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# SPATIAL PATTERNS OF FOREST COMPOSITION, SUCCESSIONAL PATHWAYS AND BIOMASS PRODUCTION AMONG LANDSCAPE ECOSYSTEMS OF NORTHWESTERN LOWER MICHIGAN

by

George Edward Host

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ABSTRACT

SPATIAL PATTERNS OF FOREST COMPOSITION, SUCCESSIONAL PATHWAYS AND BIOMASS PRODUCTION AMONG LANDSCAPE ECOSYSTEMS OF NORTHWESTERN LOWER MICHIGAN

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George Edward Host

Spatial patterns of forest composition, successional pathways, and biomass production were related to glacial landforms in a regional area of northwestern Lower Michigan. There were three general objectives: 1) to develop a geomorphic map of the study area 2) to define and describe upland forest ecosystems, and 3) to study variation in species composition, successional pattern, and biomass production among landforms and ecosystems.

Glacial landforms were mapped using field observation, airphoto interpretation, and topographic profile analysis. Eighty sample stands were located in upland landscape positions using a landform-based stratified random sampling design. Detailed observations were recorded for the overstory, understory, ground flora and soils of each stand; nine ecosystems were identified.

Compositional patterns detected in multivariate analysis of floristic data were used to form ecological species groups and relate vegetation pattern to environmental factors. Chi-squared analyses showed significant patterns of species distribution related to landform. The Interlobate Moraine, a

predominant landform in the northwestern portion of the study area, was characterized by a northern hardwood canopy, with herbaceous annuals, perennials, and ephemerals forming the ground flora. All other morainal and glaciofluvial landforms supported oak overstories with predominately ericaceous ground flora species. Stand ordination scores were significantly correlated with a soil textural index, providing indirect evidence that soil moisture availability is an important factor influencing species composition.

Potential successional pathways were studied by comparing seedling and sapling densities with current overstory composition. The results indicate that oak is not regenerating in any landscape position, and that the potential future overstory varies by ecosystem.

Total aboveground biomass and biomass increment varied significantly among landforms and ecosystems. Biomass ranged from 84 to 250 t/ha; biomass increment ranged from 1.3 to 3.6 t/ha/yr). Differences in biomass increment were correlated with the ground flora ordination, indicating that composition and production may be controlled by similar environmental factors.

Variation in the composition, production, and structure of upland forests exhibits a pattern which corresponds closely to the geomorphic surface on which the forests developed. Under homogeneous climatic conditions, landform and edaphic patterns provide an ultimate constraint on both pattern and process in forest ecosystems.

This is dedicated to my parents
and to my aunts, uncles and cousins
who have given love and support over many years

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# Chapter 1

# INTRODUCTION

## Background

The present-day forests of northwestern Lower Michigan are an expression of the post-glacial migration histories of individual species, the influence of the physical environment on species establishment and growth, and the effects of natural and man-made disturbances over the past millenium. Understanding ecosystem composition and dynamics therefore involves describing factors which operate at many spatial and temporal scales. Spatial variation ranges from the energetic, moisture, and nutrient dynamics of the volumetric space occupied by an individual plant to global climatic patterns resulting from air mass circulation and land mass distributions. Temporal variation ranges from ecophysiological effects operating in circadean cycles to the historical response of vegetation to long-term climatic change. The temporal and spatial scales of interest must be defined before relationships between the physical environment and forest communities can be studied.

This study considers the composition and dynamics of upland forest ecosystems across a five county area within the Manistee National Forest (MNF), Michigan. Spatially, the study was conducted at the scale of glacial landforms (mapped at approximately 1:60,000) and local ecosystems (mapped at approximately 1:15,000). Damman (1979) has noted that scales from 1:50,000 to 1:250,000 show the effects of parent material, bedrock lithology, and topography on vegetation pattern, while scales of 1:10,000 to 1:20,000 reveal plant-soil relationships and allow quantification of site potential. Albert et al. (1986) have recently completed a classification of the state of Michigan at a scale of 1:1,000,000. Their classification used three hierarchical units - Regions, Districts, and Subdistricts - based on differences in macroclimate and physiography. The regional landscape considered in this study includes the Newaygo and Manistee districts and the Cadillac and Grayling subdistricts. Local ecosystems were defined within these districts based on physiography, ground flora, and soils (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985). The local ecosystems represent units which occur repeatedly in characteristic landscape positions and can be identified according to simple field criteria. The major hypotheses were that local ecosystems differ not only in composition and structure, but also in ecosystem functional processes. In particular, I was interested in ecosystem variation in potential successional pathways and levels of biomass production.

Current views of landscape ecology treat a regional landscape as a mosaic of relatively homogeneous units (patches), with transfers of material, energy, and organisms within and among units (Risser et al. 1983). The mosaic nature of a regional landscape is due to many physical and biotic factors, but these factors operate in a hierarchical fashion. In his study of community organization in the Serengeti grasslands, McNaughton (1984) concludes that "...geology, topography, and climate are primary environmental factors that establish the context within which soil formation, ecosystem development, and the evolution of grazing-web members are defined and constrained." The importance of McNaughton's conclusion is that geology, climate, and topography can be used, at least in a probabilistic sense, to account for some of the spatial variation in ecosystem composition, structure, and function.

Composition

Variability in species composition is one of the most fundamental and readily-observed characteristics of the regional landscape. Composition varies according to the physical environment (space), successional status (time), and stochastic events (disturbance, chance immigration, seed source, etc.). Two schools of thought have developed over the past century regarding the fundamental nature of plant communities. One school, derived from the work of Frederick Clements in America and the Zurich-Montpellier school of phytosociology in Europe, maintains that plant communities are real taxonomic units. Braun-Blanquet (1932), in fact, developed a Latin binomial system to identify plant communities. Modern proponents of this school of thought include Daubenmire (1966), who developed the habitat typing system used in western montane regions, and Coffmann et al. (1983), who developed a similar system for the northern portions of Michigan and Wisconsin.

The second school of thought, sometimes referred to as the "Wisconsin school", maintains that species respond individually and independently to environmental factors, and that "plant associations" have no reality in nature, but are conceptual abstractions in the mind of the phytosociologist. This view was first espoused by Gleason (1926), who states "...every species of plant is a law unto itself, the distribution of which in space depends on its individual peculiarities of migration and environmental requirements." Research in Wisconsin became oriented toward the analysis of species distribution along environmental gradients, and ordination techniques were developed to analyze the multivariate data obtained when species are considered individually (Curtis and McIntosh 1951, Bray and Curtis 1957, Curtis 1959, Whittaker 1960, Beals 1984). Recent work has used gradient analysis to explain variation in species distributions over both space and time (Peet and Loucks 1977), and to model ecological processes, such as nitrogen mineralization (Pastor et al. 1984, Pastor and Post 1986). A problem with the continuum approach, however, is that it becomes difficult to extrapolate ecosystem properties across a regional landscape, or to incorporate information into a cartographic system, i.e. the continuum view has little utility in land management.

A fundamental problem with both schools is that the methods used to sample the landscape influence the outcome. Sampling species composition along a prominent environmental gradient almost invariably shows vegetation change along that gradient. Sampling homogeneous landscape units with the exclusion of "ecotonal" areas will likely show significant differences among the sample units. The "observer's perspective" has lead to considerable debate among plant ecologists over the past several decades (Gleason 1926, Daubenmire 1966, Vogl 1966, Curtis and McIntosh 1966). Studies which relate the scale and rate of change of environmental variation to biological variation appear to hold more promise than either the entirely-discrete or entirely-continuous views of community organization.

## Succession

Understanding the potential successional pathways among ecosystems would be of great value to forest management, as well as to broader-scale environmental issues. Clear views as to the actual nature of the successional process, however, are lacking. Again, ecologists are divided as to whether communities ever reach a "climax" condition, or if forests are perpetually in nonequilibrium states. Palynological studies indicate that major changes in species composition have occurred over the last 1000 years (Swain 1972), and that species are still migrating in response to climatic change (Davis 1983). This evidence precludes possibilities of equilibrium communities at the millenium scale.

At more immediate time scales, there are several conflicting models of the successional process. "Relay floristics" models propose that existing species ameliorate site conditions for incoming species, while "inhibition" models maintain that existing species inhibit invasion by resource preemption (Connell and Slayter 1977). A large scale simulation model developed for the western Great Lakes (Shugart et al. 1973) predicts different late successional communities under different soil moisture regimes. An empirical study of early successional stages (Abrams et al. 1984), however, found multiple successional pathways on very similar sites.

Northwestern lower Michigan was heavily logged in the early part of the century (Mustard 1983, Whitney 1986). The present forests represent a pulse response to this large scale disturbance. Given the longevity of tree species typical of the area, it would be inappropriate to consider these as climax or even late successional forests. The present forests are second growth forests of similar age. As such, the size class distributions of species within ecosystems can be used to examine Rowe's (1984) hypothesis that landform exerts a primary control over short and long term ecosystem development.

Production

The final point of interest was the nature of variation in total aboveground biomass and biomass increment among glacial landforms and forest ecosystems. Biomass is important both from a land management standpoint and as an ecological index of productivity. Many ecological studies have focussed on biomass production, both empirically (Whittaker et al. 1979) and from a modelling standpoint (Botkin et al. 1972, Bormann and Likens 1979, Peet 1981). Understanding the influence of site factors on productivity is of major concern to forest managers (Carmean 1975), and a primary goal of site classification work, regardless of whether the classification is by soil series (Young et al. 1981, Ferwerda and Young 1981), habitat type (Steele et al. 1981) or ecosystem (Barnes et al. 1982).

Allometric regression equations have been developed for many of the major tree species of the northeastern United States. Equations which are based on both height and diameter and predict total aboveground dry weight are applicable over a wide geographic area (Ker and van Raalte 1981, Tritton and Hornbeck 1982). To estimate total biomass levels, all available allometric regression equations were compiled into an interactive microcomputer package. The estimates were then analyzed to study variation in biomass and biomass increment among landforms and ecosystems.

Project history

The study was conducted over a three year period in association with the development of an Ecological Classification System (ECS) for the Huron-Manistee National Forest. Ecological land classification systems have long been used in German forestry (Spurr and Barnes 1980), and have recently been introduced to American forestry (Barnes et al. 1982, Jordan 1982, Pregitzer and Barnes, 1984, Spies and Barnes 1985). The ECS project for the HMNF was initiated by Dr. James B. Hart, Michigan State University and Mr. David T. Cleland, USFS, in the late 1970's; actual field sampling began in 1983. The overall sampling strategy was devised by Drs. J. B. Hart, and C. W. Ramm; Dr. K. S. Pregitzer modified and improved the vegetation sampling design. Modifications to the original sample design for improvement, expediency, or additional study were made by myself and other graduate students involved in the field work. The classification system currently in use was developed over a two year period by the three MSU principal investigators, D. Cleland and myself. The classification system has gone through several revisions, so that the ecosystem classes presented herein may not represent the most current version of the classification.

Objectives

The objectives of this study were to:

1) develop a geomorphic map of the study area.

2) define ecological species groups for upland forests of the area and describe their ecological amplitudes and associations with particular geologic features.

3) define and describe upland forest ecosystems based on combinations of physiography, soils and ground flora vegetation.

4) quantify variation in species composition, potential successional pathways, and biomass production among glacial landforms and upland forest ecosystems.

The specific hypotheses to be tested were:

1) Ground flora species bear significant associations with specific glacial landforms.

2) The spatial distribution of ground flora species and overstory species can be related to an underlying environmental gradient.

3) Ecosystems exhibit different regeneration potentials, based on the presence and abundance of species in different diameter classes.

4) Ecosystems show significant differences in total biomass and mean annual biomass increment.

## GENERAL FIELD PROCEDURES

Sample design and plot locations

Landform was used as a basis for stratified random sampling of overstory, ground flora, and soils of 80 upland forest stands in the Manistee National Forest, northern Lower Michigan. Landforms were identified using existing USFS Land

Type Association (LTA) maps, 1:15,000 color infrared aerial photography, and field reconnaissance. Potential sample stands were chosen from stands selected from the TMIS data base or by field reconnaissance. Stands were selected randomly from the pool of potential stands and evaluated according to the following criteria:

1) the overstory must be at least 40 years old.
2) the stand must be normally stocked, i.e. the canopy should be closed to the extent permitted by site conditions.
3) stocking must be uniform throughout the stand; extensive open areas or diverse age distributions are cause for rejection.
4) the topography must be representative of upland conditions.
5) the soils must be well-drained: mottling in the upper 60 cm is cause for rejection.
6) aspen (*Populus grandidentata* and *P. tremuloides*) may not constitute more than 7 $m^2$/ha of basal area.
7) the stand must have no more than 30% of the dominant overstory in multiple stems (i.e. stump sprouts).
8) the stand must not show evidence of cutting or thinning in the past forty years.
9) the stand must not have been underplanted to pine.
10) stand composition must be relatively uniform.

Four random samples were located in each stand. The first point was located at least 60 m from the nearest road, and the remaining three points were located at random distances (not exceeding 100 m) and azimuths from the first point. All sample points were marked with steel reinforcing bar. Sample stand locations were marked on 1:62,500 USGS topographic quadrangles.

