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THE TREND IN CANOPY COMPOSITION
IN A YOUNG MESIC FOREST

by

Zhenchang Li

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Submitted to the
Faculty of The Graduate College
in partial fulfillment of the
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Zhenchang Li

THE TREND IN CANOPY COMPOSITION
IN A YOUNG MESIC FOREST

Zhenchang Li, M.A.

Western Michigan University, 1985

Brewer Woods, a young disturbed mesic sugar maple-beech (Acer saccharum-Fagus grandifolia) forest in Kalamazoo Co., Michigan, was investigated by point-quarter and transition matrix methods. The results indicate that this forest is dominated by sugar maple in both canopy and understory composition. Beech is the second most important species. Fourteen species were found as canopy trees or replacements. The hypothesis that a young forest is more diverse than comparable climax forests such as Warren Woods and Hueston Woods was supported. Its successional trend is that sugar maple will become more abundant at the expense of the other species. Beech is a subdominant species at steady state. Some shade-intolerant species will be lost from the canopy as succession proceeds. A combination of three models proposed by Connell and Slatyer was used to explain the successional trends of this forest.

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CHAPTER I

INTRODUCTION

Succession is defined as the process of development from pioneer to climax community (Brewer 1979). Horn (1974) described:

Succession as a pattern of changes in species composition of a community after disturbance or after the opening of a new patch in the physical environment for colonization by plants and animals. If the physical environment remains constant, eventually the changes in the specific composition of the community become undetectably slow or cease altogether. This late stage of succession is dignified by the term "climax". (p. 25)

Generally, forest succession may be considered as the process by which a forest develops from a few seedlings to a mature forest. At the beginning, sparse trees grow in full sunlight with little inter- or intraspecific competition. Then new generations are produced by the early species. At the same time, new species may enter the site by immigration. The forest becomes denser and shade increases. However, later-arriving species are more shade tolerant. They can survive and grow under the early canopy. As soon as the canopy trees die, these saplings may capture the openings, grow quickly, and become the canopy trees. By repeating this process, one canopy tree is replaced by another. Finally the forest is dominated by a few shade-tolerant species. These final species may undergo self-replacement or reciprocal replacement. This

is called climax forest, in which the species composition remains relatively constant.

In the textbooks, commonly cited successional trends include the following: Species diversity, community productivity, and biomass often increase; the ratio of gross productivity to respiration approaches one; stock of nutrients and organic matter held in the organisms increases; stress tolerance of dominant species such as shade and drought tolerances increases; community structure is more stratified, and longevity of dominant species and community stability increase; the microclimate within the community is increasingly determined by characteristics of the community itself.

Several theories of succession have been proposed. One early theory, known as Clements' holistic organismic theory, was raised by Clements in his classic book Plant Sucession (1916) and article "Nature and Structure of the Climax" (1936). The theory states that succession is the processes of initiation, selection, continuation and termination, leading to a climatic climax. For secondary succession, it states that basic processes includes nudation, migration, ecesis, competition, reaction, and stabilization. The climax community is seen as a complex organism which arises, grows, matures, and dies. The climax formation is at the highest successional stage. The formation is a regional vegetation unit which covers a

given geographic area and is recognized by the growth-form of the dominant species (Whittaker 1980).

Odum's and Margalef's ecosystem theory parallels Clements' view of succession (McIntosh 1981). It states that succession is an orderly process which is reasonably directional and therefore predictable; it results from modification of the physical environment by the communities, i.e., "community controlled"; it culminates in a stabilized (climax or mature) ecosystem with homeostatic properties (Odum 1969, Margalef 1968, 1975). Odum and Margalef's representation of succession was described as neoClementsian because this school interprets the successional processes as organismic and holistic.

A third theory proposed in recent years (Peet and Christensen 1980) is a population approach to succession and emphasizes life-history and physiological characteristics of species in responding to environment gradients (Pickett 1976). Population processes have strong influence on the community-level properties such as species composition, diversity, and productivity.

Even though Clements' theory has been criticized since it was proposed (Gleason 1917, 1939, Tansley 1936, Whittaker 1953), it is still widely used by ecologists (Brewer 1979, McIntosh 1981, MacMahon 1981). For example, Odum's evolutionary trends toward diversity and interdependence at the community level and a stabilized

ecosystem with homeostatic properties are parallels to Clements' concepts of the ontogeny and phylogeny of the climax formation and climatic climax. Many ecologists agreed with Odum's "evolution" concepts which have been commonly cited in the literature. However, some of Odum's generalizations have been questioned by some investigators. For example, the successional changes in biomass and primary production are not consistently upward as Odum has suggested. Instead, the highest productivity and biomass are found preceding of the climax stage (Bormann and Likens 1979, Horn 1974, Loucks 1970, and Peet 1981). The tightest nutrient cycles should be expected in the central portion of successional sequences, rather than the end portion as Odum proposed (Bormann and Likens 1979). In recent years, some ecologists have given more emphasis to life-history and physiological characteristics of species to explain the succession processes.

There are several approaches to the study of forest succession. The ideal one is to follow tree growth in a specific site of natural vegetation along with the forest development (Stephens and Waggoner 1970). However, this approach makes it difficult or even impossible to obtain continuous and adequate data because of the complexity of ecological systems and the long life of many tree species. Since this method has the advantage of obtaining direct evidence succession and the disadvantage of requiring

several generations to collect sufficient data, some ecologists are searching for other approaches which may possess the advantage and overcome the disadvantage of the direct observation approach.

One of these developed approaches is the gap phase regeneration model (Brewer and Merritt 1978, Barden 1980, 1981, Runkle 1981). This model is based on succession as a tree-by-tree replacement process in which what is potentially replacing a dead tree can be observed directly. The data thus obtained can be used to construct a table of replacement probabilities, which, by transition matrix multiplication, simulates succession for a forest of a given initial composition. In recent years, the gap phase regeneration model has been applied to study forest succession under closed canopy situations. It is often called the transition matrix model (Horn 1974).

This model is based on the Markov chain process in which transitions among various "states" occur with characteristic probabilities that depend only on the current state. It assumes that forest succession is a tree-by-tree replacement process. It further assumes that (1) the transition probabilities remain constant with forest composition and with successional stages or local edaphic conditions (Horn 1975); (2) the total density of the canopy trees does not change although the species composition may shift; and (3) within a period, all

current canopy trees die and all the replacements become canopy trees (Brewer and McCann 1982). With this model, through matrix multiplications, the composition of the forest becomes either a cyclic pattern or a stationary distribution. In the latter case, the stationary distribution is the same independent of the starting distribution.

Most predictions of forest succession made by using the transition matrix model have not been tested because of the complexity of the community and the time requirement. One way to compensate for this shortage may be to choose a young disturbed forest, which is somewhat similar to a climax forest in geography, species composition and successional stage before disturbance. After choosing the potential replacements of the canopy trees, the same method can be used to predict the future canopy composition and diversity. By comparing this result with other eastern North American climax forests, light can be shed on several questions such as how much time is required for the forest to reach its climax or whether or not the forest succession is a species convergent process.

Warren Woods in Michigan and Hueston Woods in Ohio have long been known as climax forests. Much research has been conducted on these two forests so that many characteristics of the forests are recognized (Cain 1935, Brewer and Merritt 1978, Brewer 1980, Woods 1979, Woods

and Whittaker 1981, Laufersweiler 1955, Vankat et al. 1975). Brewer Woods in Kalamazoo was selected as a young disturbed forest which would be comparable to these two forests.

The present paper has four main objectives: first, to quantify the forest canopy composition and replacement composition; second, to construct a transition matrix to predict the future canopy composition; third, to compare this forest with other deciduous climax forests in eastern North America to test the hypothesis that diversity increases during the succession (Odum 1971); and fourth, to see what succession model is better in interpreting secondary succession trends.

CHAPTER II

STUDY AREA AND METHOD

Study Site

Brewer Woods is a 40-acre (16.2 ha) mesic disturbed sugar maple-beech (Acer saccharum-Fagus grandifolia) forest in Pavilion township, Kalamazoo, Michigan. The area was maple-beech forest prior to settlement (Kenoyer 1929, Hodler et al. 1981). It is known that the portion studied has been undisturbed since 1971 but only limited information on the forest's earlier history is available. It is clear from the late date of settlement of this part of the county, the pit and mound topography, and the soil development, that the forest was never cleared for cultivation.

