisturbed, broadleaf stands in the eastern United States is 0.5% to 1% (Runkle 1982). Given the extra light resources afforded, it is logical to assume that ingrowths will be clustered around canopy gaps. However, the results of this analysis suggest that the nature of this presumed relationship is more complex than previously thought.

Although substantial ingrowth occurs in the estimated canopy gaps, the species composition within gaps defies easy explanation. Early seral, shade intolerant, tree species were less prevalent in the canopy openings than late seral species. Sugar maple colonized the majority of gap areas, thus increasing its proliferation. Beech ingrowth in canopy gaps occurred in moderate numbers. Saplings of the moderately tolerant and fast growing tulip poplar did not show high fidelity to gap openings. In contrast to Williamson's (1975) hypothesis, this species regenerated in and out of shady areas. Slippery elm and black cherry opportunistically established in large numbers in the large gaps created by the tornado.

Beech grows steadily beneath closed canopies and quickly in gap openings at young ages, but its growth response is not as rapid as sugar maple. Sugar maple stems of all ages can grow rapidly in response to even the smallest gap opening (Forrester & Runkle 2000). This quick response time, coupled with its large cohort of saplings and the big canopy gaps created by the death of older beech, has helped sugar maple dominate canopy openings in the Hoot Woods. Lorimer (1980) estimated that the average mortality rate under steady-state conditions in a beech-maple forest was 6% per decade. Mortality rates in the canopy of Hoot Woods were low until 1985, when the effects of the tornado activity became evident.

Faltering reproduction of beech in Hoot Woods suggests that some biological attribute besides shade tolerance is responsible for the decline. The intense disturbance in 1980 was particularly injurious to Hoot Woods' beech population which suffered high mortality rates in the large size classes. With the toppling of large parent trees, its reproductive capacity was diminished. Not only was the source of beech seeds cut but its other primary mechanism of replacement, root sprouting, was lost. Due to the species' horizontal branching structure, beech mortalities created large gaps in the canopy. Sugar maple saplings quickly colonized these openings. Once they had grown into the mid- and high-canopy levels, these stems projected a deep shade that even their own offspring found barely tolerable.

Past studies have shown that beech-maple associations are maintained by reciprocal replacement among the codominants (Runkle 1981; Forrester & Runkle 2000). However, other studies (Poulson & Platt 1996; Kupfer et al. 1997) have discovered self-replacement patterns. The results of this analysis indicate that, in Hoot Woods, American beech is a moderately effective self-replacing species. Sugar maple, meanwhile, is a highly successful reciprocal- and self-replacing species. Given its large numbers, ability to capitalize on gap openings, and the lack of a more tolerant competitor, the continuation of sugar maple's increased representation in Hoot Woods seems likely.

### Minor Species

Tulip poplar is the most important secondary tree species in the Hoot Woods. A fast-growing and moderately tolerant tree species, tulip poplar lacks wood strength and is susceptible to decay. A quick growth rate is its main defense against adverse

environmental conditions (Loehle 1988). This has led many researchers to link tulip poplar reproduction to forest canopy openings (Williams 1936; Williamson 1975; Kupfer et al. 1997; Diggins & Kershner 2005). Other studies, however, have discovered a more general distribution (Jackson 1968). Tulip poplar is common throughout the beech-maple region and frequently cited as the third most important species in beech-maple stands (Patzger 1942; Jackson 1968; Jackson & Allen 1968; Kupfer et al. 1997; Zaczek et al. 2002; Diggins & Kershner 2005). Poorly reproducing tulip poplar populations are rarely reported for the beech-maple region (Ward 1958; Schmelz et al. 1974; Pell & Mack 1977). Though relatively intolerant of flooding, tulip poplar's dominance increases in moist, lowland stands. It was found growing well on the fertile soils of Indiana's southern Wabash River floodplain (Jackson & Allen 1968). Due to its consistent reproduction over the past 40 years, tulip poplar will almost certainly continue as an important associate of beech and sugar maple in Hoot Woods.