Overstory sampling

The overstory was sampled using a 10 BAF (English) wedge prism, with the steel reinforcing bar serving as plot center. The species, dbh, height, merchantable height (to a 10 cm top), crown class, and live crown ratio were recorded for all live tally trees > 9 cm dbh. Increment cores were taken from two dominant species at each point to determine average age at breast height (1.37 m).

Ground flora and understory sampling

The understory and ground flora vegetation were sampled using a 5 x 30 m rectangular plot centered over each of the four sample points. The percent ground cover was determined for all moss, herbaceous, and woody species in the plot using a modified Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974); the values represent cover class midpoints, as shown in Table 1.1. Octave or logrithmic abundance scales, such as the Braun-Blanquet scale, have been shown to be more efficient than straight percentage scales for ecological sampling (Gauch 1982). Cover-abundance values were determined by transversing the plot several times to compile a species list, and assigning abundance values after the list was complete. This method ensured that species were not overlooked, and aided in determining the coverage estimates. Relative frequencies for ground flora species were determined by recording the coverage of all species within six 1 $m^2$ frequency frames located at 5 m intervals along the long axis of the plot. Subsequent analyses showed that coverage values in the 1 $m^2$ frames gave poor estimates of total plot coverage, and these were later converted to binary (presence/absence) data.

Table 1.1 Cover-abundance classes used in field sampling.

| Class midpoint | Range of cover |
|---|---|
| r | Trace - 0.1 |
| + | 0.1 - 1.0 |
| 2 | 1 - 2 |
| 10 | 2 - 15 |
| 25 | 15 - 33 |
| 50 | 33 - 66 |
| 80 | 66 - 100 |

Densities of tree reproduction < 1.3 cm dbh were recorded in a subset of the sample stands using stem counts within the frequency frames. This reproduction was tallied by two size classes: stems < 30 cm in height and stems >30 cm in height but <1.3 cm dbh. Densities of woody stems 1.3 to 9 cm dbh were tallied by 2.5 cm diameter classes using stem counts in the 5 x 30 m plot.

## Soil sampling - field methods

Soil profiles for each subplot were described to 1 m using standard descriptive procedures (Soil Survey Staff 1975). The subplots were also evaluated to a depth of 4.5 m using a bucket auger to determine changes in soil texture. Within the soil pits, samples were taken at 20-30, 45-55, and 95-105 cm for textural and pH analysis. Six cores of the mineral surface horizon were extracted to a depth of 10 cm from within the frequency frames and used to determine pH and organic carbon content. The percent slope, slope shape and position, and aspect were recorded for each plot, and local topography was described.

## Soil sampling - laboratory methods

Soil pH was determined in a 1:1 soil-water mixture using a Corning 1.5 pH meter. Organic carbon was determined using the Walkley-Black titration method (Nelson and Sommers 1965). Sand size fractions and silt+clay content were determined by wet sieving; samples were shaken for two hours in a 5% sodium hexametaphosphate solution prior to sieving.

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Chapter 2

# ECOLOGICAL SPECIES GROUPS FOR UPLAND FOREST ECOSYSTEMS OF NORTHWESTERN LOWER MICHIGAN

## ABSTRACT

Ecological species groups were developed for upland forest ecosystems of northwestern Lower Michigan. Floristic data were collected in eighty upland forest stands using a stratified random sampling design, with stratification based on landform. The groups were formed using divisive classification, ordination space partitioning, and tabular analysis. Nine species groups were formed using 47 of the 93 species included in the analyses. The ecological amplitudes of the groups were related to both overstory composition and landform. The primary division in the divisive classification separated stands dominated by woody ericaceous species, sedges and grasses from stands dominated primarily by herbaceous annuals and perennials. The latter group comprised species characteristic of mesic northern hardwood sites, while the former comprised species commonly associated with oak-dominated stands on xeric or dry-mesic sites. Subsequent divisions segregated stands based on differences related to soil moisture. The groups occur in characteristic landscape positions throughout the regional study area, and may be useful indicators of selected site factors, such as moisture or nutrient availability.

# INTRODUCTION

Ground flora composition is a fundamental component of ecosystem classification systems (Barnes et al. 1982, Jordan et al. 1982, Pregitzer and Barnes 1982, Spies and Barnes 1985). Ecosystem classification seeks to identify portions of the landscape which are homogeneous with respect to vegetation, soils, and physiography (Barnes et al. 1982). Mapping by ecosystems allows for stronger interpretations of site potential than does mapping by soil or vegetation alone (Rowe 1984). Ecosystem classification is facilitated by the use of ecological species groups: groups of species with similar patterns of constancy and fidelity across a regional landscape (Mueller-Dombois and Ellenberg 1974). The use of species groups avoids problems due to the chance presence or absence of individual indicator species, and capitalizes on the ecological information available by using a significant proportion of the existing community. The objective of this study was to develop and describe ecological species groups for upland forest ecosystems of the Manistee National Forest. This specific work was part of a development of an ecosystem classification system for the Manistee National Forest.

Species groups for ecosystem classification have been formed numerically using agglomerative clustering techniques (Pregitzer and Barnes 1984) and subjectively using tabular arrangement methods (Mueller-Dombois and Ellenberg 1974, Spies 1985b). Both techniques have been used successfully, but each have inherent problems. The tabular arrangement method requires a good understanding of site and is inherently subjective. Agglomerative classification methods tend to be sensitive to "bad" fusions in the initial stages of clustering if atypical samples are present (Pielou 1984). Spies (1985b) found agglomerative clustering to be unsuccessful for forming species groups for the Sylvania Recreation Area, and suggested the use of two-way indicator species analysis (TWINSPAN), a polythetic divisive classification method (Hill 1979). TWINSPAN is designed to construct ordered species-by-sample tables (also known as synthesis tables) based on differential or indicator species. Synthesis tables are a mathematically-derived equivalent of the vegetation tables used by Spies (1985b). TWINSPAN may also be used to identify ground flora species which are important in discriminating different levels of classification.

A second approach to numerical development of species groups is ordination space partitioning (Gauch 1982). Ordination space partitioning is performed by constructing a two dimensional ordination of species and drawing partitions through sparse regions of the cloud of sample points. The ordination is based on Detrended Correspondence Analysis (DCA), a technique which avoids the problems of the "arch effect" and axis compression which occur when principle component analysis or reciprocal averaging are used with nonlinear data (Hill 1979). The clusters of species enclosed within the partitions should correspond to the groups of species derived by TWINSPAN.

While these numerical techniques are in themselves objective, the choice of techniques, the use of weighting coefficients, and the deletion of rare or "noisy" species are subjective decisions. Numerical methods are therefore not entirely objective, and are not meant to be used blindly as group-generating algorithms. They are, however, extremely valuable at detecting patterns of association based on constancy, fidelity, and abundance in vegetation data, and are therefore important techniques for the construction of ecological species groups.

## MATERIALS AND METHODS

### Sample design and field methods

Landform was used as a basis for stratified random sampling of overstory, ground flora, and soils of 80 upland forest stands in the Manistee National Forest, northern Lower Michigan. Landforms were identified using existing USFS Land Type Association (LTA) maps, 1:15,000 color infrared aerial photography, and field reconnaissance. Potential sample stands were chosen from stands selected from the U. S. Forest Service Timber Management Information System (TMIS) database and by field reconnaissance. We sampled normally stocked stands at least 40 years old, 1 ha or greater in area, with minimal evidence of recent disturbance, such as firewood cutting or windthrow. Stands with greater than 7 $m^2$/ha basal area in aspen (Populus grandidentata Michx. or P. tremuloides Michx.) were cxcluded from sampling. Much of northern Lower Michigan was heavily logged for white pine (Pinus strobus) at the turn of the century; in many cases logging was followed by fire (Mustard 1983). The intent of the selection criteria was to insure that the sample stands were minimally impacted by disturbance following their establishment at the turn of the century.

Four sample points were randomly established within each stand; these points served as loci for the sampling of overstory, ground flora, and soils. The overstory was sampled using a 10 BAF (English) wedge prism. The species, dbh, total height, merchantable height (to a 10 cm top), crown class, and live crown ratio were recorded for all live tally trees > 9 cm dbh. Increment cores were taken from two dominant treespecies at each point to determine average age at breast height (1.37 m).

Ground flora was sampled using a 5 x 30 m rectangular plot centered over each of the four sample points. Average percent ground cover was determined for all moss, herbaceous, and woody species in the plot using a modified Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974; Table 2.1). Abundance values were determined by transversing the plot several times to record the species present, and then assigning abundance values after the species list was compiled. Relative frequencies for ground flora species were determined by recording species presence/absence in six 1 $m^2$ frequency frames located at 5 m intervals along the long axis of each plot. Nomenclature for vascular plants follows Gleason (1952); nomenclature for bryophytes follows Crum and Anderson (1981).

Soil profiles for each subplot were described to 1 m using standard descriptive procedures (Soil Survey Staff 1975). Subsoils were evaluated to a depth of 4.5 m using a bucket auger to determine changes in soil texture. Percent slope, slope shape and position, and aspect were recorded for each plot, and local topography was described.

Table 2.1 Cover-abundance classes and ranks used in field sampling and data analysis.

| Class midpoint | Range of cover | Rank |
|---|---|---|
| r | Trace - 0.1 | 1 |
| + | 0.1 - 1.0 | 2 |
| 2 | 1 - 2 | 3 |
| 10 | 2 - 15 | 4 |
| 25 | 15 - 33 | 5 |
| 50 | 33 - 66 | 6 |
| 80 | 66 - 100 | 7 |

Statistical Methods

Ground flora species from 80 upland forest ecosystems were classified using the FORTRAN program TWINSPAN (Hill 1979). TWINSPAN divides samples into groups by repeated dichotomization, and identifies the major indicator species at each level of division. The divisions are based on reciprocal averaging, a variation of principle component analysis which simultaneously ordinates stands and species. The analysis was performed using the stand level mean rank cover-abundance values of 93 herbaceous, woody and moss species. Species with less than 5% frequency at the stand level were excluded from analysis. In addition, rare species (species with less than 0.1% coverage) which occurred on only 1 plot/stand were also excluded. Deletion of characteristically rare species has been shown to remove very little information from the data set (Gauch 1982).

Species were also subjected to DCA using the FORTRAN program DECORANA (Hill 1979). Ordination space partitioning (DCASP; Gauch 1982) was used to identify clusters of species and corroborate the groups derived from TWINSPAN.

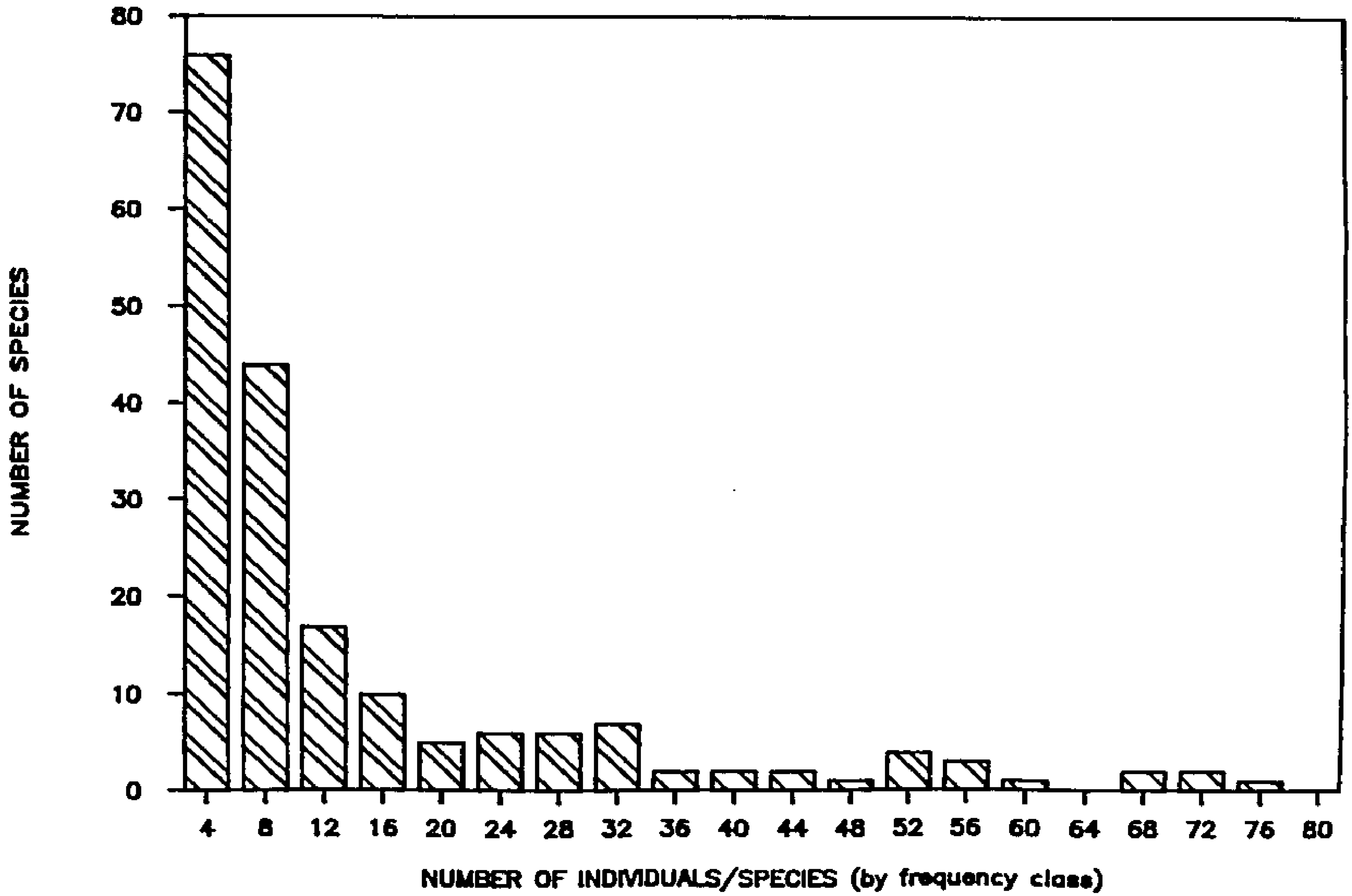
Ecological species groups were derived from interpretation of the TWINSPAN synthesis table, the indicator species identified by TWINSPAN, and the species clusters identified by DCASP. Tree seedlings and species represented by a few sporadic occurrences were not used as species group members.