Aerial photography from 1950 shows the forest to be composed of small-crowned trees, suggesting that timber cutting had occurred sometime in the preceding quarter-century. A 1960 photograph shows a canopy that was dense and uniform without large gaps. The 1967 photograph differed markedly. Small crowns and many gaps indicated timber cutting sometime between 1960 and 1967. A 1974 photograph shows that most of the big gaps appearing in the 1967 photograph had disappeared, although the canopy looks less mature than the 1950 photograph. The year of

the lumbering episode, dated by aerial photography as between 1960 and 1967, was established as 1962 based on tree growth responses determined by increment boring (R. Brewer and Z.C. Li, original data).

The forest is dominated by sugar maple and beech. Basswood and red maple are the next important species. Some other minor species are also present in the forest. The ground-cover is composed of ferns, grass, a few sedges, some shrubs and a variety of herbs, especially spring ephemerals. The canopy is now almost uniform with only a few breaks. Adjacent areas to the south, east, and half of the north sides are cultivated fields. The west side is a similar forest, while the west half of the north side is bordered by a young forest.

Top soil is somewhat poorly drained, moderately coarse textured with high organic matter. The subsoil is moderately fine textured to 24-42 inches; below this, the subsoil is coarse textured. Geologically, the area was characterized as thin outwash over ground moraine by Martin (1958); however, in several spots, till reaches the surface (Brewer, personal communication).

Study Method

Most sampling was done in the summer of 1984. The point-quarter method described by Brewer and McCann (1982) was applied. Thirty points were previously chosen, each

with a metal stake marking a 50 by 50 meter grid. To obtain more intensive sampling, 36 more points were chosen which were the alternative points of the original thirty (Fig. 1). Sample points were restricted to the upland at least 35 meters from any edge.

At each point, the space was divided into northeast, northwest, southeast and southwest quarters by compass. The canopy tree closest to the center for each quarter was chosen and its species was identified. Its diameter at breast height (DBH) and distance from the point were measured and recorded. For each canopy tree, the tree most likely to replace it was identified as the "first replacer". This was the non-canopy tree thought most likely to fill the gap should the canopy tree be lost immediately. A "second replacer" was chosen as the most likely replacement for the canopy tree should the first replacer be lost. For first and second replacers, their DBH, distances from the canopy tree and species were recorded.

The canopy trees were defined by the criterion used by Brewer (unpublished) and Vankat et al. (1975), namely, that a tree receiving incident sunlight directly is a canopy tree. However, in Brewer Woods, unlike the climax forests, the structural differentiation of the canopy and subcanopy is not so apparent. It was difficult to define the canopy trees in former openings and broken canopy

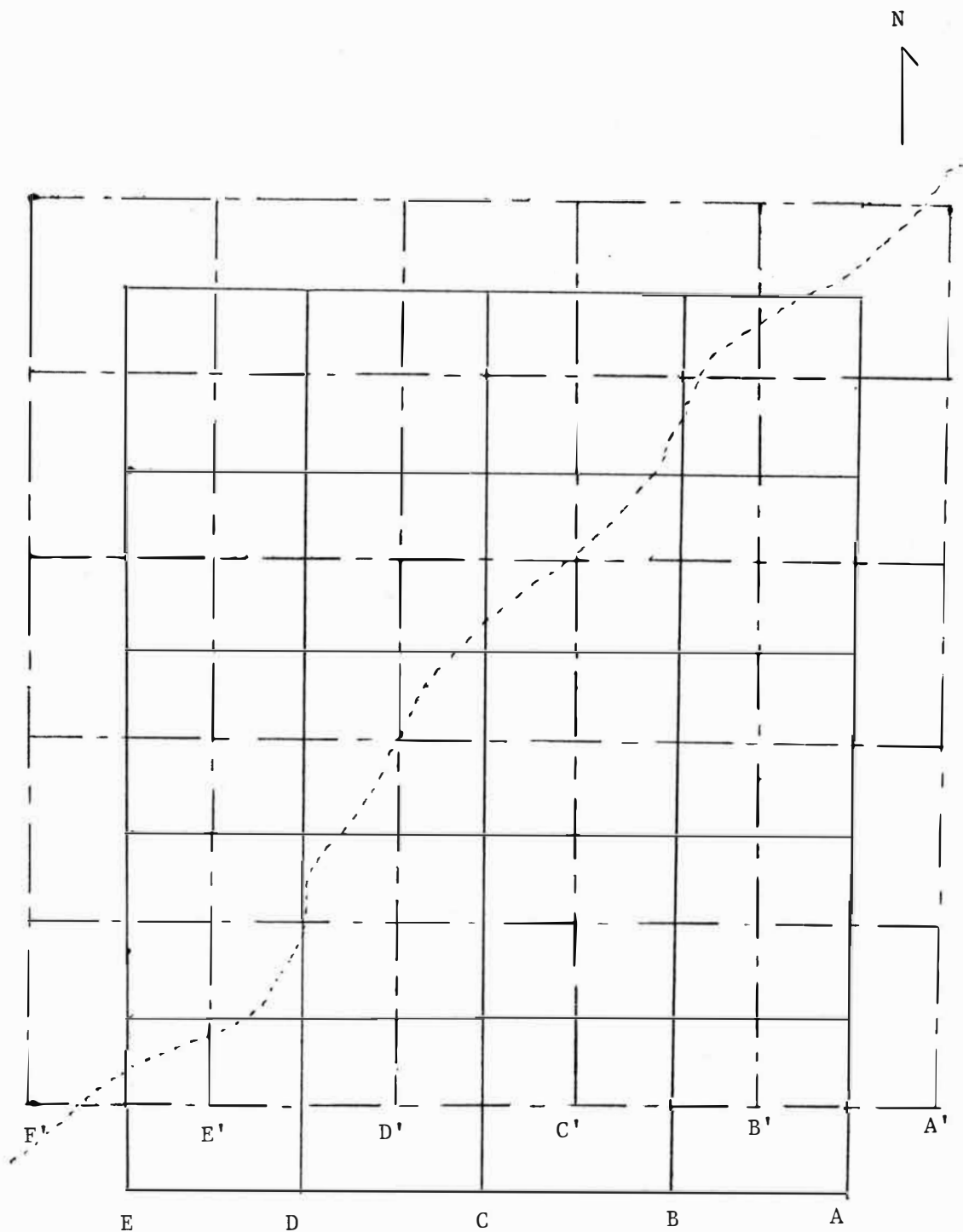


Figure 1. Point-quarter samplings. A B C D E are previously chosen coordinates at 50-M intervals marked with metal stakes. A' B' C' D' E' F' are additional lines added for this sampling. is the previous pathway.

areas. To deal with this problem, two criteria were applied: (1) A tree which was big and old, although it was about the same height as the surrounding trees in the relatively broken areas was selected as the canopy tree; and (2) a tree which was bigger and much taller than its surroundings in the relatively open area was grouped in the canopy category.

When selecting replacers, several considerations were taken into account. A non-canopy tree that was closest to and under the crown of the canopy tree, with greatest height, largest DBH among the non-canopy trees, healthy and growing vigorously was selected as the first replacer. The second replacer was determined in the same way with more emphasis on its position and growth rate. Growth rates were adapted from the description of Brewer (1979), Marks (1975), Stephens and Waggoner (1970) and Bormann and Likens (1979), (i.e., growing speed is in the increasing order of red oak, beech, sugar maple, hickory, red maple, basswood, elm, ash, black cherry, tuliptree and cottonwood). Other things being equal, a sapling with a greater growing speed was preferred as the replacement. In addition, even if a tree was taller than some nearby canopy trees, but was located directly under a canopy tree, it was still considered as the replacer.

Because elm trees usually die before reaching canopy size from Dutch elm disease, whenever either elm species

(american elm [Ulmus americana] or slippery elm [U. rubra]) was chosen as a replacer, a third replacer was also selected.

To obtain a better representation of replacement probabilities for rare species (defined as those with fewer than 10 trees in the original samples), a supplementary sampling was conducted during the spring of 1985. The area was divided into 30 quadrats, 20 of which were 50 by 50 meters and 10 of which were 50 by 25 meters (Fig. 2). The starting quadrat was chosen randomly by flipping a coin. In each quadrat, canopy trees of any rare species were selected as previously described. To avoid locational bias, no more than two canopy trees of rare species were taken per quadrat. When the defined quota of ten trees (including ones obtained in regular samples) had been reached, sampling of that species was discontinued. When all 30 quadrats were sampled, even though some rare species were still below 10, the sampling was ended.

Since this study is the beginning of a long-term research project, all trees sampled were marked with numbered aluminum tags. Canopy trees were tagged with circular tags, first replacers with triangles and second replacers with rectangles.