Dutch elm disease reached the Midwestern United States in the 1930s. It appeared in Indiana forests near Indianapolis in 1937 and, by the mid-1950s, had spread to all parts of the state. High elm mortality rates have been widely reported ever since (Brewer 1980; Parker et al. 1985; Parker 1989; Cowell et al. unpublished). By causing mortality of tree stems before they reach maturity, the disease consigns elms to the subcanopies of forests. It has substantially affected the native vegetation of the region and altered the structure of many old-growth forests. Beals and Cope (1964) reported that half of the elm population at Lewis Woods, a beech-maple forest located in eastern Indiana, was dead or dying of Dutch elm disease. The authors predicted that sugar maple would come to occupy the vacated canopy space. Dutch elm disease represented a mild

disturbance in Hoot Woods. American and slippery elm constituted only a small proportion of the canopy during the 1965 census. By that time, damage from the infection would have likely been underway.

Rogers (1981) envisioned American elm's occurrence in presettlement beech-maple forests as "common." But Ward (1958) described the species' presence in several Wisconsin beech-maple stands as "rare." He reported slippery elm success in beech-maple stands where the two codominants occupied slightly less than half of the canopy and argued that large beech populations retard elm reproduction. American and slippery elm occur in a wide variety of environments. American elm fares best on moist sites and in bottomlands. Slippery elm prefers soils with high organic content and can tolerate drier conditions (Beals & Cope 1964; Boggess & Geis 1967). In Hoot Woods, slippery elm has demonstrated strong reproduction in the wake of the 1980 tornado. Miceli et al. (1977) made a similar finding at Brownfield Woods, where the species increased in density from 6 to 18 trees per acre following American elm mortality in the 1950s. Though still a component of Hoot Woods and other old-growth forests, elms are likely to remain relegated to the subcanopy.

Oaks once dominated much of the Eastern Deciduous forest. But in many contemporary forests, they have been steadily replaced by shade-tolerant species (Abrams 2003). Oak decline has been reported in Midwestern forests for some time (Esten 1932; Williams 1936; Jackson & Allen 1968; Miceli et al. 1977; Cowell & Jackson 2002). Only rarely are oak populations reported as being self-replacing (Boggess & Geis 1967). In beech-maple stands, white and northern red oaks are the most common species. Beech and sugar maple occur only in relatively low densities where

oaks are able to reproduce (Ward 1956). White oak is a moderately shade-tolerant species, but unable to successfully compete in mature beech-maple stands. Gap-phase disturbance does not favor oaks because they grow at a slower rate than their mesophytic counterparts (Ward 1958; Parker 1989). Density competition from shade-tolerant species may not directly cause failed regeneration, but it prevents oak seedlings from maturing into subcanopy trees (Lorimer et al. 1994). These circumstances describe the dynamics in Hoot Woods, where oak representation in the subcanopy and canopy has been low since the study's inception, although several massive oaks exist in the stand. The white oak population suffered the most from the 1980 tornado. All six individuals greater than 80 cm dbh were killed as a result of the disturbance. Oak basal area increased in the larger size classes, indicating growth by the older trees. Low figures in the smaller size classes, however, indicate these trees are not being replaced. The coming decades will likely see the elimination of oak trees from Hoot Woods.

White ash is a moderately shade tolerant species, known to resist grazing pressures and benefit from open canopy conditions. It consistently bears seed crops that germinate well, but cannot effectively compete with beech or sugar maple. White ash is thought to be similar to tulip poplar in its reliance on canopy gaps to maintain itself in beech-maple communities (Williams 1936; Williamson 1975; Parker et al. 1985). Some studies have found good reproduction among white ash populations (Patzger 1942; Jackson & Allen 1968). But more recent accounts have indicated its decline in forest stands, particularly in smaller size classes (Schmelz et al. 1974). Ward (1958) found that white ash fared best in environments where beech and maple existed in moderate levels. Disease may contribute to white ash mortality. Ash dieback, often induced by periods of

drought, has been known to produce heavy mortalities among white ash populations. There is no evidence of this illness in Hoot Woods, however. The presence and importance of both white and green ash have decreased over the course of the study, and these species are likely to remain of only minor importance in the stand.