## RESULTS AND DISCUSSION

Seventy-seven of the 80 sample stands were used in the multivariate analyses; three stands were considered outliers; these had atypical overstories or were not representative of typical upland forest. One hundred ninety ground flora species were recorded in the 77 stands. Of these, 120 species had stand level frequencies of 5% or higher, and 93 had sufficient coverage and frequency within stands to be included in the analysis. Species frequency data approximated a truncated log-normal distribution pattern (Figure 2.1) as described by Preston (1948).

The first level division of TWINSPAN was related to differences in overstory composition (Table 2.2). This division separated species characteristic of oak-dominated stands from those characteristic of stands dominated by northern hardwoods. In general, the ground flora of oak-dominated stands was dominated by woody ericaceous species, such as Vaccinium angustifolium and Gaultheria procumbens, while northern hardwood stands were dominated by herbaceous species, such as Osmorhiza claytonii and Viola canadense. It was noted during field sampling that many of the northern hardwood stands also support a diverse spring ephemeral flora, whereas spring ephemerals were absent from oak-dominated stands. Subsequent TWINSPAN divisions appeared to be related primarily to moisture availability. Within oak forests, the next TWINSPAN division separated species characteristic of extremely well drained glacial outwash, such as Deschampsia flexuosa and Arctostaphylos uva-ursi, from those found in more mesic landscape positions. The major division within the northern hardwood forests also

Figure 2.1 Stand level frequency distribution of 120 ground flora species.



NUMBER OF SPECIES
0
10
20
30
40
50
60
70
80
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
72
76
80
NUMBER OF INDIVIDUALS/SPECIES (by frequency class)

Table 2.2 Ecological species groups for the upland forest ecosystems in the Manistee National Forest. Values are cover classes used by TWINSPAN.[a] Vertical divisions separate classes of stands with similar ground flora composition.

| | STANDS (coded by stand number) | | | | | |
|---|---|---|---|---|---|---|
| | Oaks | | | | Northern Hardwoods | |
| ECOLOGICAL SPECIES GROUPS | 545554556<br>580399145 | 6771672673 233 1113447 355667<br>68987593181983481259566302818З | 7667811124<br>7290036707 | 1167 46<br>40024544 | 35334724522<br>717250451613 | 2222433<br>64672367 |
| **Deschampsia group** | | | | | | |
| Deschampsia flexuosa | 33543-1-1 | -1——1—2————1— | ———— | ——— | ————— | ——— |
| Andropogon gerardii | 121—11— | ———————— | ———— | ——— | ————— | ——— |
| Arctostaphylos uva-ursi | -13112-11 | ———————— | ———— | ——— | ————— | ——— |
| Pleurozium scheberi | 1——1111 | ——1—————11— | -1——— | ——— | ————— | ——— |
| Comptonia peregrina | -233331-1 | 1———11-11-11——1—— | ———— | ——— | ————— | ——— |
| Cladina rangiferina | 1—11-— | -1——1—111———— | ———— | ——— | ————— | ——— |
| **Vaccinium group** | | | | | | |
| Dicranum polysetum | 2—121111 | -1——1—21111111-1111-1111—1 | -1-1—1— | ——— | ————— | ——— |
| Melampyrum lineare | 112111-1- | -11—11-22-112111111111-11-1-1- | -1-11—— | 1——— | ————— | ——— |
| Gaylussacia baccata | 1——1— | 332-1-131-1-3331-131-13111—22 | 2—1——— | ——— | ————— | ——— |
| Epigaea repens | —111—— | —————1-1-112——111— | -1——1— | ——— | ————— | ———1- |
| Vaccinium angustifolium | 424343252 | 33-1334342333232123334333344444 | 4312212122 | 1112-1-2 | ————— | ——— |
| Gaultheria procumbens | 11121—— | 1—1112212121111122221-11-3121 | -212212111 | 1122-1-1 | ————— | ——— |
| Leucobryum glaucum | ———— | -1———1——1—11—1——— | ——11—— | ——— | ————— | ——— |
| **Hamamelis group** | | | | | | |
| Hamamelis virginiana | ———1— | —222-31-211-121—32222231333 | 1-341-1221 | 22222314 | —1———— | ——— |
| Sassafras albidum | ————3 | -2—33133313332333123-332-43332 | 43232-2123 | 112-1233 | ————— | ——— |
| **Pteridium group** | | | | | | |
| Pteridium aquilinium | 122342312 | 4214465662334332322232244334343 | 5245414212 | 12333422 | 3—111—11- | ——— |
| Amelanchier spp. | 1-12211-1 | 2112221111111111-211122111213-22 | 3233211111 | 1-321112 | 11—111—— | ——1— |
| Carex pensylvanica | 566666666 | 5556666666545553232323323434343 | 5343511312 | 1224-123 | 11-3—32—11 | 1211—— |
| **Trientalis group** | | | | | | |
| Trientalis borealis | ———— | ——————1—11———1-1- | —1—11-1- | 112111— | —1——— | ——— |
| Aster macrophyllum | ———— | ——11—1————1————1—1- | 11111——1- | 1111—11 | ————— | ———1— |
| **Desmodium group** | | | | | | |
| Desmodium spp. | ———— | ————1—————1——1—— | 4-1-1——— | -1-11243 | ———1—— | ——— |
| Viola pubescens | ———— | ———————— | ———— | 11-211— | ————— | 1——— |
| Cornus florida | ———— | —1——————1——— | ———— | —36165 | ————— | 11-1—— |

Table 2.2 - continued page 2

STANDS (coded by stand number)

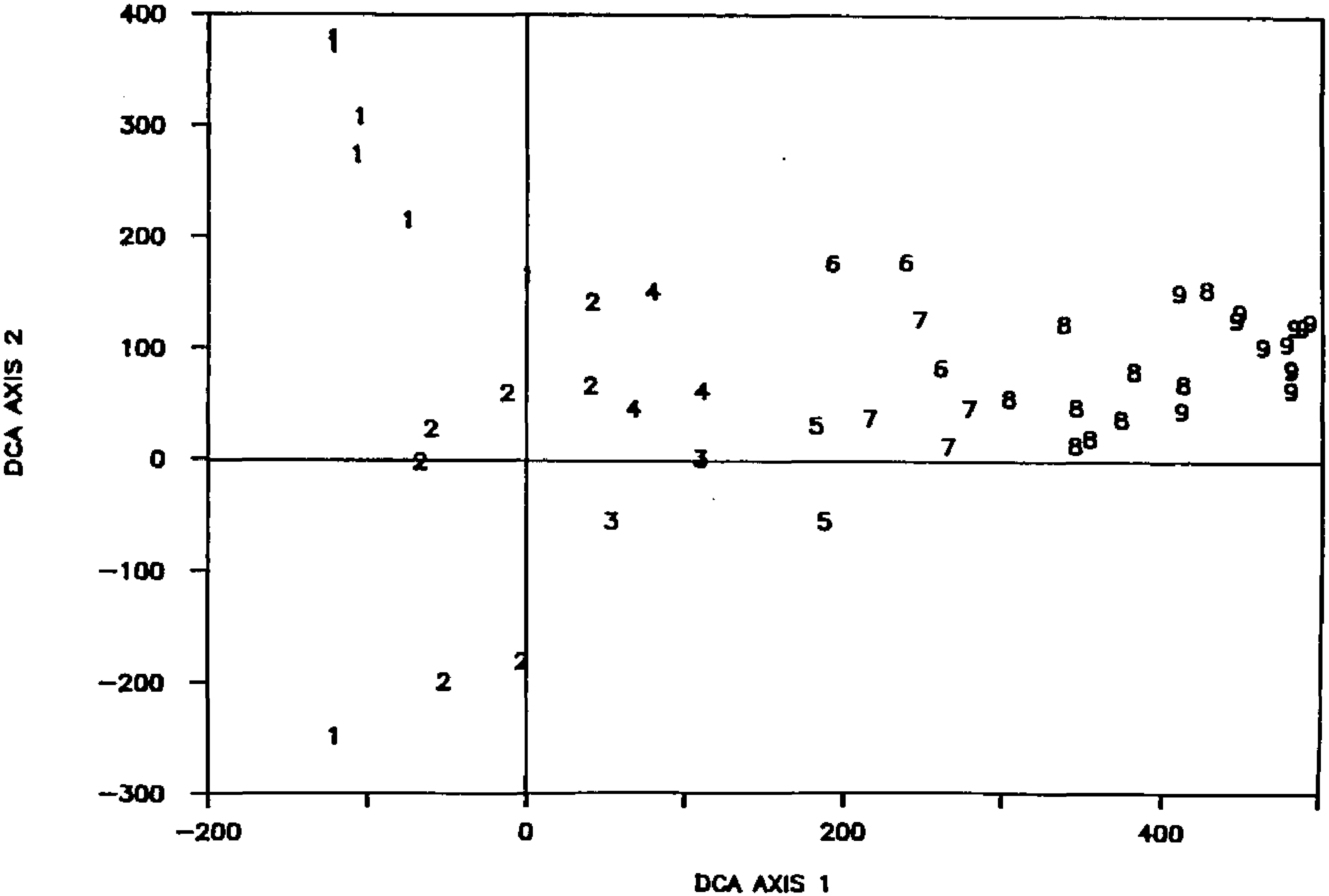
| | Oaks | | | | Northern Hardwoods | |
|---|---|---|---|---|---|---|
| | 545554556 | 6771672673 233 1113447 355667 | 7667811124 | 1167 46 | 35334724522 | 2222433 |
| ECOLOGICAL SPECIES GROUPS | 580399145 | 68987593181983481259566302818 3 | 7290036707 | 40024544 | 717250451613 | 64672367 |
| Viburnum group | | | | | | |
| Viburnum acerifolium | ——————— | ——111——————11111111—121-2 | 3332212-11 | 41442334 | —222-2——1- | -2-11—— |
| Aralia nudicaulis | ——————— | ————————————————————————1- | 21211————1 | 2111-1-1 | ——1——111- | 12-1211- |
| Medeola virginiana | ——————— | —————————————————————————— | —————————— | 1—1——— | ——————————1- | ———————— |
| Mitchella repens | ——————— | ——————————————1———————————— | ———————1--1- | -211--1 | --1-111--- | ----1 |
| Maianthemum group | | | | | | |
| Maianthemum canadense | ——————— | —————————————————1—————1- | 111-11111- | 11221—— | 112111111211 | 22111222 |
| Epifagus virginiana | ——————— | —————————————————————————— | —————1———— | ————————— | ——————————1-1 | ———————— |
| Polygonatum biflorum | ——————— | —————————————————————————— | ——————————11 | 1——11—— | 1-211-111—— | 11—2111 |
| Lycopodium lucidulum | ——————— | —————————————————————————— | —————————— | ————————— | ——————1—11 | ———————— |
| Carex deweyana | ——————— | —————————————————————————— | —————————— | ————————— | -11--1—11— | 1————11- |
| Lycopodium obscurum | ——————— | —————————————————————————— | —————————— | ——1————— | ——————1-211 | ———————— |
| Carex pedunculata | ——————— | —————————————————————————— | —————————— | ————————— | 1-11-1-111-- | 1——————— |
| Solidago caesia | ——————— | —————————————————————————— | 1—————————1 | ————————— | -121—1—————— | ————21—— |
| Dryopteris spinulosa | ——————— | —————————————————————————— | —————————— | ———1———— | ——————————1 | ——1——11 |
| Osmorhiza group | | | | | | |
| Osmorhiza claytonii | ——————— | —————————————————————————— | —————————— | -1—————— | ——1———1——— | 32143114 |
| Adiantum pedatum | ——————— | —————————————————————————— | —————————— | ————————— | ———————————— | 11———1 |
| Mitella diphylla | ——————— | —————————————————————————— | —————————— | ————————— | ———————————— | 11-221— |
| Tiarella cordifolia | ——————— | —————————————————————————— | —————————— | ————————— | ———————————— | 12-11--- |
| Allium tricoccum | ——————— | —————————————————————————— | —————————— | ————————— | ———1———————— | 32-121— |
| Hepatica acutiloba | ——————— | —————————————————————————— | —————————— | ————————— | ——1————————— | -1——1—— |
| Uvularia perfoliata | ——————— | —————————————————————————— | —————————— | ————————— | ———————————— | ——121-2 |
| Actaea alba | ——————— | —————————————————————————— | —————————— | ————————— | ———————————— | ——————1 |
| Botrychium virginianum | ——————— | —————————————————————————— | —————————— | ————————— | ———————————— | 11-111— |
| Caulophyllum thalictroides | ——————— | —————————————————————————— | —————————— | ————————— | ———————————— | 12-111-1 |
| Carex plantaginea | ——————— | —————————————————————————— | —————————— | ————————— | —11—————1- | 111111— |
| Viola canadense | ——————— | —————————————————————————— | —————————— | ——————1- | -1-1———————— | 12121-11 |

[a] Cover class values: 1 - <2%, 2 - 1-2%, 3 - 2-15%, 4 - 15-33%, 5 - 33-66%, 6 - 66-100%.

appeared to be related to soil moisture, with a diverse herbaceous ground flora community occurring in the most mesic landscape positions.