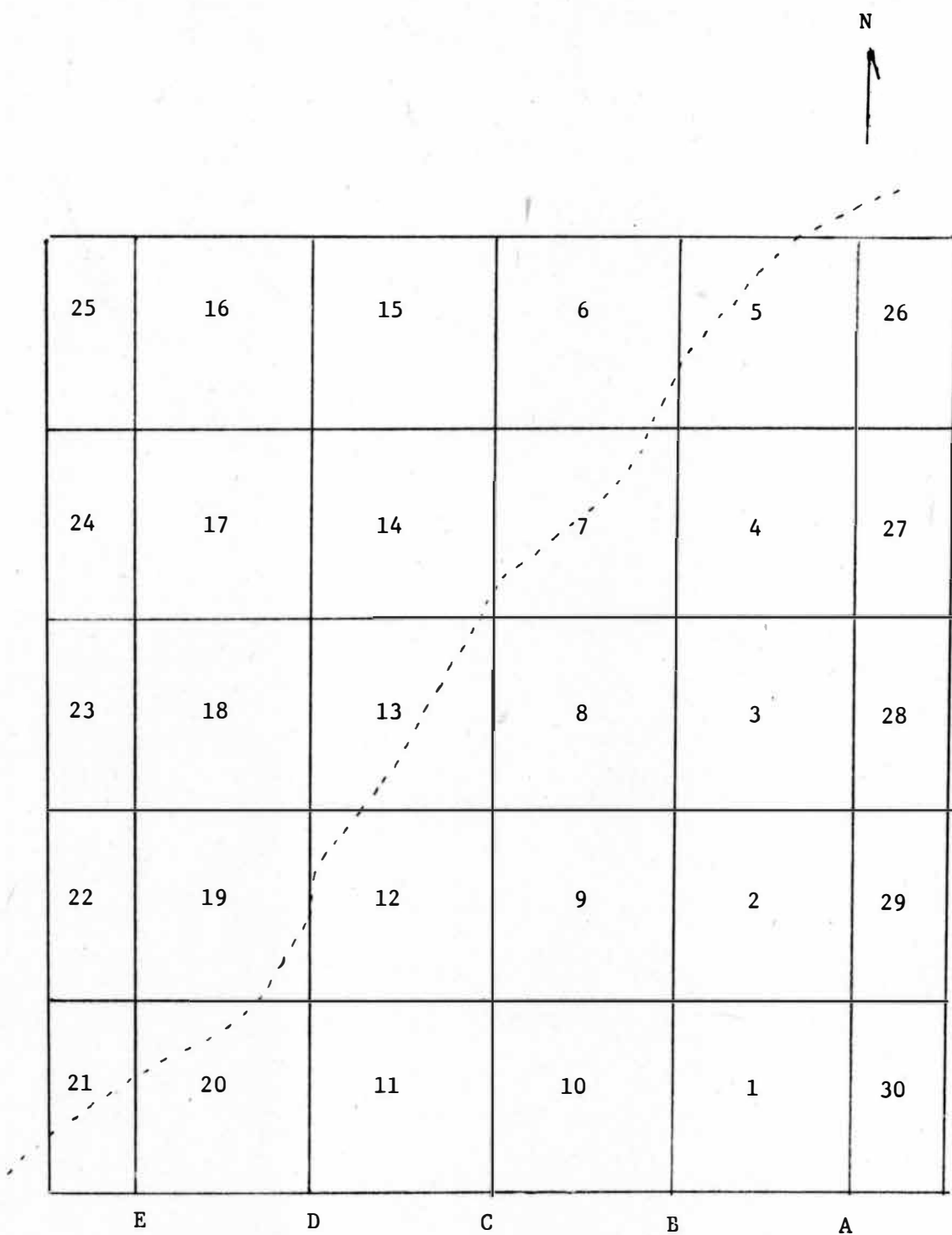


Figure 2. Sampling quadrats for rare species. Other explanations are the same as Fig. 1.

Data Analysis

From the original 66 points (264 canopy trees), canopy composition and importance values were calculated by the method of Brewer and McCann (1982). Several parameters were obtained by the following formulae:

$$\text{Frequency}(F) = \frac{\text{points of occurrence for species } i}{\text{total number of points sampled}}$$

$$\text{Relative frequency}(RF) = \frac{\text{frequency of species } i}{\text{sum of frequencies for all species}}$$

$$\text{Relative dominance}(RB) = \frac{\text{basal area for species } i}{\text{sum of basal areas for all species}}$$

$$\text{Relative density}(RD) = \frac{\text{number of trees of species } i}{\text{total number of trees of all species}}$$

$$\text{Importance value} = RF + RB + RD$$

The frequency composition of first replacers was computed for each canopy species and, from this, the transition matrix was compiled. Starting with the current canopy composition, the transition probabilities were used to estimate the numbers of each species in the canopy for the next generation. Then, given the canopy composition in the second generation, the same transition probabilities were used to estimate the canopy composition of the third generation. The process was repeated until the canopy composition was stationary.

The significance of interactions among the canopy trees and replacers was tested by contingency analysis (Vann 1972, Brewer and McCann 1982). To eliminate the zero observations of some minor species, a 4 by 4 table was constructed.

CHAPTER III

RESULTS

Current Canopy Composition

The density of canopy trees on the study area was 172 trees per hectare (Table 1). Among the canopy species,

Table 1
Canopy composition of Brewer Woods, 1984

| Species | Number | Relative density(%) | Trees/hectare |
|-----------------------|--------|---------------------|---------------|
| Sugar maple | 142 | 53.8 | 91 |
| Beech | 34 | 12.9 | 22 |
| Basswood | 34 | 12.9 | 22 |
| Red maple | 21 | 8.0 | 14 |
| Shagbark hickory | 9 | 3.4 | 6 |
| Bitternut hickory | 7 | 2.7 | 5 |
| Ashes (red and white) | 7 | 2.7 | 5 |
| Tuliptree | 3 | 1.1 | 2 |
| Cottonwood | 3 | 1.1 | 2 |
| Black cherry | 2 | 0.8 | 1 |
| American elm | 1 | 0.4 | 1 |
| Hop-hornbeam | 1 | 0.4 | 1 |
| Total | 264 | 100 | 172 |

sugar maple was most abundant, with 142 trees occurring in the forest canopy. Its relative density accounts for more than 50% of the canopy stems indicating that this species is most important in the forest. Densities of beech and basswood were identical, with about 13% of the total value. Red maple (Acer rubrum) is a fourth major species in the forest. The other species of tuliptree (Liriodendron tilipifera), shagbark hickory (Carya ovata), bitternut hickory (C. cordiformis), white ash (Fraxinus americana), red ash (F. pennsylvanica), black cherry (Prunus serotina), american elm, cottonwood (Populus deltoides) and hop-hornbeam (Ostrya virginiana) comprise the remaining fraction of the canopy.

According to Curtis (1971) , and Brewer and McCann (1982), importance value (IV) may be a better representation than density of forest composition. Sugar maple has almost half of the total IV (Table 2), indicating that it plays a major role in determining the forest structure and physiognomy. It may be noted that sugar maple IV is slightly below 50 percent because of a relatively low RF value, which does not correlate with RB and RD. This suggests that sugar maple as a canopy tree is not evenly distributed over the forest.

Beech and basswood make up 14 and 13%, respectively, of the total IV. Even though both species have the same RD value, because of its relatively larger size and more even

Table 2
Importance values for canopy trees

| Species | P | Q | BA | F | RF | RB | RD | IV | IV(%) |
|-------------------|----|-----|-------|-------|-------|-------|-------|-------|-------|
| Sugar maple | 57 | 142 | 21.94 | .864 | .401 | .544 | .538 | 1.483 | 49 |
| Beech | 21 | 34 | 5.75 | .318 | .148 | .143 | .129 | .420 | 14 |
| Basswood | 19 | 34 | 5.01 | .288 | .134 | .124 | .129 | .387 | 13 |
| Red maple | 17 | 21 | 3.82 | .258 | .120 | .095 | .080 | .295 | 10 |
| Shagbark hickory | 8 | 9 | .97 | .125 | .058 | .024 | .034 | .116 | 4 |
| Bitternut hickory | 7 | 7 | 1.01 | .106 | .049 | .025 | .027 | .101 | 3 |
| White ash | 3 | 3 | .58 | .045 | .021 | .014 | .011 | .046 | |
| Red ash | 2 | 4 | .36 | .030 | .014 | .009 | .015 | .038 | |
| Tuliptree | 3 | 3 | .31 | .045 | .021 | .008 | .001 | .040 | |
| Cottonwood | 1 | 3 | .21 | .015 | .007 | .005 | .011 | .023 | |
| Black cherry | 2 | 2 | .25 | .030 | .014 | .006 | .008 | .028 | |
| American elm | 1 | 1 | .03 | .015 | .007 | .001 | .004 | .012 | |
| Hop-hornbeam | 1 | 1 | .08 | .015 | .007 | .002 | .004 | .013 | |
| Toatl | | 264 | 40.32 | 2.154 | 1.001 | 1.000 | 1.000 | 3.001 | |

Note: P = No. of points of occurrence; Q = No. of trees; BA = Basal area; F = frequency; RF = relative frequency; RB = relative dominance; RD = relative density, and IV = importance value.

spread throughout the forest, beech has a higher IV than basswood. Red maple is 8% of the RD, but due to the large size of the trees, its IV accounts for 10% of the total value. Hickory, including shagbark and bitternut hickory, occupies a good portion of the forest canopy, holding 7% of the IV. The remaining 7% is shared by seven minor species.