Black walnut is a valuable timber tree, native to most of the eastern United States. Indiana produces several hundred thousand seedlings of the species annually for commercial use (Bey & Williams 1974). Its condition in natural settings is occasionally remarked upon. In Cox Woods, Potzger (1942) noted the species' unique spatial arrangement; they were clustered near the bottom of slopes where greater moisture was available. Black walnut's preference for moist conditions has been confirmed by other studies. Jackson and Allen (1968) noted the species' increased importance in sinkholes. In Potzger's Woods, it ranked third in importance at 5%. Overall, the species performs best on mesic sites with moist, fertile, alluvial deposits (Beals & Cope 1964; Seischab 1985). In Hoot Woods, black walnut declined 200% in density and 3.68% in basal area over the course of the study. It had an importance value of just 0.3% in 2005.

Flowering dogwood is a shade-tolerant understory tree that lives up to 125 years. Its moderate presence has been noted in several beech-maple forests (Jackson & Allen 1968; Zaczek et al. 2002). In Hoot Woods, several dogwoods grew into the stand during the first half of the study. But the species declined 700% in density during the last census. Red maple is at times an important canopy species in locations that meet its specific demands, principally high moisture (Jackson 1968; Zhang et al. 2000). More commonly though, the species is site-restricted and shows poor reproduction (Schmelz et al. 1974). In beech-maple forests, its saplings do not survive well (Williams 1936). In

Hoot Woods, it was not present until 1975 and averaged just over one ingrowth per year. Black gum very rarely is an important minor species in beech-maple forests. In Potzger's Woods, it ranked fifth in importance (Jackson & Allen 1968). Although consistent from year to year in terms of density and basal area, it ranked 15<sup>th</sup> in importance during the last census. Hop hornbeam is common throughout the whole range of the beech-maple region and often cited as a dominant understory tree. It rarely exceeds 30 cm in dbh and is never a canopy species, but can constitute a large proportion of trees in the small size classes (Potzger 1935; Buell & Cantlon 1951; Ward 1958; Peet 1984). In Hoot Woods, hop hornbeam representation is quite low. The ingrowth of a few stems has increased the species' density by 75%. Hickories, as a group were unimodally distributed in the medium size classes and showed limited regeneration.

### Management Prescriptions

The utility of the present study is not restricted to biogeographers and forest ecologists. Changing forest composition and structure is an emerging issue in natural resource management and one that can profoundly affect wildlife communities within natural areas (Rodewald 2003). Long-term studies of vegetation dynamics are useful to citizen's groups, state conservation departments, and federal agencies attempting to determine top administrative priorities. Proper management decisions balance the goals of biodiversity, protection, ecological function, and economic production. Given the lack of empirical data on the dynamics of old-growth forest ecosystems, comprehensive research that can inform management decisions is inherently valuable. Documentation of compositional turnover through direct observation of stand dynamics is critical for



understanding the processes of compositional change. Permanent plot studies, in general, provide important findings which affect conservation strategies, but the number of mapped permanent plots in the eastern hardwoods region is limited (Potzger & Friesner 1943; Lindsey & Schmelz 1969).

Midwestern vegetation patterns reflect past and present human landuse practices. Whether due to changes to their surroundings or successional dynamics these remnants are shifting in composition and structure. Therefore, protecting old-growth remnants with the motivation of retaining forest primeval conditions is erroneous. Old-growth forests are nevertheless valuable for their record of change, aesthetic quality, and significance to future generations (Ziegler 2004). Management strategies that mimic natural disturbances, such as treefall gaps, have become a hot topic among researchers and conservationists. The belief is that the ecological processes of landscapes can be better maintained in this way. Shade-intolerant species, it is argued, can maintain themselves better under active management regimes (Turner et al. 2001).