The differences in ground flora composition between oak and northern hardwood stands were also evident in the first axis of the detrended correspondence analysis (Figure 2.2); species common in oak-dominated stands received negative or low first axis scores, while species common in northern hardwood stands received high first axis scores. The first axis accounted for 70% of the first four summed eigenvalues; the second axis accounted for 15%. The species clusters in the ordination space corresponded closely with the groups derived by TWINSPAN. In contrast with TWINSPAN's divisive classification, however, the ordination shows that species composition along this underlying ecological gradient changes in a continuous, rather than discrete fashion. This continuous pattern of compositional change was also evident in studies of Wisconsin forests (Bray and Curtis 1959, Peet and Loucks 1977).

Figure 2.2 Detrended correspondence analysis of 49 ground flora species. Values represent ecological species group membership: 1 - Deschampsia, 2 - Vaccinium, 3 - Hamamelis, 4 - Pteridium, 5 - Trientalis, 6 - Desmodium, 7 - Viburnum, 8 - Maianthemum, 9 - Osmorhiza.


400
300
200
100
0
−100
−200
−300
−200
0
200
400
DCA AXIS 1
DCA AXIS 2

# ECOLOGICAL SPECIES GROUPS

Nine ecological species groups were produced using 48 of the 93 species included in the analysis. Seven of the species groups were associated with oak forests; the remaining two groups were associated with northern hardwood forests. The species groups, their ecological amplitudes, and their relationship to other groups are presented in Table 2.2 and described below.

## Deschampsia group

The Deschampsia group is characteristic of xeric, extremely well-drained sandy outwash plains under open upland pin oak-black oak canopies. *Carex pensylvanica* and *Deschampsia flexuosa* are very abundant (generally > 60% ground coverage) and form a dense continuous mat across the forest floor. *Comptonia peregrina*, *Arctostaphylos uva-ursi* and *Chimaphila umbellata* occur in scattered clonal patches. The Deschampsia group is almost always associated with the Pteridium and Vaccinium groups, but is restricted to extremely xeric sand plains.

## Vaccinium group

The Vaccinium group is widely distributed across well drained sand plains and hills under white oak-black oak overstories. Canopy closure is complete but not dense. *Vaccinium angustifolium*, *Gaultheria procumbens*, and *Gaylussacia baccata* have the highest abundance. Seedlings of

*Quercus velutina* and *Q. alba* are also abundant. *Epigaea repens*, *Dicranum polysetum*, and *Melampyrum lineare* are less abundant and occur as scattered individuals. This group is commonly associated with both the Pteridium and Deschampsia groups, but is not as widely distributed as the Pteridium group.

Pteridium group

The Pteridium group comprises species which are widely distributed with relatively high frequency across most of the upland landscape. *Pteridium aquilinium* is found in high abundance in stands with open canopies. *Amelanchier* spp. typically occurs as a low shrub under a variety of canopy conditions. *Carex pensylvanica* is one of the most frequent species, occurring in over 85% of the sample stands. The greatest coverage of *Carex pensylvanica* occurs under open oak canopies on xeric outwash plains, where it forms an extensive lawn-like mat (typically > 60% coverage) over most of the forest floor.

Hamamelis Group

The Hamamelis group occurs on well drained sand hills and plains under white and red oak overstories. Canopy closure is complete but not dense. This group is commonly associated with the Vaccinium and Pteridium groups, but typically is absent from xeric outwash plains.

Trientalis group

The Trientalis group is widely distributed across well-drained to moderately well-drained ice contact landforms under closed red oak-white oak canopies. Commonly associated with the Vaccinium and Viburnum groups, the Trientalis group occupies an intermediate position on the moisture gradient. On hilly landforms, these species are more frequent on upper slope positions along with members of the Vaccinium group, while the Viburnum group is more frequent on lower slope positions.

Viburnum group

The Viburnum group is widely distributed across well drained to moderately well drained ice contact landforms under closed red oak-white oak canopies. Viburnum acerifolium occurs as a low shrub ( < 30 cm in height) in scattered clones. Trientalis borealis, Aralia nudicaulis and Aster macrophyllum are common. The Viburnum group is typically associated with the Vaccinium and Pteridium groups, but indicative of somewhat more mesic soil conditions.

Desmodium group

The Desmodium group is characteristic of well drained to moderately well drained moraines, ground moraines or glacio-lacustrine deposits under closed red oak-red maple canopies. Cornus florida and Desmodium spp. are found with high abundance, generally greater than 25% coverage. Viburnum acerifolium occurs as a tall shrub (40-60 cm) in large clonal patches. The Desmodium group appears to be restricted to sites having loamy surface horizons or loam-textured bands within 4.5 m.

Maianthemum group

The Maianthemum group occurs under dense sugar maple-beech-red oak canopies and is characterized by having very sparse coverage of the forest floor (generally less than 5% total coverage). Most of the forest floor is covered with a heavy litter layer of hardwood leaves. Maianthemum canadense and the two species of Lycopodium generally occur in large clonal patches. This group is associated with the Osmorhiza and Viburnum groups.

Osmorhiza group

The Osmorhiza group occurs with high fidelity on soils having thick A horizons with high pH and organic carbon contents. The soils are generally well drained sands to loamy sands underlain by nonpedogenic sandy clay loam to clay loam bands. The group is typically found under a closed sugar maple-basswood canopy: Allium tricoccum and Dicentra spp. are dominant members of the spring ephemeral community, while Osmorhiza claytonii, Viola canadense, and Carex plantaginea are abundant later in the growing season. The Osmorhiza group exhibits high species diversity and complete coverage of the forest floor. The Maianthemum group is a common associate.

## SUMMARY

Nine ecological species groups have been identified for upland areas of the Manistee National Forest using two way indicator species and detrended correspondence analyses. Differences in the ecological amplitudes of these groups seem to be related primarily to current overstory composition and soil moisture holding availability. Two groups are common to northern hardwood forests, while seven are associated with oak overstories. The groups tend to occur in characteristic landscape positions. The Deschampsia group, for example, is most common on extremely well drained level outwash plains, whereas the Viburnum group occurs on well to moderately well-drained rolling ice contact or morainal hills. Groups which have relatively narrow ecological amplitudes may be useful in site classification work, as they indicate a limited range of site conditions. The indicator values of the groups appear to be consistent across this regional landscape, but will likely shift with changes in climatic or physiographic boundaries.

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Chapter 3

# THE ROLE OF LANDFORM IN THE COMMUNITY ORGANIZATION OF UPLAND FORESTS IN NORTHWESTERN LOWER MICHIGAN

## ABSTRACT

The ground flora, overstory, and soils of 80 upland forest stands were related to the glacial geomorphology of a five county area in northwestern Lower Michigan. Glacial landforms were mapped using field observation, air photo interpretation, and topographic profile analysis; nine classes of landforms were identified based on parent materials and surface configuration. Binary discriminant and detrended correspondence analyses were used to study the relationship of species distribution patterns with landform.

Chi-squared tests of association showed patterns of species distribution to be significantly related to landform. The Interlobate Moraine, a predominant landform in the northwestern portion of the study area, was characterized by a northern hardwood canopy, primarily sugar maple, basswood, and red oak, with herbaceous annuals, perennials, and ephemerals forming the ground flora. All other morainal and glaciofluvial landforms had oak overstories with woody ericaceous ground flora species. Outwash plains, the most xeric landforms, had high basal areas of black and white oak (9.3 and 8.4 t/ha, respectively) and high coverages of *Carex pensylvanica* and *Deschampsia flexuosa*. More mesic landforms

had higher proportions of red oak and a concomitant change in ground flora composition.

Moisture availability, as evidenced by soil textures and the presence of subsurface textural discontinuities, was significantly related to the composition and abundance of both overstory and ground flora species. Since moisture availability is a function of depositional and post-glacial history, glacial landform provides a means of predicting species composition, at least in a probabilistic sense. Moreover, the occurrence of specific assemblages of overstory and ground flora species in characteristic landscape positions should allow identification of landscape ecosystems, i.e. spatial units which are relatively homogeneous in composition and structure. It is likely that landscape ecosystems vary in process, such as successional dynamics and biomass production, as well as in spatial pattern. Maps of landscape ecosystems would therefore allow functional processes to be extrapolated across regional areas.

# INTRODUCTION

Studies of the Lake States forests have reported that forest composition varies continuously along complex ecological gradients (Cottam 1949, Curtis and McIntosh 1951, Bray and Curtis 1957). Initial studies in Wisconsin by Curtis and McIntosh (1951) described patterns of compositional change, but did not separate temporal from environmental effects. Peet and Loucks (1977) identified complex moisture-nutrient and successional gradients as the predominant factors explaining forest composition, and showed that successional sequences became longer and more complex as conditions became more mesic. Pastor et al. (1982) showed that species composition under fixed climatic conditions varied as a response to a complex soil texture-N mineralization gradient, which in turn was related local geology. More recently, Pastor and Post (1986) produced a computer simulation model driven by moisture and temperature to predict production and species composition. While the general association of species composition to geologic history has long been recognized (Jenny 1941, Major 1955), there have been few quantitative studies of relationships between species distribution patterns and specific geomorphic features of the Lake States forests. The objective of this study was to identify and map glacial landforms across a regional landscape in northwestern Lower Michigan, and to study the relationship of vegetation pattern to landform.

In a study of community organization in the Serengeti grasslands, McNaughton (1984) concluded that geology, topography, and climate are the primary environmental factors which define and constrain soil formation and ecosystem development. Within a relatively homogeneous climatic region in northwestern Lower Michigan, it was expected that the landscape pattern imparted by glacial and post-glacial geomorphic events should explain a significant proportion of the variation in species distribution patterns. Rowe (1984) has stated that landform, defined as surficial topography + parent materials, provides the stable morphologic base upon which soil formation and ecosystem development take place. The nature of geologic parent materials affects the development, moisture-holding capacity and fertility of soils, which in turn exerts a stong influence on species composition (Peet and Loucks 1977, Pregitzer and Barnes 1982, Pregitzer et al. 1983, Pregitzer and Barnes 1984, Hupp and Osterkamp 1985, Spies and Barnes 1985a). Surficial topography controls patterns of insolation and drainage. Topographic breaks influence the rate of wildfire spread and their areal extent. Grimm (1984) has attributed the current overstory composition of the Big Woods of Minnesota to the landform-mediated history of fires in that area. By understanding how landforms vary in topography and parent materials across a regional landscape, it should be possible to predict some of the pattern of community composition, even in highly disturbed regions.

Significant patterns in species distribution data can be obfuscated by unpatterned variation in the data matrix. Unpatterned variation is a result of the chance distribution and establishment of individuals, random local disturbances, and environmental heterogeneity at scales below that of the sample area (Gauch 1982). Various techniques have been derived to minimize unpatterned variation. One such approach is the use of ecological species groups, i.e. groups of species with similar patterns of constancy and fidelity (Mueller-Dombois and Ellenberg 1974). The use of ecological species groups capitalizes on the ecological information obtained in using a significant proportion of the existing community, and minimizes the effects of the chance presence or absence of an individual indicator species (Spies and Barnes 1985b). Pregitzer and Barnes (1982) have shown select species groups to be strongly associated with specific edaphic factors, such as soil drainage or reaction. Relationships between species and categorical units, such as landform or soil type, can be evaluated statistically using binary discriminant analysis (BDA), a two stage technique combining contingency table and principal component analyses (Strahler 1978). Hupp and Osterkamp (1985) used BDA discriminant analysis to relate the distribution of woody species to fluvial landforms in Virginia. This study uses BDA and detrended correspondence analysis (DCA; Hill 1979) to evaluate spatial patterns of ground flora species, ecological species groups, and overstory species in relation to glacial landforms in a five county area of northwestern Lower Michigan.

## MATERIALS AND METHODS

### Study area

Sample stands were located on upland sites throughout the Manistee National Forest in Manistee, Wexford, Mason, Lake, and Newaygo counties in northwestern Lower Michigan. The study area was generally north of the "tension zone"; the transition zone between boreal and temperate communities (Potzger 1946). The area occupies portions of the Newaygo and Manistee Districts and the Cadillac and Grayling Subdistricts of the recently completed physiographic and climatic classification of Michigan (Albert et al. 1986). The growing season ranges from 126 days in western part of the study area to 115 days in the east, although actual climatic patterns in this region are extremely variable (Albert et al. 1986).