Current Replacement Composition

The replacement composition is important in describing understory behavior of the forest. The results from regular sampling and the combination of regular and rare species sampling are shown in Tables 3 and 4, respectively. Since the results from these two tables are almost the same, the data in Table 3 will be used in the later discussion. These results show that sugar maple was most abundant with about 70% of the replacement composition. The second most abundant replacer was beech making up about 10%. Basswood was the third most often selected. Three canopy species, shagbark hickory, cottonwood and hop-hornbeam, were not found in the samplings. Ash, red oak and black cherry were occasionally encountered. Elm species, which occurred in very small numbers in the canopy of regular samples, held the fourth position of selected replacements.

Table 3
Replacement composition from regular samples
at Brewer Woods

| Species | First replacer | | Second replacer | |
|-------------------|----------------|-----|-----------------|-----|
| | Number | % | Number | % |
| Sugar maple | 175 | 66 | 185 | 70 |
| Beech | 28 | 11 | 25 | 9 |
| Basswood | 20 | 8 | 18 | 7 |
| Red maple | 13 | 5 | 2 | 1 |
| Bitternut hickory | 0 | 0 | 1 | |
| Ashes | 0 | 0 | 2 | 1 |
| Tuliptree | 11 | 4 | 8 | 3 |
| Black cherry | 1 | | 4 | 2 |
| Elms | 14 | 5 | 17 | 6 |
| Red oak | 2 | 1 | 2 | 1 |
| Total | 264 | 100 | 264 | 100 |

Tables 3 and 4 do not reveal interspecific and intraspecific interactions. One way to deal with this problem is to find out the probabilities of a given species replacing different canopy trees. These results are listed in Tables 5, 6, 7 and 8. Elms were treated either as replacements like the other species or eliminated because of the high likelihood of death from Dutch elm disease before reaching the canopy. When the

Table 4

Replacement composition of Brewer Woods from the combination of regular and rare species samplings

| Species | First replacer | | Second replacer | |
|-------------------|----------------|-----|-----------------|-----|
| | Number | % | Number | % |
| Sugar maple | 197 | 67 | 207 | 70 |
| Beech | 28 | 10 | 29 | 10 |
| Basswood | 23 | 8 | 22 | 7 |
| Red maple | 13 | 4 | 2 | 1 |
| Bitternut hickory | 0 | 0 | 1 | |
| Ashes | 0 | 0 | 2 | 1 |
| Tuliptree | 12 | 4 | 8 | 3 |
| Black cherry | 2 | 1 | 4 | 1 |
| Elms | 17 | 6 | 17 | 6 |
| Red oak | 2 | 1 | 2 | 1 |
| Total | 294 | 101 | 294 | 100 |

latter was done, the second and third replacers were moved accordingly. The probabilities as given in Tables 7 and 8 form the transition matrices.

Among 142 canopy trees of sugar maple, 104 were replaced by sugar maple (Tables 5 and 7). The replacement probability is 0.732. This species also has high replacement probabilities for other canopy species. Basswood tends to replace itself: 13 of its 20 replacers are basswood. The rare species are most often replaced by

Table 5
Numbers of replacers by canopy species.*

| First replacer | Canopy trees | | | | | | | | | | | | |
|-------------------|--------------|----|----|----|----|----|----|----|----|----|----|----|----|
| | SM | BE | BW | RM | TT | BC | EL | RO | SH | BH | AS | CW | HB |
| SM | 104 | 20 | 17 | 8 | 3 | 9 | 6 | 3 | 7 | 10 | 10 | 0 | 0 |
| BE | 10 | 10 | 3 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| BW | 3 | 2 | 13 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| RM | 5 | 2 | 0 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| TT | 6 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| BC | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EL | 11 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 |
| RO | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 142 | 34 | 34 | 21 | 6 | 10 | 10 | 3 | 10 | 10 | 10 | 3 | 1 |

* SM = sugar maple; BE = Beech; BW = Basswod; RM = red maple;
TT = tuliptree; BC = black cherry; El = elms; RO = red oak; SH =
shagbark hickory; BH = bitternut hickory; AS = ashes; CW = Cottonwood,
and HB = hop-hornbeam.

Table 6

Numbers of replacers by canopy species eliminating elms as replacers. The abbreviations are the same as in Table 5.

| First replacer | Canopy Trees | | | | | | | | | | | | |
|-------------------|--------------|----|----|----|----|----|----|----|----|----|----|----|----|
| | SM | BE | BW | RM | TT | BC | EL | RO | SH | BH | AS | CW | HB |
| SM | 114 | 20 | 17 | 8 | 4 | 9 | 6 | 3 | 7 | 10 | 10 | 0 | 0 |
| BE | 10 | 10 | 3 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| BW | 3 | 2 | 13 | 1 | 0 | 1 | 4 | 0 | 1 | 0 | 0 | 0 | 0 |
| RM | 5 | 2 | 0 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| TT | 6 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| BC | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| RO | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| BH | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Toatl | 142 | 34 | 34 | 21 | 6 | 10 | 10 | 3 | 10 | 10 | 10 | 3 | 1 |

Table 7

The probabilities of replacement by canopy species.
The abbreviations are the same as in Table 5.

| First replacer | Canopy trees | | | | | | | | | | | | |
|-------------------|--------------|-------|-------|-------|-------|-------|------|------|------|------|------|------|----|
| | SM | BE | BS | RM | TT | BC | EL | RO | SH | BH | AS | CW | HB |
| SM | .732 | .588 | .500 | .381 | .500 | .900 | .60 | 1.00 | .70 | 1.00 | 1.00 | 0 | 0 |
| BE | .071 | .294 | .088 | .190 | 0 | 0 | 0 | 0 | .10 | 0 | 0 | 0 | 0 |
| BW | .021 | .059 | .382 | .048 | 0 | .100 | .20 | 0 | .10 | 0 | 0 | 0 | 0 |
| RM | .035 | .059 | 0 | .238 | 0 | 0 | 0 | 0 | .10 | 0 | 0 | 0 | 0 |
| TT | .042 | 0 | 0 | .143 | .167 | 0 | 0 | 0 | 0 | 0 | 0 | .667 | 0 |
| BC | .008 | 0 | 0 | 0 | .166 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EL | .077 | 0 | .030 | 0 | .167 | 0 | .20 | 0 | 0 | 0 | 0 | .333 | 1 |
| RO | .014 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1 |

Table 8

The probabilities of replacement by canopy species (elm replacers eliminated). The abbreviations are the same as Table 5.

| First replacer | Canopy trees | | | | | | | | | | | | |
|-------------------|--------------|-------|-------|-------|-------|-------|------|-----|------|-----|-----|-----|-----|
| | SM | BE | BW | RM | TT | BC | EL | RO | SH | BH | AS | CW | HB |
| SM | .803 | .588 | .500 | .381 | .667 | .90 | .60 | 1.0 | .70 | 1.0 | 1.0 | 0 | 0 |
| BE | .071 | .294 | .088 | .190 | 0 | 0 | 0 | 0 | .10 | 0 | 0 | 0 | 0 |
| BW | .021 | .059 | .382 | .048 | 0 | .10 | .40 | 0 | .10 | 0 | 0 | 0 | 0 |
| RM | .035 | .059 | 0 | .238 | 0 | 0 | 0 | 0 | .10 | 0 | 0 | 0 | 0 |
| TT | .042 | 0 | 0 | .143 | .167 | 0 | 0 | 0 | 0 | 0 | 0 | 1.0 | 0 |
| BC | .014 | 0 | 0 | 0 | .166 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| RO | .014 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.0 |
| Toatl | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.00 | 1.0 | 1.00 | 1.0 | 1.0 | 1.0 | 1.0 |

sugar maple. After removal of elm replacers, the same general tendencies were found. The slight differences in replacement probabilities are the result of most of the value of the elm replacers being added to the sugar maple category.