Long-term protection and management of old-growth forests is made difficult by their characteristic small size and isolation. Current management primarily involves protection from anthropogenic factors. Efforts to control native biota via the reintroduction of fire or other active management strategies are less prevalent. Some old-growth forests are part of public parks and are susceptible to overuse and vandalism. These stands require trails and fencing to direct human traffic in and around the protected area. Those forests that are isolated, such as Hoot Woods, enjoy relatively less damage from human use. However, these stands must deal with their own anthropogenic threats. These impacts include urban construction, soil erosion, agricultural pollution, land

drainage, strip mining, and invasion by non-native plant species due to greater edge environment and nearby seed sources. Many isolated old-growth forests are affected by landuse practices on adjoining lands. The effects of roads, buffers, corridors, edges, and harvest systems adjacent to old growth are not always readily apparent but may become significant over the long term (Parker 1989).

Management of forests to maintain particular structural and compositional configurations requires careful consideration. Stand manipulation intended to favor certain tree species, such as thinning, coarse woody debris reduction, diseased tree removal, or the reintroduction of fire are not desirable management options for most old-growth stands (Zaczek et al. 2002). It is difficult to predict what effects active management might have on these ecosystems (Rodewald 2003). Partial overstory removal and prescribed fire in conjunction with partial cutting followed by complete overstory removal are thought to be effective means of reinvigorating failing cohorts of shade-intolerant species. But in some cases, thinning techniques have proven incapable of arresting the succession of shade-tolerant species. Maintenance of natural disturbance regimes in remnant forests has also proven insufficient for deriving desired forest patterns (Kupfer et al. 1997). Prescribed burning, for instance, can produce unforeseen negative impacts (Parker 1989; Parker et al. 1985). Given the observed composition of its canopy gaps, it is doubtful whether these methods could be successfully employed in Hoot Woods to restore the position of beech. In addition, the matter of using fire to derive desired landscape features is politically tenuous. Fire suppression has been long-practiced and where there are large human populations it is still very desirable.

Public land-holding agencies must cope with limited budgets. The average privately-owned Indiana forest changes ownership approximately every 15 years. As possession is exchanged land use practices are typically altered. Continuous tenure, therefore, represents a valuable defense against the loss of forested lands. Stable farm ownership is particularly helpful for old-growth maintenance. Old-growth remnants are more likely to persist on parcels with slow rates of turnover. Medley et al. (2003) found that lands classed as having low, moderate, and high rates of turnover averaged 30, 20, and 12 percent, respectively, in terms of the proportion of the property still in forest. Mean patch sizes of forests were also significantly greater on lands with low turnover. Given these details, there is no certainty that forests adjacent to areas containing Indiana's old-growth sites will remain intact.

Some research suggests that public agencies use proximity index (PX) maps in their decision-making processes to help identify high priority areas for acquisition or re-vegetation. Edge areas can be reduced through tree planting or by allowing natural succession to take place. Younger forests that surround old-growth remnants are advantageous in this regard and should be considered high priorities for future land acquisitions (Spetich et al. 1997). The destruction of privately-controlled forest ecosystems is unrelenting. Nature conservation efforts, therefore, must go beyond the protection of old-growth stands to include the restoration of adjacent land patches (Medley et al. 2003). Old-growth preservation should occur at the ecosystem level and include participation by private landowners (Goebel et al. 2005).

For a quarter-century, the Nature Conservancy has protected Hoot Woods from harm. It is encouraging to know the stand will remain under the organization's

supervision and be permitted to develop according to the laws of nature. The Nature Conservancy would be wise to maintain its current policy of protection, as well as adopt a few new strategies. No effort should be made to promote public awareness of the Hoot Wood's whereabouts. Heavy human traffic would degrade understory conditions, upset the remaining permanent plot markers, and possibly alter successional pathways. The forest's isolation in an agricultural matrix is an unlikely asset in this regard.