Geologically, northwestern Lower Michigan is covered by Wisconsinan-age glacial drift, which lies unconformably on top of Paleozoic sediments (Dorr and Eschmann 1970). The surficial geology of Michigan has been mapped by Leverett and Taylor (1915), Martin (1955), and more recently by Farrand (1984). Four major morainal systems have been identified in this part of the state. The massive Interlobate Moraine occupies the northeastern portion of the study area, and formed in the reentrant angle between the Michigan and Saginaw Lobes of the Laurentide glacier. The Valparaiso-Charlotte Morainal system was deposited penecontemporaneously with the Interlobate Moraine (approx. 14,500 ybp.) and extends southward into southwestern Michigan. The younger Lake Border Moraine comprises a discontinuous series of hills occurring to the west of the Valparaiso-Charlotte Moraine. The Port Huron Moraine, extending into the northwestern portion of the study area, is the most recent morainal landform in the vicinity (approx 13,000; Lusch 1982). These morainal systems are surrounded by relatively level outwash plains composed of well-sorted sands. The outwash surfaces range in elevation from 207 to 290 meters above sea level and occupy extensive portions of the forest, particularly in Lake and Newaygo counties.

Geomorphic analysis

The surficial geology of the study area was mapped using field observation and soil sampling, topographic profile analysis, and airphoto interpretation. The working hypotheses during development of the map were that (1) the local Late Wisconsinan ice margin retreated to the west and north into the Lake Michigan basin, with general meltwater drainage to the south and west into an early stage of Lake Chicago, and (2) that ice-marginal retreat did not progress uniformly, but was characterized by a series of advances, retreats, and readvances. A series of parallel NW-SE trending topographic profiles were constructed perpendicular to the hypothesized orientation of the retreating ice front. These profiles allow visualization of the form and relative elevations of discrete landforms and facilitate the intepretation of the mode and developmental sequence of the landform assemblage.

Sample design and methods

Landform was used as a basis for stratified random sampling of the vegetation and soils of 80 upland forest stands. Stands were sampled between 1983 and 1985. Only well-stocked stands with minimal evidence of recent disturbance (windthrow, firewood cutting, etc.) were selected for sampling. Stands with greater than 7 $m^2$ basal area/ha in aspen (Populus grandidentata Michx. and P. tremuloides Michx.) were excluded from sampling. Vegetation was divided into three structural layers: overstory (stems > 9 cm dbh), understory (stems 1-9 cm dbh), and ground flora (woody vegetation < 1 cm dbh, herbaceous species and mosses). Four sample points were randomly located in each stand; these points served as loci for sampling of soil and vegetation.

At each point, the overstory was sampled using a 10 BAF (English) wedge prism. The species, dbh, height, merchantable height (to a 10 cm top), crown class, and live crown ratio were recorded for all live tally trees > 9 cm dbh. Increment cores were taken from two dominant species at each point to determine average age at breast height (1.37 m).

The ground flora vegetation was sampled using a 5 x 30 m rectangular plot centered over each of the four sample points. The average percent ground cover was determined using a modified Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974). Relative frequencies for ground flora species were determined by recording species presence/absence in six 1 $m^2$ frequency frames located at 5 m intervals along the long axis of the plot.

Soil profiles for each subplot were described to a depth of 1 m using standard procedures (Soil Survey Staff 1975). Additionally, each subplot was sampled to a depth of 4.5 m using a bucket auger to record changes in subsoil textures. Within the soil pits, samples were taken at 50 and 100 cm for particle size analysis. The percent slope, slope shape and position, and aspect were recorded for each plot, and local topography was described. Sand size fractions and silt+clay content from the 50 and 100 cm samples were determined in the laboratory by wet sieving; samples were shaken for two hours in a 5% sodium hexametaphosphate solution prior to sieving. Mean weighted particle diameters were determined according to Hillel (1982). The mean weighted particle diameters and presence of textural bands (defined here as > 15 cm cumulative thickness of sandy clay loam or finer textures between 1 and 4.5 m) were used to derive an index of soil moisture holding capacity. This index has an implicit assumption that banded soils have greater moisture availability than unbanded soils. The index was created by coding banded soils as 0, unbanded soils as 1, and adding these values to the mean weighted particle diameter. Low indices represent soils with high moisture availability. This index was used to rank stands by moisture availability for nonparametric statistical tests.

Statistical analyses

Stands and ground flora species were classified using two-way indicator species analysis (TWINSPAN; Hill 1979) and ordination space partitioning (Gauch 1982). These techniques have previously been used to form ecological species groups for upland forests of this region (Chapter 2). Ground flora species were subjected to binary discriminant analysis (BDA), using landform as a categorical unit. BDA is a two-step process, involving a chi-squared test of association for each species-landform combination, calculation of standardized residuals for significant species (Haberman 1973), and analysis of the standardized residuals matrix by principal component analysis (Strahler 1978). The magnitudes and signs of the standardized residuals indicate the degree of positive or negative association of species or species groups with landforms. Principal component analysis was used to ordinate the species or species groups according to their patterns of preference or avoidance of landforms. Landforms with $< 4$ stands were not included in the analysis (Ostle 1977).

Ground flora and overstory species were also subjected to detrended correspondence analysis (DCA) using DECORANA (Hill 1979). DCA is an ordination technique which minimizes the scale compression and "arch" effects inherent in principle component analysis (Hill and Gauch 1980). The use of both DCA and BDA allows a comparison of ordinations and factor loadings, and provides a validation of techniques and results (Hupp and Osterkamp 1985). DCA was performed on basal area data for overstory species and abundance data for ground flora species. Species which occurred in < 10% of the sample stands were deleted and rare species were downweighted. The stand scores from the overstory and ground flora DCA ordinations were compared using regression analysis. Stand ordination scores were related to the soil moisture index using Spearman's rank order correlation (Conover 1971).

## RESULTS

### Geomorphic analysis

Three main classes of landforms were recognized within the study area: level outwash plains, kame complexes, and moraines (Figure 3.1). Outwash plains were defined as extensive areas of well-sorted medium and coarse sands with little or no topographic relief (Figure 3.2b). Kame complexes, areally-compact, coarse-drift areas of moderate to strong relief, include heads-of-outwash and heavily pitted

Figure 3.1. Predominant glacial landforms of a five county area of northwestern Lower Michigan.

PHM - Port Huron Moraine
ILM - Interlobate Moraine
VCM - Valparaiso-Chalotte Moraine

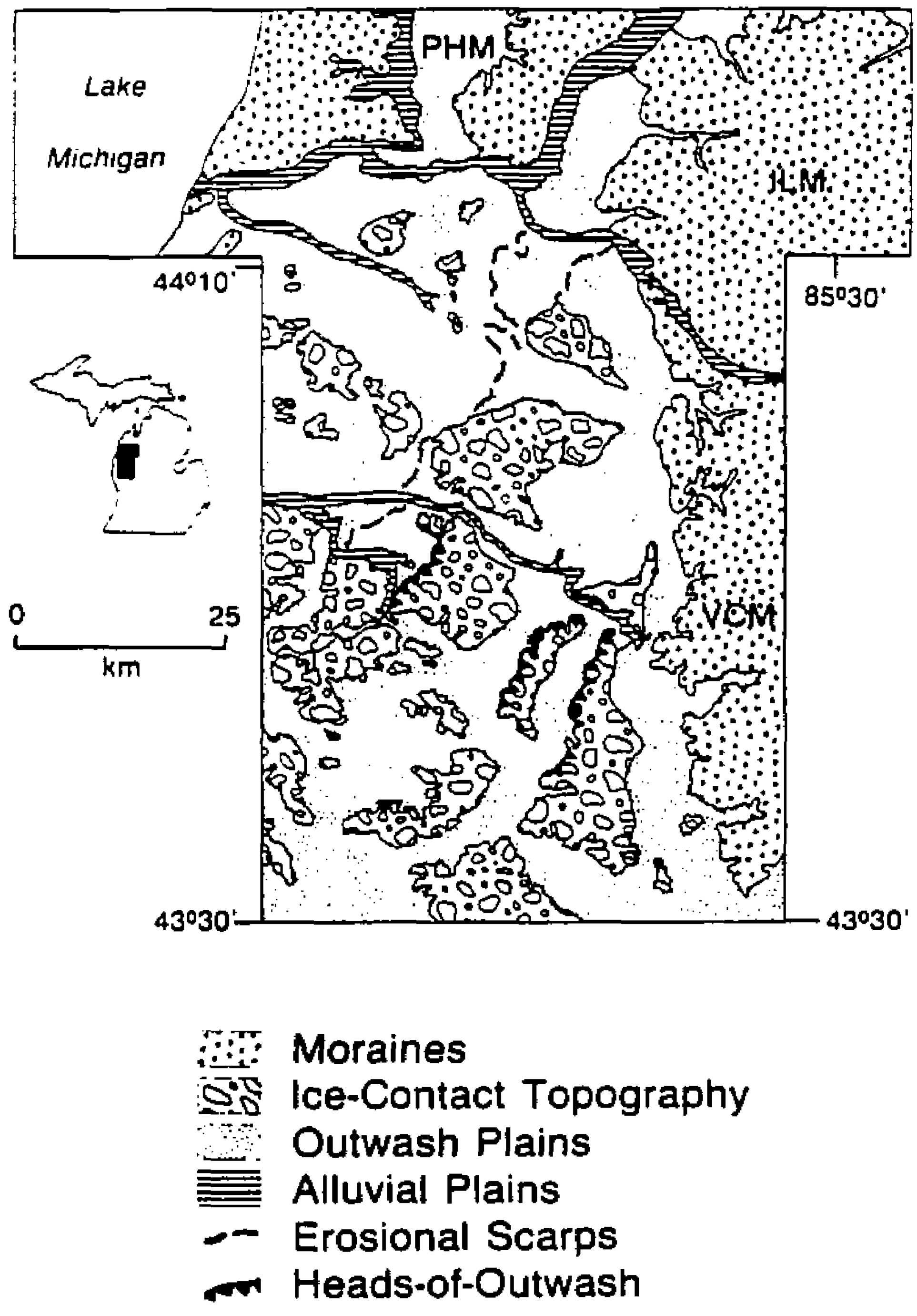
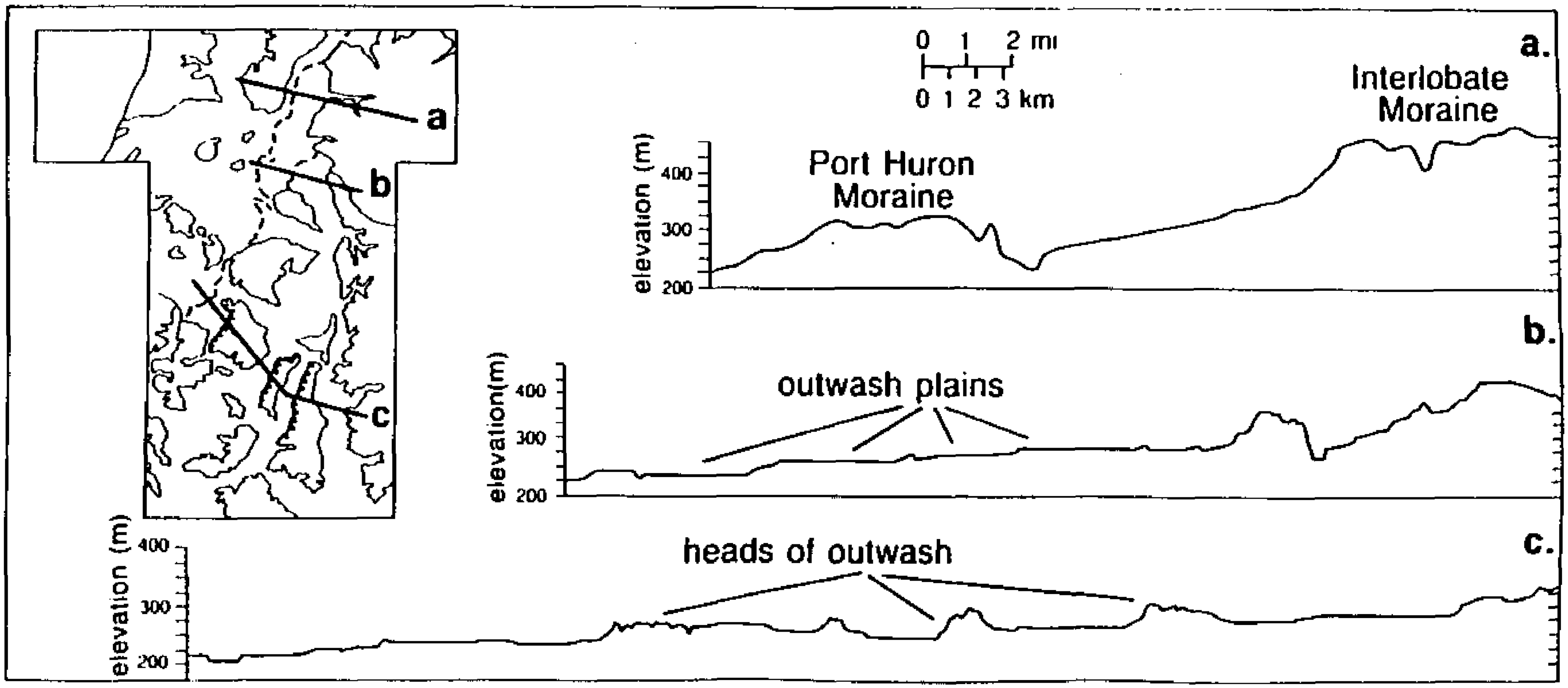