Predicted Future Canopy Composition

The transition probabilities were used as transition matrices to be multiplied by current canopy composition (in Table 1) as the column vector. Using a modification of the CHANGE program (Brewer and McCann 1982), the projected future canopy composition was produced. The results (Tables 9 and 10) indicate that (1) after three multiplications, composition approaches a stationary distribution; (2) sugar maple is most abundant and beech is second; (3) sugar maple becomes more important in the forest; (4) in the absence of Dutch elm disease, elm would be well represented in the climax canopy; (5) without elm, sugar maple is projected as even more numerous, but basswood is less well represented; and (6) at the steady state, 7 or 8 species remain in the canopy.

Table 9

The predicted future canopy composition of Brewer Woods

| Species | Generations of the forest | | | | | |
|-------------------|---------------------------|-----|-----|-----|-----|-----|
| | 0 | 1 | 2 | 3 | 4 | 5 |
| Sugar maple | 142 | 173 | 176 | 178 | 179 | 179 |
| Beech | 34 | 28 | 25 | 23 | 23 | 23 |
| Basswood | 34 | 20 | 17 | 16 | 16 | 16 |
| Red maple | 21 | 13 | 11 | 10 | 10 | 10 |
| Shagbark hickory | 9 | 0 | 0 | 0 | 0 | 0 |
| Bitternut hickory | 7 | 0 | 0 | 0 | 0 | 0 |
| Ashes | 7 | 0 | 0 | 0 | 0 | 0 |
| Tuliptree | 3 | 11 | 11 | 11 | 11 | 11 |
| Cottonwood | 3 | 0 | 0 | 0 | 0 | 0 |
| Black cherry | 2 | 2 | 3 | 3 | 3 | 3 |
| Elms | 1 | 15 | 19 | 20 | 20 | 20 |
| Hop-hornbeam | 1 | 0 | 0 | 0 | 0 | 0 |
| Red oak | 0 | 2 | 2 | 2 | 2 | 2 |
| Total | 264 | 264 | 264 | 263 | 264 | 264 |

Table 10

The predicted future canopy composition
(elm replacers eliminated)

| Species | Generations of the forest | | | | | |
|-------------------|---------------------------|-----|-----|-----|-----|-----|
| | 0 | 1 | 2 | 3 | 4 | 5 |
| Sugar maple | 142 | 184 | 194 | 197 | 198 | 198 |
| Beech | 34 | 28 | 26 | 25 | 24 | 24 |
| Basswood | 34 | 20 | 14 | 12 | 11 | 11 |
| Red maple | 21 | 13 | 11 | 11 | 11 | 11 |
| Shagbark hickory | 9 | 0 | 0 | 0 | 0 | 0 |
| Bitternut hickory | 7 | 0 | 0 | 0 | 0 | 0 |
| Ashes | 7 | 0 | 0 | 0 | 0 | 0 |
| Tuliptree | 3 | 12 | 12 | 12 | 12 | 12 |
| Cottonwood | 3 | 0 | 0 | 0 | 0 | 0 |
| Black cherry | 2 | 2 | 5 | 5 | 5 | 5 |
| Elm | 1 | 0 | 0 | 0 | 0 | 0 |
| Hop-hornbeam | 1 | 0 | 0 | 0 | 0 | 0 |
| Red oak | 0 | 3 | 3 | 3 | 3 | 3 |
| Total | 264 | 262 | 265 | 265 | 264 | 264 |

CHAPTER IV

DISCUSSION

General Description of the Forest

One of the generally accepted principles in forest ecology is that dominant species play a major role in forest development, because these species bear the brunt of external environmental forces. They are most important for classification of a community. Applying this to the studied area, Brewer Woods may be classified as a sugar maple-beech forest. As discussed above, sugar maple is a dominant species since it has a large number of the canopy trees per hectare, about 50% of the relative density and importance value (Tables 1 and 2). In understory composition, it accounts for more than 65% either in first or second replacers (see Table 5). The next important species is beech. Its importance value and replacement composition are arranged in the second place. Basswood and red maple may have a certain influence on the community, since they make up more than 20% of the canopy composition.

It is of interest to compare this disturbed forest with Warren Woods as an example of a similar old-growth

Table 11

Diameter size class distribution of the canopy trees (cm) at Brewer Woods. Four important species are shown. "Others" include tuliptree, elms, ashes, hickories, red oak, black cherry, cottonwood and hop-hornbeam.

| Species | Canopy class | | | | | |
|-------------|--------------|-------------|-------------|-------------|-------------|-----|
| | 20- 29.9 | 30- 39.9 | 40- 49.9 | 50- 59.9 | 60- 69.9 | 70- |
| Sugar maple | 10 | 43 | 66 | 17 | 5 | 1 |
| Beech | 5 | 6 | 11 | 10 | 2 | 0 |
| Basswood | 2 | 11 | 14 | 6 | 1 | 0 |
| Red maple | 0 | 3 | 11 | 6 | 0 | 1 |
| Others | 7 | 14 | 8 | 4 | 0 | 0 |
| Total | 24 | 77 | 110 | 43 | 8 | 2 |

forest. They differ not only in species composition and density, but also in canopy structure (Tables 11 and 12).

From these comparisons, several differences in the two forests are apparent: (1) The largest class of canopy trees in Brewer Woods is between 40-50 cm DBH with 70% of the canopy trees clustered in 30-50 cm, while in the Warren Woods, the peak value is between 60-70 cm DBH, with 78% of the canopy trees between 40-90 cm; (2) of 264 canopy trees, only two larger than 70 cm DBH were found in Brewer Woods. However, 31% (91) of the canopy trees were larger than this value in Warren Woods; and (3) Brewer

Table 12

Diameter size class distribution of canopy trees at Warren Woods. "Others" include basswood, tuliptree, black cherry, elms, hickories, white ash, red oak and sycamore. Data were from Brewer (unpublished).

| Species | Canopy class | | | | | | | |
|-------------|--------------|-------------|-------------|-------------|-------------|-------------|-------------|------------------|
| | 20- 29.9 | 30- 39.9 | 40- 49.9 | 50- 59.9 | 60- 69.9 | 70- 79.9 | 80- 89.9 | 90- 99.9 100- |
| Sugar maple | 6 | 3 | 6 | 14 | 5 | 7 | 11 | 2 2 |
| Beech | 3 | 19 | 26 | 36 | 56 | 27 | 20 | 9 6 |
| Red maple | 0 | 1 | 5 | 3 | 3 | 0 | 0 | 1 1 |
| Others | 2 | 3 | 4 | | 5 | 0 | 0 | 2 3 |
| Total | 11 | 25 | 41 | 53 | 69 | 34 | 31 | 14 12 |

Woods has a narrower diameter distribution than Warren Woods. It may be concluded from these data that Brewer Woods is not a climax forest at the present time. Its structure is less stratified and differentiated.

The current canopy trees in Brewer Woods show a more or less even age structure (Table 11), suggesting that the canopy trees could have grown from about the same size of sapling or subcanopy trees. If all trees which were larger than 30 cm DBH were removed from the forest at the time of disturbance (Brewer, personal communication), the current canopy trees would have gained about 18 cm DBH in 22 years (assuming that the average DBH of them was 25 cm at the

time of disturbance). The average growth rate, then, was about 0.8 cm DBH per year. One of the explanations for this high growth rate may be that before the timber cutting of 1962, the saplings were suppressed by canopy trees. Timber cutting not only opened the canopy, making light available for substory trees, but also reduced the competition between canopy and understory trees. In addition, opening of the forest accelerated the nutrient cycle through litter decomposition by microorganisms. The nutrients so released were taken up by remaining trees and used for their growth and reproduction.

Successional Trends

One of the successional trends generalized by Odum (1969) is that during succession, species diversity and stability of the ecosystem often increase. However, this generalization was questioned and even rejected by some ecologists (May 1972, 1974, 1976; Drury and Nisbet 1973). May used several mathematical models derived from the Lotka-Volterra model and confirmed that a system with more complexity in the sense of more species and a richer structure of interdependence was more fragile; that is, the higher the stage of succession, the less stable the community. In addition, some ecologists observed that, though species diversity increased in the early stage of secondary succession, peak diversity came prior to the

climax (Horn 1974, Auclair and Goff 1971, Bormann and Likens 1979, Whittaker 1975). To see what the successional trend for species diversity may be in Brewer Woods, the Shannon-Wiener index (H') (Shannon and Weaver 1963) was calculated.