Spetich et al. (1997) advocated management strategies that would stabilize landuse practices on property bordering Indiana's old-growth forests and recommended lowering the average nearest neighbor distances between old-growth stands to 11,588 meters. Hoot Woods possesses the third highest PX value of all of Indiana's old-growth sites at 718.5, indicating that it is relatively large and positioned close to other forests. The Nature Conservancy should investigate the possibility of acquiring properties directly adjacent to the stand. Management programs that entice the current owners of those lands to maintain favorable landuse practices are an attractive second option. Species competition, disturbance agents, local environmental variations, and global change will continue to alter Hoot Woods. Its future as an old-growth forest that fulfills many ecological and aesthetic roles is dependent on appropriate management decisions (Potzger 1942; Quinby 2001).

## CHAPTER SIX

### CONCLUSIONS

This study examines how ingrowth, survival, and mortality contributed to changes in the structural, compositional, and spatial attributes of an undisturbed old-growth beech-maple forest over forty years. It considers which factors could have affected such changes and assesses which trends are likely to continue into the future. Taken together, the results warrant the conclusion that a considerable change in forest composition of Hoot Woods has been in progress for the past forty years. The forces operating to bring about this change continue to function at present. That beech formerly exhibited greater stand dominance than it now does is clear. A change in species dominance continued throughout the study, indicating a steady shift from the co-dominance of beech and maple to more singular sugar maple dominance. Mortality increased and stand density decreased as a result of the 1980 tornado; most of the large trees lost in this event were beech. Thereafter, stand basal area and average stem diameter increased, sugar maple survivors grew well, and the loss of beech accelerated.

Disturbance events can advance succession to later seral stages, rather than set them back. This has been known to occur in oak forests with understories composed of sugar maples (Abrams & Nowacki 1992). External stimuli in the form of the 1980 tornado prompted a major response in canopy composition. Breaks in the canopy resulting from heavy beech mortality were quickly filled by other species. Species

diversity is sometimes anemic in undisturbed old-growth communities. More diverse forest conditions stem from disturbances. This analysis indicates that the intensity and type of disturbance matters greatly. Low-intensity gap-phase disturbance was insufficient to maintain canopy diversity. High-intensity tornadic disturbance, meanwhile, allowed a handful of minor species to succeed. Conditions in Hoot Woods suggest that accelerated succession is possible even when forest overstories are composed of shade-tolerant, late-seral species.

The tornado helped escalate sugar maple's stand dominance as well. But it was not the sole reason for the species' rise. That development can also be traced to the life history strategies of beech and maple. Several natural disturbance agents, including pathogens, insects, herbivore predation, and drought, are ruled out as causal agents due to lack of evidence. Anthropogenic influences, such as fire suppression and fragmentation caused by agricultural landuse, cannot be linked to the changing composition of Hoot Woods either. According to the precipitation and temperature records of Spencer, Indiana, local climate conditions changed little over the course of the study. These results are commensurate with a view of old-growth forests as dynamic, changing communities, rather than stable, pristine climaxes.

Prediction of future crown cover is a common component of studies of this nature (Bakker et al. 1996). But the increased recognition of the importance of disturbance events in vegetation dynamics has reduced confidence in compositional forecasts (Parker et al. 1985; Peterken & Jones 1987). The intensity and configuration of disturbances are largely unpredictable, with the possibility that a stand-replacing disturbance will initiate the development of a new forest (Cowell & Parker 2004; Ziegler 2004). The decline of

beech in Hoot Woods has been steep and dramatic. Although a small increase in representation in small size classes during the last census and mildly increased rates of ingrowth raise the possibility that beech will rebound, this seems unlikely.

Most of the beech-maple forest that spent centuries accumulating the energy of the sun's rays is now gone, sacrificed to American progress (Cronon 1991). Old-growth remnants of this original forest are priceless artifacts of nature. Interesting patterns of vegetation dynamics, a lack of direct anthropogenic disturbance, and a rich tradition of academic study combine to make Hoot Woods one of the finest old-growth forests on record. Future work in Hoot Woods should center on long-term changes and relating the stand to the forest complex of the surrounding region as a whole. It is heartening to believe that this study will continue for many years to come.

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