PHM
Lake
Michigan
JLM
44°10'
85°30'
0
25
km
VCM
43°30'
43°30'
Moraines
Ice-Contact Topography
Outwash Plains
Alluvial Plains
Erosional Scarps
Heads-of-Outwash

Figure 3.2 NW-SE trending topographic profiles (locations shown in inset) depicting outwash plains, morphosequences, and moraines in the study area. Vertical exaggeration is 20x.


a
b
c
0 1 2 mi
0 1 2 3 km
a.
Interlobate Moraine
Port Huron Moraine
elevation (m)
400
300
200
b.
outwash plains
elevation(m)
400
300
200
c.
heads of outwash
elevation (m)
400
300
200

outwash. The Interlobate, Port Huron, and Valparaiso-Charlotte moraines were all characterized by typical morainal topography: extensive areas of moderate to high relief (Figure 3.2a) with well-developed dendritic drainage systems. In contrast, some of the discontinuous hills which previous workers (Leverett and Taylor 1915, Martin 1955, Farrand 1984) have mapped as the Lake Border Moraine exhibited a distinctly non-morainic form. These hills typically had steep, ice-contact bluffs facing to the west, with gentle grades to the east (Figure 3.2c). Auger samples from stands on these features revealed that the upper 4.5 m of surface materials were composed of stratified sands and gravel. These asymmetrical landforms closely resemble the outwash morphosequence profiles described by Koteff and Pessl (1981). The combined textural and topographic data suggest that at least parts of the Lake Border Moraine are actually outwash morphosequences, with hilly heads-of-outwash grading into level outwash plains (Figure 3.2c). For this reason, stands on features west of the Valparaiso-Charlotte Moraine were considered representative of hilly ice-contact topography or outwash plains rather than moraines. In general, the elevations of outwash systems decreased to the south; this is in accord with Farrand and Eschmann (1974), who postulated meltwater drainage from the Port Huron maximum flowing south-southwest through Wexford and Lake counties into the Lake Michigan basin.

The ice-contact and morainal landforms frequently had layers of nonpedogenic, fine-textured sediments (sandy loam to clay) within the upper 4.5 m. The presence of these fine-textured bands has an influence on both species composition and site productivity (Cleland et al. 1984, Hannah and Zahner 1970). The presence or absence of bands was therefore included as a criterion in identifying landforms and categorizing stands in the BDA. Using surficial topography and presence of banding as criteria, nine landforms were identified for the geomorphic map (Table 3.1). The predominant soils on the ice-contact and morainal landforms were Entic or Typic Haplorthods, whereas soils on the outwash plains were primarily Typic Udipsamments. Average textures of the solum were generally coarser on sites underlain by deep sands compared with soils on the banded sites (Table 3.1). Soils associated with deep sands on the three morainal systems and the kame complexes were very similar in degree of development and texture.

Vegetation analysis

The greatest difference in forest composition occurred between the Interlobate Moraine and the other landforms. The Interlobate Moraine was consistently dominated by northern hardwoods, whereas all other stands, with the exception of two stands on the Port Huron Moraine, were dominated by oak (Table 3.1). Within these two major overstory types, however, patterned variation in species composition related

Table 3.1. Forest composition and soil properties among glacial landforms of northwestern Lower Michigan.

| | Landform | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | OUTWASH | KAME COMPLEXES UNBANDED | PORT HURON MORAINE UNBANDED | VALPARAISO-CHARLOTTE MORAINE UNBANDED | INTERLOBATE MORAINE UNBANDED | KAME COMPLEXES BANDED | PORT HURON MORAINE BANDED | VALPARAISO-CHARLOTTE MORAINE BANDED | INTERLOBATE MORAINE BANDED |
| | (n = 22) | (n = 12) | (n = 6) | (n = 3) | (n = 8) | (n = 10) | (n = 4) | (n = 3) | (n = 8) |
| Overstory | | | | | | | | | |
| Density (stems/ha) | 659 (39.4) | 657 (66.8) | 731 (116.9) | 719 (72.8) | 789 (78.8) | 543 (80.1) | 651 (133.8) | 728 (54.3) | 741 (53.1) |
| Total basal area (sq m/ha) | 19.7 (0.7) | 22.1 (0.8) | 22.3 (1.3) | 24.6 (1.2) | 26 (2.6) | 26.0 (1.1) | 27.1 (0.8) | 27.8 (1.8) | 28.9 (0.7) |
| Species basal area (sq m/ha) | | | | | | | | | |
| Quercus velutina | 9.3 (1.2) | 7.8 (1.5) | 2.5 (0.5) | 9.0 (4.7) | - | 1.5 (1.3) | - | 0.2 (0.2) | - |
| Quercus alba | 8.4 (0.9) | 6.3 (0.9) | 9.7 (1.0) | 6.7 (1.9) | - | 5.4 (1.6) | 0.9 (0.7) | 2.8 (1.3) | - |
| Quercus rubra | 1.1 (0.7) | 7.3 (2.0) | 11.2 (2.3) | 4.1 (1.8) | 6 (3.1) | 17.0 (2.6) | 15.6 (3.5) | 17.1 (2.5) | 4.7 (2.6) |
| Acer rubrum | 0.3 (0.2) | 1.2 (0.5) | 1.8 (1.0) | 3.4 (1.7) | 2 (1.1) | 4.2 (1.5) | 3.4 (1.3) | 3.7 (1.0) | 0.1 (0.1) |
| Acer saccharum | - | - | - | - | 7 (2.1) | - | 3.5 (2.9) | 1.2 (0.6) | 11.6 (1.8) |
| Fagus grandifolia | - | - | - | 0.6 (0.6) | 3 (0.9) | - | 1.7 (1.7) | 1.5 (1.5) | 1.9 (1.0) |
| Fraxinus americana | - | - | - | - | 3 (1.1) | 0.1 (0.1) | 0.3 (0.3) | - | 2.3 (1.3) |
| Prunus serotina | - | - | - | - | 3 (2.0) | 0.2 (0.1) | - | - | 1.4 (0.6) |
| Tilia americana | - | - | - | - | 2 (0.7) | - | - | - | 5.6 (1.7) |
| Soils | | | | | | | | | |
| Mean weighted particle diameter (mm) (100 cm depth) | 0.37 (0.01) | 0.34 (0.01) | 0.34 (0.01) | 0.34 (0.03) | 0.32 (0.02) | 0.27 (0.03) | 0.30 (0.01) | 0.29 (0.02) | 0.29 (0.02) |
| % cs+ms (100 cm depth) | 76 (3) | 69 (2) | 66 (2) | 69 (2) | 65 (6) | 47 (7) | 46 (7) | 57 (10) | 51 (8) |
| % si+cl (100 cm depth) | 2 (0.4) | 3 (1) | 3 (0.5) | 4 (1) | 2 (0.5) | 19 (4) | 9 (3) | 12 (6) | 10 (3) |

Note: Values represent means (standard error).

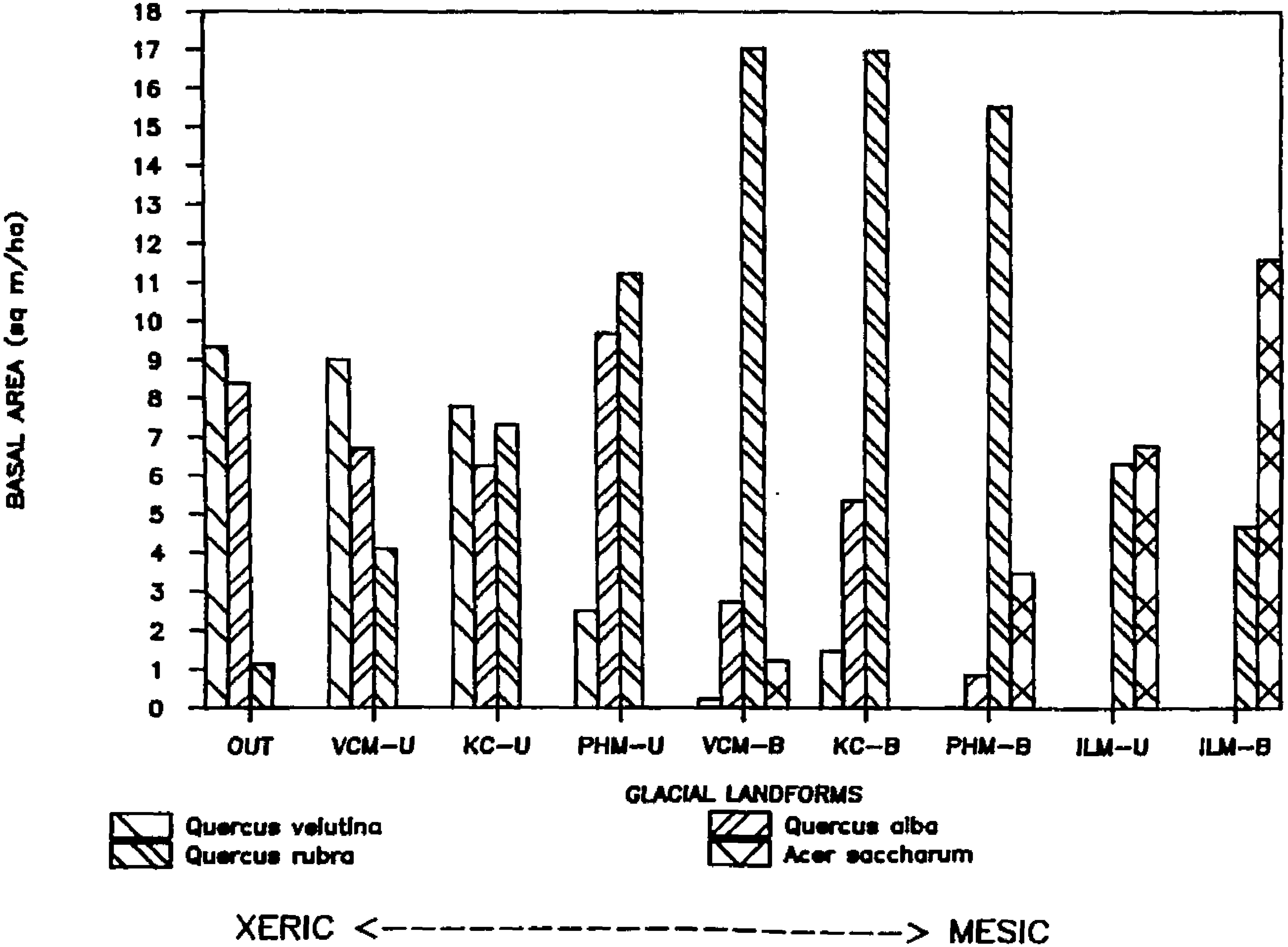
to landform was observed. When oak-dominated landforms were ranked along a soil moisture gradient (based on solum textures and the presence of banding), overstory species exhibited bell-shaped, J-shaped or reversed J-shaped distribution patterns (Figure 3.3), similar to those reported by Curtis (1959). Sugar maple and basswood dominated the banded mesic sites on the Interlobate Moraine, while unbanded Interlobate sites were dominated by sugar maple and red oak. At the opposite extreme, black and white oaks dominated the outwash plains and dry ice-contact and morainal hills (Figure 3.3). Mesic banded sites within these hills, however, had high basal areas ( > 15 $m^2$/ha) of red oak. Sample stands were of similar age and history, developing after the logging activities of the early 1900s.

Ground flora composition exhibited patterned variation that was related to both overstory composition and landform. The initial TWINSPAN division separated species and stands of the Interlobate Moraine from those found on oak-dominated landforms. Using the TWINSPAN algorithm, species with similar patterns of abundance, constancy, and fidelity to the sample classification units were clustered together. Geologically, divisions based on ground flora composition separated stands by relief and presence or absence of fine-textured materials in the subsurface horizons.

The chi-squared test of association, which was the first phase of the binary discriminant analysis, showed that most of the individual ground flora species used in the ecological

Figure 3.3 Basal areas of major overstory species summarized by landform. Oak-dominated landforms are ordered by soil moisture availability (xeric to mesic), based on soil texture and presence or absence of textural bands. Landform codes are as follows:

OUT - Outwash plains
VCM-U - Valparaiso-Charlotte Moraine - unbanded
KC-U - Kame complexes - unbanded
PHU-U - Port Huron Moraine - unbanded
VCM-B - Valparaiso-Charlotte Moraine - banded
KC-B - Kame complexes - banded
PHM-B - Port Huron Moraine - banded
ILM-U - Interlobate Moraine - unbanded
ILM-B - Interlobate Moraine - banded


BASAL AREA (sq m/ha)
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
OUT
VCM-U
KC-U
PHM-U
VCM-B
KC-B
PHM-B
ILM-U
ILM-B
GLACIAL LANDFORMS
Quercus velutina
Quercus rubra
Quercus alba
Acer saccharum
XERIC <-------------------------> MESIC

species groups bore statistically significant associations with landform (Table 3.2). The associations with landform were correlated, in part, with differences in overstory composition. The Deschampsia, Vaccinium, Pteridium, Hamamelis, and Trientalis groups were negatively associated with the Interlobate Moraine (which is dominated by northern hardwoods), and positively associated with landforms dominated by oak. Within this initial dichotomy, however, distinct patterns of ground flora/landform association were observed. The Deschampsia group was strongly associated with outwash plains, and was less abundant on landforms with finer particle sizes and greater relief. The Vaccinium group had a wider amplitude, occurring on outwash plains and sandy ice-contact hills and moraines, but was absent from sites with textural banding. The Hamamelis and Trientalis groups occupied more intermediate positions; they were absent from the outwash plains, but present on both sandy and banded hills. The Desmodium group was strongly associated with banded ice-contact landforms. Two groups were strongly associated with the Interlobate Moraine. The Osmorhiza group was strongly associated with sites having textural banding. The Maianthemum group was most common on deep sands, but also occurred on banded sites. Under similar canopy conditions, soil moisture holding capacity and relief appear to be the major factors influencing the distribution of ground flora species.