The results (Table 13) show that for canopy species richness, Brewer Woods and Warren Woods are equal. However, because of the differences in equitability, H' is much higher in Brewer Woods than in Warren Woods. For the first and second replacers, both species richness and H' are higher in Brewer Woods than in Warren Woods. The results also indicate that canopy diversity in Brewer Woods is higher than in Hueston Woods. It should be noted

Table 13

Species richness and diversity comparison of three eastern North American sugar maple-beech forests

| Forest | Canopy | | Substory | |
|-------------------------|-------------|------|-------------|------|
| | Species No. | H' | Species No. | H' |
| Brewer Woods | 13 | .68 | 12 | .53 |
| Brewer Woods(predicted) | 9 | .52 | - | - |
| Warren Woods | 13 | .45 | 9 | .36 |
| Hueston Woods | 8 | .64 | 12 | .73 |

Sources: Data on Warren Woods from Brewer (unpublished); data on Hueston Woods from Vankat et al. (1975).

that the diversity of the predicted forest canopy composition of Brewer Woods is similar to that of Warren Woods. These findings suggest that (1) Brewer Woods is undergoing succession and as the succession proceeds, its diversity will decrease; and (2) a forest before reaching the equilibrium stage is more diverse than that at the climax stage.

What is the cause of the differing diversities of Brewer Woods and the climax forests? It is generally known that Warren Woods and Hueston Woods are beech-maple codominant climax forests. They have been externally undisturbed for a long time. They are considered to be steady state, self-regenerating communities. Basically, in a climax forest, the most important ecological factor is light. This factor determines the opportunity for shade-intolerant species to reach the canopy. Only in multiple-tree gaps created by wind throw or after catastrophic disturbance, such as fire and hurricane, is there more than an accidental chance of their reaching the canopy. Without external disturbance in Warren Woods and Hueston Woods, the shade-intolerant species maintain themselves as components of the canopy only by capturing the multi-tree gaps (Barden 1980, 1981, Williamson 1975). Therefore, the limited diversity is controlled by the community itself.

In contrast to Warren Woods and Hueston Woods, Brewer Woods is a young disturbed forest. All large trees were cut 22 years ago. This cutting created many openings in the forest, which offered opportunities for shade-intolerant species invasion and establishment. This disturbance released the saplings, including shade-tolerant and shade-intolerant species, creating many safe sites which were necessary for buried seeds to germinate (Oosting and Humphreys 1940) and seedlings to become established (Harper 1977).

It was reported that there existed a non-random replacement of tree species in eastern North American forests (Fox 1977, Woods 1979, Woods and Whittaker 1981, Poulsen and Platt n.d., Runkle 1981). Saplings of sugar maple did better under the canopy of beech trees and saplings of beech did better under the sugar maple canopy. However, Runkle (1981) and Barden (1980) also found that in more diverse forests, non-random replacement among species was weak or absent.

To determine whether non-random replacement occurs in Brewer Woods, a chi-square test was used (Table 14). It was found that there were no significant differences of association of sugar maple replacers with different canopy trees. This implies that sugar maple replaces all canopy species equally. On the other hand, there were stronger

Table 14

Interactions among canopy and replacement species. "Others" include red maple, tuliptree, ashes, elms, hickories, black cherry, red oak, cottonwood and hop-hornbeam. Significance values: ** = $p < .01$. * = $p < .05$.

| First replacer | Canopy species | | | |
|----------------|----------------|-------|----------|--------|
| | Sugar maple | Beech | Basswood | Others |
| Sugar maple | 104 | 20 | 17 | 56 |
| Beech | 10 | 10** | 3 | 5 |
| Basswood | 3* | 2 | 13** | 5 |
| Others | 25 | 2 | 1 | 18 |

associations for beech and basswood. Both species show significant tendencies toward the self replacement.

(Partial chi-square = 14.1 for beech, 1 df, $p < 0.01$; partial chi-square = 40.2 for basswood, 1 df, $p < 0.01$). A significant chi-square value was found for the interaction among canopy and replacement species as a whole (chi-square = 73.18, 9 df, $p < 0.01$).

The interpretation of these results may be that basswood sprouts prolifically at the root collar following injury by fire or cutting. Circular stumps of several trunks typically occur around decaying stumps on cutover area. Seven (30%) of basswood replacers were found growing close (< 1.0 meter) to the trunks of its canopy trees.

Unlike basswood, beech did not develop many sprouts around its trunks. Therefore, what contributes to the beech behavior of self replacement remains to be determined. That sugar maple has a high probability of replacing each of the canopy species may be interpreted as a result of its heavy reproduction coupled with its high shade tolerance. When the forest was opened during timber cutting, many sugar maple seedlings and saplings which had already been present there grew fast throughout the forest. Hence, its special association with any one of the canopy species is weak or absent.

In some climax beech-maple forests, because of the abundance of small individuals of sugar maple, a prediction based solely on its basal area tends to underestimate its importance, and a value based only on density tends to overestimate it. The reverse is true for beech, because it has fewer small individuals and a relatively large size of replacers (Runkle 1981). In general, a better fit between observed and predicted canopy composition in beech-maple forests may be obtained by averaging relative dominance and relative density than by using either alone. To see the differences in the future canopy compositions predicted by relative density, relative dominance, and relative density with replacers larger than 15 cm DBH, three transition matrices were constructed for calculating the future canopy

compositions. Both relative density and relative dominance methods produced the same result for sugar maple (Table 15), suggesting that sugar maple has a good representation of relative density and relative dominance in the substory. Beech, on the other hand, has fewer small saplings (no selected replacers were under 10 cm DBH) and a relatively large portion of the bigger replacers. Therefore, the value predicted by relative dominance is higher than that by relative density. If the prediction of beech from relative dominance is a better fit, the percentage of beech in the future canopy will be close to that of the present time. Predictions of either method show the reduction of other species in the future.

Table 15

Comparison of predicted canopy compositions by three different methods. "Others" include basswood, red maple, tuliptree, elms, black cherry and red oak.

| Species | Relative density | Relative dominance | Relative density with replacers larger than 15 cm DBH* |
|-------------|------------------|--------------------|--|
| Sugar maple | 68% | 68% | 65.7% |
| Beech | 8 | 12 | 14.5 |
| Others | 24 | 20 | 19.8 |

* From Table 17.

It has been observed that trees between seedling and sapling size (smaller than 15 cm DBH) suffer a high mortality rate (Woods 1979). If the replacers under this size are eliminated from calculations of the transition matrix, predictions for future canopy composition are different from those obtained by relative density and relative dominance. There were 92 replacers which were less than 15 cm DBH. Among them, 70% (64 trees) are sugar maple 26% (24 trees) are the other species, and only 4% (4 trees) are beech.

These figures are not proportional to frequencies of the total replacers (Table 3). Therefore, the replacement probabilities are changed (Tables 16 and 17). Future canopy composition predicted by these changed probabilities indicate that sugar maple and beech increase while other species decrease (Table 15). Especially, beech increases by a much higher proportion than sugar maple does. This suggests that the canopy composition, predicted on the basis of the replacers in Table 5, underestimates the eventual contribution of beech. This is because many of the less-than-15-cm-DBH trees will die before the corresponding canopy trees do. This implies that transition probabilities are not constant during succession.

Table 16

Larger than 15 cm DBH replacement composition and probability. "Others" include non-sugar maple-beech species.

| Replacer | Canopy trees | | | | | |
|-------------|--------------|-------------|-------|-------------|--------|-------------|
| | Sugar maple | | Beech | | Others | |
| | # | Probability | # | Probability | # | Probability |
| Sugar maple | 68 | 0.716 | 9 | 0.474 | 34 | 0.586 |
| Beech | 9 | 0.095 | 8 | 0.421 | 7 | 0.121 |
| Others | 18 | 0.189 | 2 | 0.105 | 17 | 0.293 |

Table 17

Prediction of future canopy composition with larger than 15 cm DBH replacers. Data are from Table 16.

| Species | Generation | | | |
|-------------|------------|-----|-----|-----|
| | 0 | 1 | 2 | 3 |
| Sugar maple | 95 | 111 | 113 | 113 |
| Beech | 19 | 24 | 25 | 25 |
| Others | 58 | 37 | 34 | 34 |
| Total | 172 | 172 | 172 | 172 |

Interpretation of the Succession

To interpret forest succession, Connell and Slatyer (1977) summarized three models of mechanisms of succession in natural communities and their role in community stability and organization, namely, facilitation, inhibition and tolerance models. In the facilitation model, after colonization of pioneer species in a site or region, the species modify the environment so that it is unsuitable for their own further recruitment. In contrast to the facilitation model, the inhibition model describes that once the early successional species occupy a site, they inhibit the invasion of later species or suppress the growth of those already present. The tolerance model is based on different responses to the environments in different species of the communities. The early species neither increase nor decrease the rate of establishment, recruitment and growth of later species. The "later" species may arrive at a site at the very beginning or later and appearing later in the canopy are simply because they cannot grow as rapidly as early successional species. On the other hand, they have the advantage of shade tolerance, stress tolerance and development of appropriate proportion of roots and shoots.