Table 3.2. Standardized residuals and chi-squared values for individual herbaceous and woody species distributed on nine upland landforms.

| | Landform[a] | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | OUT | KC-U | PHM-U | VPM-U | ILM-U | KC-B | PHM-B | VPM-B | ILM-B | Chi-squared |
| DESCHAMPSIA GROUP | | | | | | | | | | |
| Deschampsia flexuosa | 3.88[b] | 0.64 | -0.12 | -0.84 | -1.42 | -1.61 | -0.98 | -0.84 | -1.42 | 16.64 *[c] |
| Arctostaphylos uva-ursi | 4.35 | -1.20 | -0.81 | -0.56 | -0.95 | -1.08 | -0.65 | -0.56 | -0.95 | 16.97 * |
| Comptonia peregrina | 5.93 | 0.37 | -0.69 | -1.13 | -1.91 | -2.17 | -1.31 | -1.13 | -1.91 | 35.83 * |
| Cladina rangiferina | 3.14 | 0.95 | 0.06 | -0.77 | -1.29 | -1.47 | -0.89 | -0.77 | -1.29 | 12.45 |
| Pleurozium schreberi | 3.83 | -0.77 | 1.23 | -0.77 | -1.29 | -1.47 | -0.89 | -0.77 | -1.29 | 16.72 * |
| Andropogon gerardii | 4.00 | -1.11 | -0.75 | -0.52 | -0.88 | -0.99 | -0.60 | -0.52 | -0.88 | 14.32 * |
| VACCINIUM GROUP | | | | | | | | | | |
| Vaccinium angustifolium | 2.87 | 2.33 | 1.58 | 1.09 | -4.84 | 1.34 | -1.03 | -0.23 | -4.84 | 56.01 * |
| Gaultheria procumbens | 1.35 | 2.72 | 1.84 | 0.03 | -4.15 | 1.73 | -0.68 | 0.03 | -4.15 | 44.42 * |
| Gaylussacia baccata | 1.52 | 2.99 | 1.58 | 2.31 | -2.28 | -1.89 | -1.57 | -1.35 | -2.28 | 26.52 * |
| Melampyrum lineare | 3.54 | 1.89 | 2.55 | 1.77 | -2.99 | -3.39 | -1.03 | -0.59 | -2.99 | 44.89 * |
| Dicranum polysetum | 3.33 | 2.09 | 2.69 | 0.68 | -2.09 | -3.22 | -0.92 | -1.68 | -2.84 | 39.02 * |
| Leucobryum glaucum | 0.65 | 0.24 | 2.71 | -0.95 | -1.61 | -0.19 | 0.13 | 0.47 | -1.61 | 11.60 |
| Epigaea repens | 0.19 | 1.62 | 3.87 | -1.16 | -1.16 | -1.50 | 0.88 | -1.16 | -1.97 | 22.12 * |
| PTERIDIUM GROUP | | | | | | | | | | |
| Pteridium aquilinium | 2.53 | 1.71 | 1.16 | 0.80 | -3.60 | 1.54 | 0.93 | 0.80 | -6.58 | 57.60 * |
| Amelanchier spp. | 2.29 | 1.55 | 1.05 | 0.73 | -3.02 | 0.43 | 0.85 | 0.73 | -5.14 | 36.78 * |
| Carex pensylvanica | 2.17 | 1.47 | 0.99 | 0.69 | -6.58 | 1.32 | -0.72 | 0.69 | -1.05 | 44.48 * |
| HAMAMELIS GROUP | | | | | | | | | | |
| Hamamelis virginiana | -2.12 | 2.76 | 2.30 | 1.59 | -3.32 | 3.05 | -0.22 | 0.41 | -3.32 | 41.88 * |
| Sassafras albidum | -0.89 | 2.58 | 2.18 | 1.51 | -3.51 | 2.21 | -0.33 | 0.31 | -3.51 | 36.29 * |
| TRIENTALIS GROUP | | | | | | | | | | |
| Trientalis borealis | -2.75 | -0.83 | 4.27 | -1.06 | -0.94 | 2.60 | 2.27 | 0.28 | -1.79 | 36.39 * |
| Aster macrophyllum | -1.91 | -0.47 | 1.42 | -0.22 | -0.89 | 3.51 | 0.44 | 2.19 | -2.41 | 27.75 * |
| VIBURNUM GROUP | | | | | | | | | | |
| Viburnum acerifolium | -4.82 | 1.12 | 2.06 | 1.43 | -2.17 | 2.74 | 1.66 | 1.43 | 0.12 | 33.67 * |
| Aralia nudicaulis | -4.10 | -1.85 | 1.34 | -0.27 | 1.32 | 2.71 | 1.43 | 2.13 | 0.56 | 27.04 * |
| Mitchella repens | -2.99 | -2.03 | 0.67 | -0.95 | 2.88 | 3.68 | 1.36 | -0.95 | -0.71 | 30.93 * |
| Medeola virginiana | -1.48 | -1.00 | -0.68 | -0.47 | 0.71 | 1.84 | 3.60 | -0.47 | -0.79 | 17.61 * |

Table 3.2. -continued page 2

| Species | OUT | KC-U | PHM-U | VPM-U | ILM-U | KC-B | PHM-B | VPM-B | ILM-B | Chi-squared |
|---|---|---|---|---|---|---|---|---|---|---|
| DESMODIUM GROUP | | | | | | | | | | |
| Desmodium spp. | -0.26 | -1.29 | -0.88 | -0.61 | -1.03 | 2.15 | -0.70 | 5.15 | -1.03 | 10.93 |
| Cornus florida | -2.41 | 0.09 | -1.11 | -0.77 | -0.27 | 3.18 | -0.89 | -0.77 | 2.81 | 20.42 * |
| Viola pubescens | -1.63 | -1.11 | -0.75 | -0.52 | -0.88 | 4.04 | 1.30 | -0.52 | 0.51 | 18.64 * |
| MAIANTHEMUM GROUP | | | | | | | | | | |
| Maianthemum canadense | -4.55 | -2.52 | 0.00 | -1.77 | 2.99 | 2.04 | 2.05 | 1.77 | 2.99 | 43.66 * |
| Polygonatum biflorum | -3.90 | -1.97 | -0.88 | -1.24 | 4.27 | -0.21 | 1.84 | 1.27 | 3.48 | 45.18 * |
| Dryopteris spinulosa | -2.04 | -1.38 | -0.94 | -0.65 | 3.53 | -0.19 | -0.75 | -0.65 | 3.53 | 26.27 * |
| Solidago caesia | -1.86 | -0.88 | -1.16 | -0.80 | 0.63 | 2.96 | 0.43 | 2.33 | -0.37 | 13.40 * |
| Epifagus virginiana | -1.63 | -1.11 | -0.75 | -0.52 | 3.28 | -0.99 | 1.30 | -0.52 | 1.90 | 17.36 * |
| Lycopodium lucidulum | -1.63 | -1.11 | -0.75 | -0.52 | 1.90 | -0.99 | 3.21 | -0.52 | 1.90 | 18.96 * |
| Lycopodium obscurum | -1.77 | -1.20 | -0.81 | -0.56 | 2.93 | 0.09 | 1.12 | -0.56 | 1.63 | 14.17 * |
| Carex deweyana | -1.63 | -1.11 | -0.75 | -0.52 | 6.06 | -0.99 | -0.60 | -0.52 | 0.51 | 34.91 * |
| Carex pedunculata | -1.91 | -1.29 | -0.88 | -0.61 | 5.06 | -1.16 | -0.70 | -0.61 | 2.63 | 32.95 * |
| OSMORHIZA GROUP | | | | | | | | | | |
| Osmorhiza claytonii | -2.41 | -1.63 | -1.11 | -0.77 | 0.76 | -0.54 | -0.89 | 0.85 | 6.91 | 51.88 * |
| Carex plantaginea | -2.29 | -1.55 | -1.05 | -0.73 | 3.02 | -1.40 | 0.61 | -0.73 | 5.14 | 37.91 * |
| Adiantum pedatum | -1.31 | -0.89 | -0.60 | -0.42 | -0.70 | -0.80 | -0.48 | -0.42 | 5.99 | 32.88 * |
| Uvularia perfoliata | -1.48 | -1.00 | -0.68 | -0.47 | 2.22 | -0.90 | -0.55 | -0.47 | 3.73 | 18.11 * |
| Botrichium virginianum | -1.77 | -1.20 | -0.81 | -0.56 | 0.34 | -1.08 | -0.65 | -0.56 | 6.80 | 43.61 * |
| Caulophyllum thalictroides | -1.77 | -1.20 | -0.81 | -0.56 | 1.63 | -1.08 | -0.65 | -0.56 | 5.51 | 32.50 * |
| Mitella diphylla | -1.63 | -1.11 | -0.75 | -0.52 | 1.90 | -0.99 | -0.60 | -0.52 | 4.67 | 25.34 * |
| Allium tricoccum | -1.63 | -1.11 | -0.75 | -0.52 | 0.51 | -0.99 | -0.60 | -0.52 | 6.06 | 34.91 * |
| Tiarella cordifolia | -1.63 | -1.11 | -0.75 | -0.52 | 0.51 | -0.99 | -0.60 | -0.52 | 6.06 | 34.91 * |
| Actaea alba | -1.77 | -1.20 | -0.81 | -0.56 | 0.34 | 1.27 | -0.65 | -0.56 | 4.22 | 20.28 * |
| Viola canadensis | -2.53 | -1.71 | -1.16 | -0.80 | 1.62 | 1.16 | -0.93 | -0.80 | 5.59 | 37.92 * |
| Hepatica acutiloba | -1.48 | -1.00 | -0.68 | -0.47 | 2.22 | -0.90 | -0.55 | -0.47 | 3.73 | 19.11 * |

[a] Landform abbreviations are: OUT, outwash plains, KC-U, kame complexes - unbanded, PHM-U, Port Huron Moraine - unbanded, VPM-U, Valparaiso-Charlotte Moraine - unbanded, ILM-U, Interlobate Moraine - unbanded, KC-B, kame complexes - banded, PHM-B, Port Huron Moraine - banded, VPM-B, Valparaiso-Charlotte Moraine - banded, ILM-B, Interlobate Moraine - banded.

[b] A positive residual indicates frequent occurrence on a particular landform; negative residuals indicate that the group is rarely found there.