The facilitation model has been rejected by some ecologists (Egler 1954, Drury and Nisbet 1973, Horn 1974,

Botkin 1981). Egler (1954) proposed that each successional group, including the climax group, exists from the start of the succession (the initial floristic composition model). This theory was supported by Horn (1974), Drury and Nisbet (1973) and Franklin and Hemstrom (1981). After analysis of sequences of vegetation types, Drury and Nisbet concluded that the successional processes were not an orderly replacement of early species by members of later communities. Instead, almost all species were established before the succession started or colonized during the first few years. Recognized growth-form is indeed a reflection of the conspicuousness of certain species mixed with species having different sizes and maturity. It is not the purpose of this paper to argue which model is correct, but rather, to seek a proper explanation of the succession of Brewer Woods by consulting these models.

A combination of Connell and Slatyer's models with some evolutionary views may give a better explanation of successional trends. This combination, which is similar to the ideas suggested by Botkin (1981), states that during ecosystem evolution, life history and physiological characteristics of a species are important in determining the succession process. The early species modify the environment making it suitable for later successional species. Their giving way to later species is not a result

of creating an unsuitable habit for themselves, but rather, the modified environments make it easier for later species to invade that site. Consequently, because of a high competitive and tolerant capacity, the later species finally become dominant, while the early species are gradually lost from the community.

The causes producing current forest composition have been briefly discussed. Now the question is how sugar maple and beech have become and will continue to be dominant in Brewer Woods. The main evolutionary strategies responsible for this forest succession include a high reproductive rate, high competitiveness, greater shade and stress tolerance and long life of these two species.

Sugar maple has a high reproductive rate. It was reported that sugar maple produced a large number of seeds and many of them could germinate (Curtis 1971). These seedlings establish themselves on most sites, including under dense canopy. However, they survive less well there and grow very slowly. Many gaps were created in Brewer Woods during the timber cutting. This perhaps is a main factor favoring sugar maple seedlings and saplings' growth. This high productive strategy may be especially important in later successional processes.

Sugar maple and beech develop a highly competitive and tolerant strategy. (1) They employ an indeterminate growth pattern in which the winter bud carries a few

primordia and embryonic leaves, and these expand as the bud opens and extension growth begins in the spring (Bormann and Likens 1979). The advantages of this growth pattern are apparent: fewer preformed leaves would obtain enough nutrition during the winter so that they maintain a healthy state. By using the stored energy, these leaves expand very rapidly in the early growing season. This not only permits the plant to exploit the temporarily favorable environment at the beginning of the growing season, but also makes extension growth possible since the growing condition is good. In the early spring, on April 18, 1985, it was observed that the leaves of sugar maple and beech were nearly fully expanded, while leaves of hickories were only in the beginning stages. (2) They apply a long run growth strategy. Sugar maple shows a resistant type of shade tolerance, and beech, a slow performance type of shade tolerance (Poulson and Platt n.d.). The achievement of the tolerant growth pattern is through a greater expenditure of energy for root growth and a better geometry of leaves and branches. Sugar maple and beech have a higher root to shoot ratio in seedling and sapling stages than later successional species such as basswood. Their roots grow deeper than early successional species such as basswood and cottonwood (Bormann and Likens 1979). (3) They develop a competitive or tolerant strategy. Sugar maple and beech are monolayer at the

canopy scale of organization (Horn 1971, Poulson and Platt, n.d.), which offers these species an ability to inhibit other species by shading. They have a lower bifurcation ratio than early successional species (Horn 1971, Whitney 1976). Sugar maple also develops multilayer leaves in an inside scale of crown organization and produces heterophyll leaves with deeply indented sinues, and the leaves are held more vertically at high intensities (Steingraeber 1982). These geometrical characteristics, including early growth and deeper root systems, all contribute to the high degree of competitiveness and shade tolerance. (4) Long life span of both species, up to 300 or 400 years, may be another strategy contributing to their high competition capacity (Mark 1975). (5) Sugar maple may produce exudates which inhibit other species. Hence, allelopathy may play a role in survival of species on sites where sugar maple is abundant (Tubbs 1976).

Implication

The destruction of ecosystems has become an issue of public concern all over the world. How to maintain ecosystems in balance and preserve rare species is an urgent task facing us. We not only request lumber from the forests but also demand a sense for aesthetic

appreciation. To meet these demands, different types of management should be applied to the forest.

First, proper cutting is an ecologically acceptable procedure in forest management (Bormann and Likens 1979). The result of this study indicates that the canopy trees of Brewer Woods are developing at a high growth rate and the forest has not reached the high lumber yield and quality. Therefore, it is not the best time for timber cutting if one wants to manage this forest for lumber purposes. Another 10 to 50 years may be needed for the forest to reach its highest lumber-producing value.

Second, the finding of this study is consistent with the conclusion that continuous preservation of a forest will eventually result in loss of species (Brewer 1980). Therefore, preservation with frequent disturbance is necessary to maintain diversity of the forest (Loucks 1970, Heinzelman 1973, Pickett 1976). If this forest is going to be managed for stewardship purposes, a certain kind of disturbance should be applied because a mosaic forest may better satisfy an aesthetic appreciation.

Third, both management purposes may be combined. Small-scale, infrequent disturbances create the gaps which are necessary for maintaining species composition and diversity. This implies that selective cutting may not only satisfy the condition of shade-intolerant species regeneration, but also meets human requirements for timber

use. This method should be considered in future management.

Suggestions of Continuing this Research

The marking of trees in the forest studied may allow testing the validity of the transition model. The important assumptions of this model as mentioned above are that the succession is a tree-by-tree replacement process; canopy trees die in a limited period of the time; the transition probabilities are constant. To evaluate the methodology, this study should be continued in the future.

1. Repeating this study with the same method within a certain time interval for several tree generations is necessary. This study may give an answer as to whether replacement probability is constant or changeable.

2. The assumption of a tree-by-tree replacement process may be less reliable in a young forest than a climax forest, because the density of a young forest is not constant. To weigh this hypothesis, it is useful to study gap phase regeneration of this forest as previous investigators did elsewhere (Brewer and Merritt 1978, Barden 1980, Runkle 1981).

3. It might be useful to survey the interaction of understory and canopy more closely, for example, under what influence index (proposed by Woods and Whittaker

1981) will a sapling die or survive. This result may help us to explain the successional driving forces.

CHAPTER V

CONCLUSION

1. There are three major succession theories. They are holistic organismic succession, ecosystematic succession, and population succession.

2. Brewer Woods is a sugar maple-beech forest. Sugar maple is the most important species, and occupies about 50% of the canopy, 66% of the first replacers and 70% of the second. Beech is the second most important species making up 14% of the importance value of the canopy trees. Its replacer composition is in second place. Following these two species is basswood. Red maple takes the fourth position both in the canopy and understory composition. Eleven other minor species are found in this forest.

3. Brewer Woods is a young disturbed forest. Its structure is less stratified and differentiated than climax forest. The comparison of this forest with climax forest of North America supports that the species composition and diversity are higher in the preceding stage of the climax.

4. There is a different replacement pattern from Warren Woods and Hueston Woods where a reciprocal replacement pattern is dominant. Sugar maple replace all

canopy species randomly. Beech and basswood tend to replace their own.

5. The successional trends of this forest are that sugar maple, a shade tolerant species, will become more and more abundant at the expense of the others, especially of rare species. The composition of the future canopy, predicted by the transition matrix method, will be dominated by sugar maple and beech. Without external disturbance, several species such as hickories, ashes and cottonwood may be eliminated from the forest. When the forest reaches a steady state, it is similar to the climax forests of eastern North America.

6. Three succession models proposed by Connell and Slatyer were described. A combination of these three models is suggested for an explanation of successional trends of Brewer Woods. This combination states that the life history and physiological characteristics of a species are important, and that greater competition and higher stress tolerant capacities are the main driving force in the forest succession.

7. The result that species will be lost during the climax stage suggests that if the forest is managed for stewardship purposes, moderate disturbances are necessary because the creation of gaps may allow early successional species invasion, survival and growth. Selective cutting is a sound method for forest management.

8. It is recommended that this research be continued in order to evaluate the validity and reliability of the methodology.

BIBLIOGRAPHY

- Auclair, A. N., & F. G. Goff. 1971. Diversity relations of upland forest in the western great lakes area. Am. Nat. 105:499-529.
- Barden, L. S. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. Oikos 36:15-19.
- _____. 1981. Forest development in canopy gaps of a diverse hardwood forest of the south Appalachian Mountains. Oikos 37:205-209.
- Bormann, F. H., & G. E. Likens. 1979. Pattern and process in a forest ecosystem. New York: Springer-Verlag.
- Botkin, D. B. 1981. Causality and succession. pp 37-55. In D. C. West, H. H. Shugart & D. B. Botkin (eds.). Forest succession: Concepts and application. New York: Springer-Verlag.
- Botkin, D. B., J. F. Janak, & J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60:849-872.
- Brewer, R. 1979. Principles of ecology. Philadelphia: W. B. Saunders Company.
- _____. 1980. A half-century of changes in the herb layer of a climax deciduous forest in Michigan. J. Ecol. 68:823-832.
- Brewer, R., & M. T. McCann. 1982. A laboratory and field manual of Ecology. Philadelphia: Saunders College publishing.
- Brewer, R., & P. G. Merritt. 1978. Wind throw and tree replacement in a climax beech-maple forest. Oikos 30:149-152.
- Cain, S. A. 1935. Studies on virgin hardwood forest: III. Warren Woods, a beech-maple climax forest in Berrien County, Michigan. Ecology 16:500-513.
- Christensen, N. L., & R. K. Peet. 1984. Convergence during secondary forest succession. J. Ecol. 72:25-36.
- Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation. Washington, D. C.:

Carnegie Inst. Pub. 242.

- _____. 1936. Nature and structure of the climax. J. Ecol. 24:252-284.
- Connell, J. H., & R. D. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.
- Curtis, J. T. 1971. The vegetation of Wisconsin. Madison: University of Wisconsin Press.
- Drury, W. H., & I. C. T. Nisbet. 1973. Succession. J. Arnold. Arbor. 54:331-368.
- Egler, F. E. 1954. Vegetation science concepts. I. Initial development. Vegetatio 4:412-417.
- Fox, J. F. 1977. Alternation and coexistence of tree species. Am. Nat. 111:69-89.
- Franklin, J. F., & M. A. Hemstrom. 1981. Aspects of succession in the coniferous forest of the Pacific Northwest. pp 212-228. In D. C. West, H. H. Shugart & D. B. Botkin (eds.), Forest succession: Concepts and application. New York: Springer-Verlag.
- Gleason, H. A. 1917. The structure and development of the plant association. Bull. Torrey Bot. Club. 43:463-481.
- _____. 1939. The individualistic concept of the plant association. Am. Midland. Bot. 21:92-110
- Harper, J. L. 1977. Population biology of plants. London: Academic Press.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. 3:329-382.
- Hodler, T. W., R. Brewer, L. G. Brewer, & H. A. Raup. 1981. Presettlement vegetation of Kalamazoo County, Mich. (Map). Kalamazoo: Western Michigan Univ., Department of Geography.
- Horn, H. S. 1971. The adaptive geometry of trees. Monogr: Pop. Biol. 3. Princeton, New Jersey: Princeton University Press.

- _____. 1974. The ecology of secondary succession. Ann. Rev. Ecol. Syst. 5:25-37.
- _____. 1975. Markovian properties of forest succession. pp196-211. In M. L. Cody & J. M. Diamond (eds.), Ecology and evolution of communities. Cambridge, Massachusetts: Harvard University Press.
- _____. 1976. Succession. pp 187-204. In R. M. May (ed.), Theoretical ecology. Oxford, England: Blackwell.
- _____. 1981. Some causes of variety in patterns of secondary succession. pp 24-35. In D. C. West, H. H. Shugart & D. B. Botkin (eds.), Forest Succession: Concepts and application. New York: Springer-Verlag.
- Kenoyer, L. A. 1929. Ecological notes on Kalamazoo County, Michigan, based on the original land survey. Papers Mich. Acad. Sci. 11:211-217.
- Laufersweiler, C. G. 1955. Changes with age in the proportion of the dominants in a beech-maple forest in central Ohio. Ohio J. Sci. 55:73-80.
- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. Am. Zool. 10:17-25.
- MacMahon, J. A. 1981. Successional Processes: Comparisons among biomes with special reference to probable roles of and influences on animal. pp 277-304. In D. C. West, H. H. Shugart & D. B. Botkin (eds.), Forest succession: Concepts and application. New York: Springer-Verlag.
- Margalef, R. 1975. Diversity, stability and maturity in natural ecosystem. pp 151-160. In W. H. van Dobben & R. H. Lowe-McConnell (eds.), Unifying concepts in ecology. The Hague: W. Junk.
- _____. 1968. Perspectives in ecological theory. Chicago: University of Chicago Press.
- Marks, P. L. 1975. On the relation between extension growth and successional status of deciduous trees of north-eastern United States. Bull. Torrey Bot. Club. 102:172-177.
- Martin, H. M. 1958. Outline of the geological history of Kalamazoo County. Lansing: Michigan Department of Conservation, Geological Survey Division.

- May, R. M. 1976. Theoretical ecology. Philadelphia: Saunders.
- _____. 1972. Will a complex system be stable? Nature 238:413-414.
- _____. 1974. Stability in ecosystems: Some comments. pp 161-168. In W. H. van Dobben & R. H. Lowe-McConnell (eds.), Unifying concepts in ecology. The Hague: W. Junk.
- McIntosh, R. P. 1981. Succession and ecological theory. pp 10-23. In D. C. West, H. H. Shugart & D. B. Botkin (eds.), Forest succession: Concepts and application. New York: Springer-Verlag.
- Odum, E. P. 1969. The strategy of ecosystem development. Science 196:262-270.
- _____. 1971. Fundamentals of ecology (3rd. ed.). Philadelphia: Saunders.
- Oosting, H. J., & M.E. Humphreys. 1940. Buried viable seeds in a successional series of old field and forest soils. Torrey Bot. Club. Bull. 67:253-273.
- Peet, R. H. 1981. Changes in Biomass and production during secondary forest succession. pp 324-338. In D. C. West, H. H. Shugart & D. B. Botkin (eds.), Forest Succession: Concepts and application. New York: Springer-Verlag.
- Peet, R. H., & N. L. Christensen. 1980. Succession: a population process. Vegetatio 43:131-140.
- Pickett, S. T. A. 1976. Succession: an evolutionary interpretation. Am. Nat. 110:107-119.
- Poulsen, T. L., & W. J. Platt. No date (1981). Dynamics of beech-maple coexistence at Warren Woods, Michigan.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62:1041-1051.
- Shannon, C. E., & W. Weaver. 1963. The mathematical theory of communication. Urbana: Univ. of Illinois Press.
- Shugart, H. H., D. C. West, & W. R. Emanuel. 1981. Patterns and dynamics of forest: An application of

- simulation models. pp 74-94. In D. C. West, H. H. Shugart & D. B. Botkin (eds.), Forest succession: Concepts and application. New York: Springer-Verlag.
- Steingraeber, D. A. 1982. Heterophylly and neoformation of leaves in sugar maple. Amer. J. Bot. 69:1277-1282.
- Stephens, G. R., & P. E. Waggoner. 1970. The forest anticipated from 40 years of natural transitions in mixed hardwoods. Conn. Agric. Stat. Bull. 707.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284-307.
- Tubbs, C. H. 1977. Root crown relations of young sugar maple and yellow birch. USDA For. Serv., Res. Note NC-225. Minnesota: North Central Forest Experiment Station, St. Paul.
- Vankat, J. L., W. H. Blackwell, & W. E. Hopkins. 1975. The dynamics of Hueston Woods and a review of the question of successional status of southern beech-maple forest. Castanea 40:290-308.
- Vann, E. 1972. Fundamentals of biostatistics. Massachusetts: D. C. Heath and Company.
- Williamson, G. B. 1975. Pattern and seral composition in an old-growth beech-maple forest. Ecology 56:727-731.
- Whitney, G. G. 1976. The bifurcation ratio as an indicator of adaptive strategy in woody plant species. Bull. Torrey Bot. Club. 103:67-72.
- Whittaker, R. H. 1975. Communities and ecosystem (2nd. ed.). New York: Macmillan.
- _____. 1953. A consideration of climax theory: The climax as a population and pattern. Ecol. Monogr. 23:41-78.
- _____. 1980. Classification of plant communities. The Hague: W. Junk.
- Woods, K. D. 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. Oikos 33:31-39.
- Woods, K. D., & R. H. Whittaker. 1981. Canopy-understory interaction and the internal dynamics of mature

hardwood and hemlock-hardwood forests. pp 305-323.
In D. C. West, H. H. Shugart & D. B. Botkin (eds.),
Forest succession: Concepts and application.
New York: Springer-Verlag.