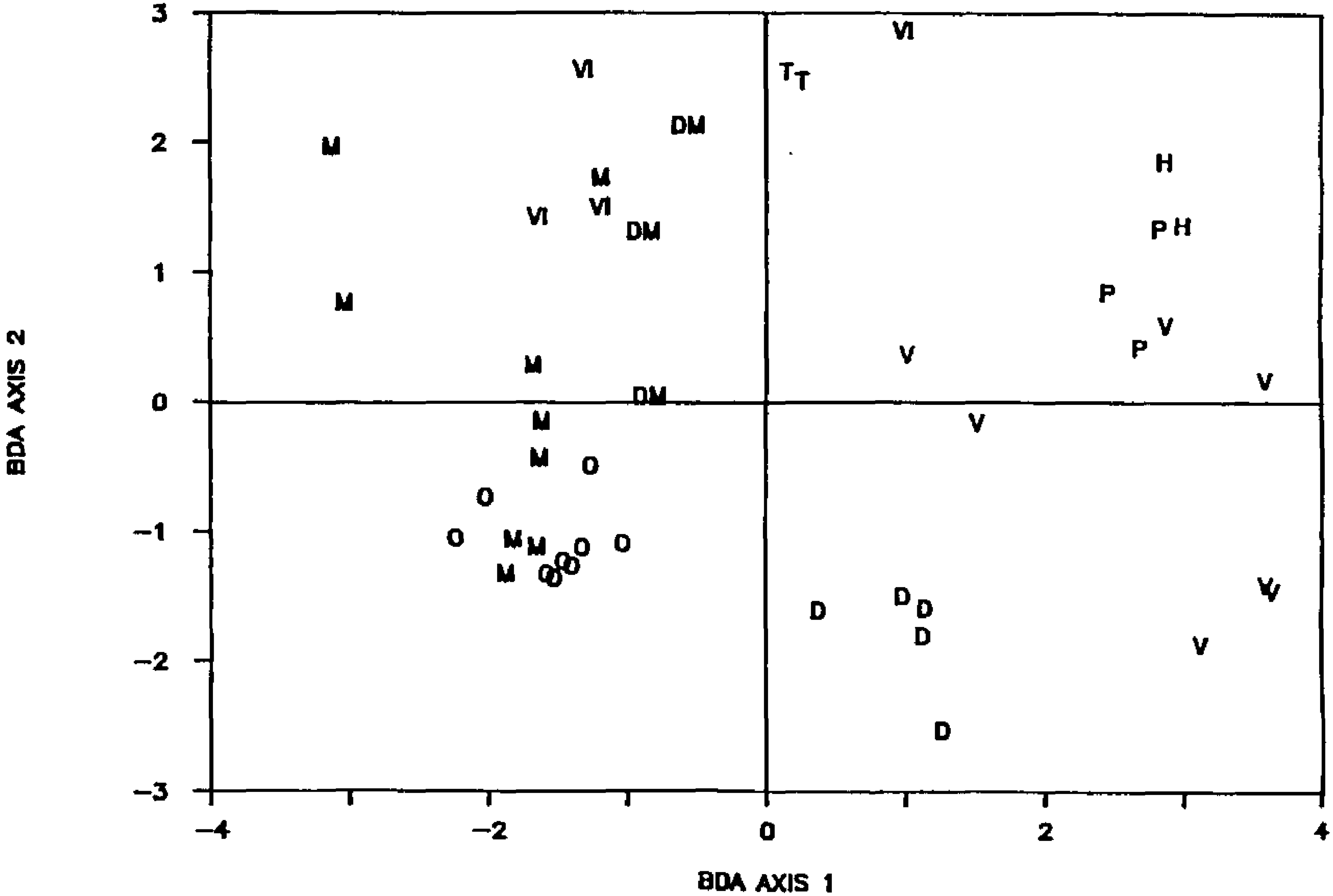
[c] * significant at $p<0.05$

In the second phase of the BDA, the first and second principal component axes explained 44 and 24% of the variation in the standardized residuals matrix, respectively. On the first principal component axis, species characteristic of ice contact hills and outwash plains received high positive factor loadings, whereas species common on the Interlobate Moraine received high negative loadings (Table 3.3). Ordination of species on the first two PC axes effectively grouped species by preference to landform, but a strong arch effect (i.e. quadratic dependence of the second axis on the first) was manifest in the second axis (Figure 3.4). Arctostaphylos uva-ursi, characteristic of the most xeric outwash plains, was relatively close in the two dimensional ordination space to Adiantum pedatum, characteristic of mesic morainal positions. For this reason, further interpretations of species-landform relationships were made using detrended correspondence analyses.

Table 3.3. Factor loadings (eigenvectors) from a principal component analysis of standardized residuals from the species by landform contingency tables.

| Landform | Eigenvector 1 |
|---|---|
| Outwash plains | 0.34 |
| Kame complexes - unbanded | 0.47 |
| Port Huron Moraine - unbanded | 0.35 |
| Valparaiso-Charlotte Moraine - unbanded | 0.37 |
| Interlobate Moraine - unbanded | -0.44 |
| Kame complexes - banded | -0.03 |
| Port Huron Moraine - banded | -0.17 |
| Valparaiso-Charlotte Moraine - banded | -0.05 |
| Interlobate Moraine - banded | -0.40 |

Figure 3.4 Species distribution on the first two axes of a binary discriminant analysis. Symbols are species group codes: D - Deschampsia, V - Vaccinium, P - Pteridium, H - Hamamelis, T - Trientalis, VI - Viburnum, DM - Desmodium, M - Maianthemum, O - Osmorhiza.


BDA AXIS 2
BDA AXIS 1
3
2
1
0
−1
−2
−3
−4
−2
0
2
4
VI
TT
DM
M
H
P H
P
V
D
O

The first DCA axis from an ordination of ground flora (Q-type analysis) also represented a compositional gradient from xeric-site species to species characteristic of mesic landforms; the 20 most heavily weighted species for the first axis are presented in Table 3.4. The relationship of species to landforms using DCA was similar to the relationships expressed by the standardized residuals from the BDA. Species with the highest DCA scores were all members of the Osmorhiza species group, which is strongly associated with banded sites on the Interlobate Moraine. Members of the Maianthemum group received slightly lower scores; this group was most frequent on unbanded sites on the Interlobate Moraine. Species of the Deschampsia and Vaccinium groups received negative scores on the first axis. These groups typically occured under black oak-white oak canopies on outwash plains and dry sandy hills. The Trientalis and Viburnum groups occupied intermediate positions on the gradient, occurring under red oak-white oak canopies on more mesic (banded or finer-textured) landforms. Since DECORANA calculates only the first four axes, it is not possible to present the exact proportion of variation explained by a single axis. A relative estimate of variation explained can be obtained by calculating the percentage of an eigenvalue relative to the sum of first four eigenvalues (Boerner 1985). Using this method, the first DCA axis accounted for 70% of the summed eigenvalues. The second DCA axis accounted for 14% of the summed eigenvalues, and appeared to separate the

Deschampsia and Vaccinium groups. No arch effect was evident in this ordination.

Table 3.4. The 20 terminal species on DCA ordination axis 1; Eigenvalue = 0.653.

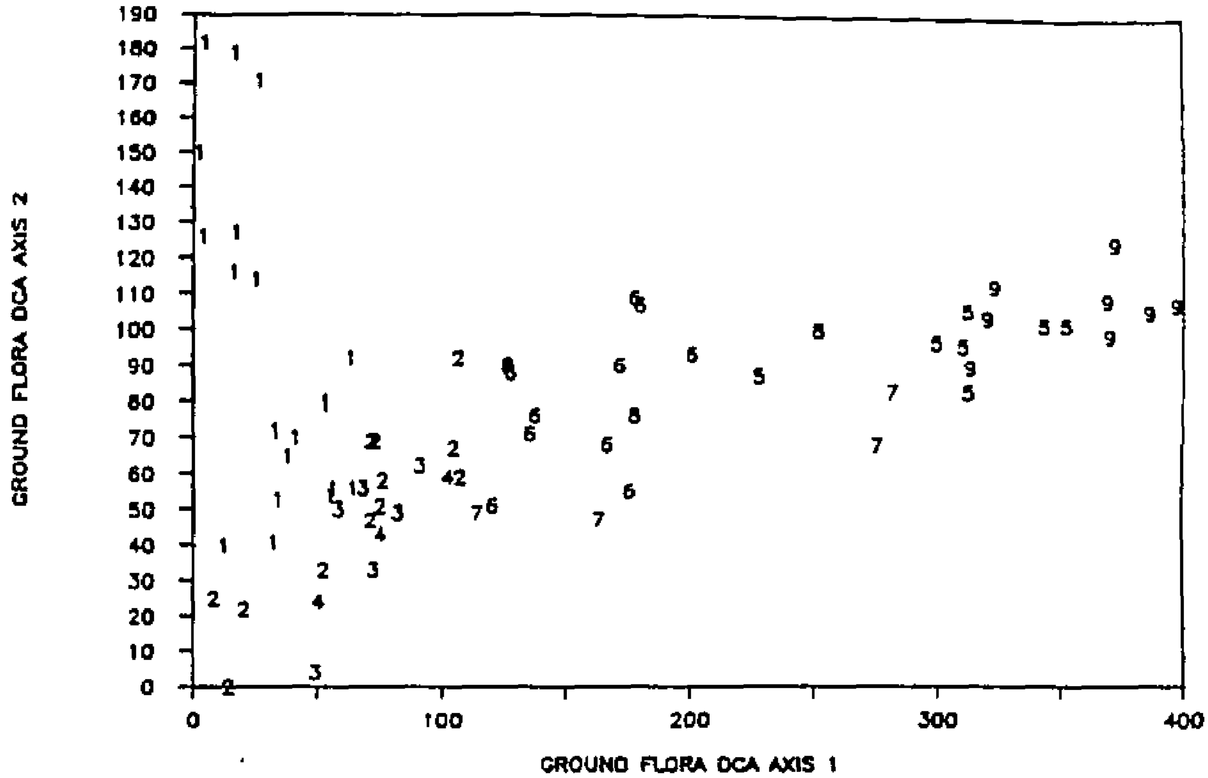
| Highest scores | Lowest scores |
|---|---|
| Dicentra canadensis | Pinus banksiana |
| Uvularia perfoliata | Arctostaphylos uva-ursi |
| Tiarella cordifolia | Cladina rangiferina |
| Mitella diphylla | Lycopodium tristachyum |
| Adiantum pedatum | Comptonia peregrina |
| Allium tricoccum | Rubus hispidus |
| Caulophyllum thalictroides | Deschampsia flexuosa |
| Botrychium virginianum | Lupinus perennis |
| Osmorhiza claytonii | Quercus ellipsoidalis |
| Hepatica acutiloba | Cladonia crista-tella |
| Carex plantaginea | Polytrichum piliferum |
| Tilia americana | Galium circaezans |
| Trillium grandiflorum | Polytrichum juniperinum |
| Dryopteris spinulosa | Pleurozium shreberi |
| Epipactis helleborine | Dicranum polysetum |
| Carex deweyana | Hieracium venosum |
| Actaea alba | Melampyrum lineare |
| Viola canadensis | Comandra umbellata |
| Acer saccharum | Gaylussacia baccata |
| Galium boreale | Quercus velutina |

A two-dimensional ordination of stands by ground flora vegetation (R-type analysis) showed that landforms were clearly separated by ground flora composition (Figure 3.5a). All of the stands occurring on the Interlobate Moraine received first axis scores of 200 or higher. The central portion of the gradient (DCA Axis 1 scores 100-200) comprised stands with high proportions of the Trientalis, Viburnum, and Desmodium groups. These stands occurred on ice-contact or

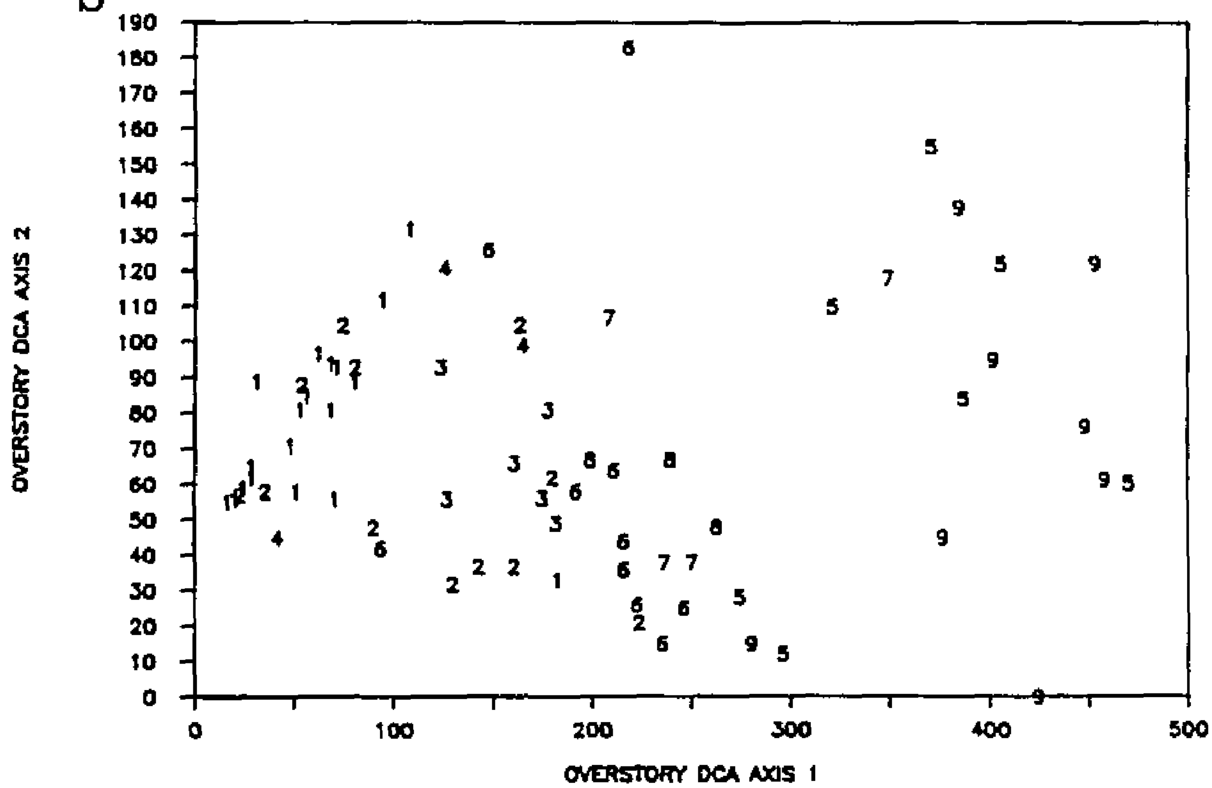
Figure 3.5 Detrended correspondence analysis of stands by ground flora and overstory vegetation: a) ordination based on ground flora, b) ordination based on overstory. Values represent landform codes:

1 - Outwash plains
2 - Kame complexes - unbanded
3 - Port Huron Moraine - unbanded
4 - Valparaiso-Charlotte Moraine - unbanded
5 - Interlobate Moraine - unbanded
6 - Kame complexes - banded
7 - Port Huron Moraine - banded
8 - Valparaiso-Charlotte Moraine - banded
9 - Interlobate Moraine - banded

a


GROUND FLORA DCA AXIS 2
GROUND FLORA DCA AXIS 1

b


OVERSTORY DCA AXIS 2
OVERSTORY DCA AXIS 1

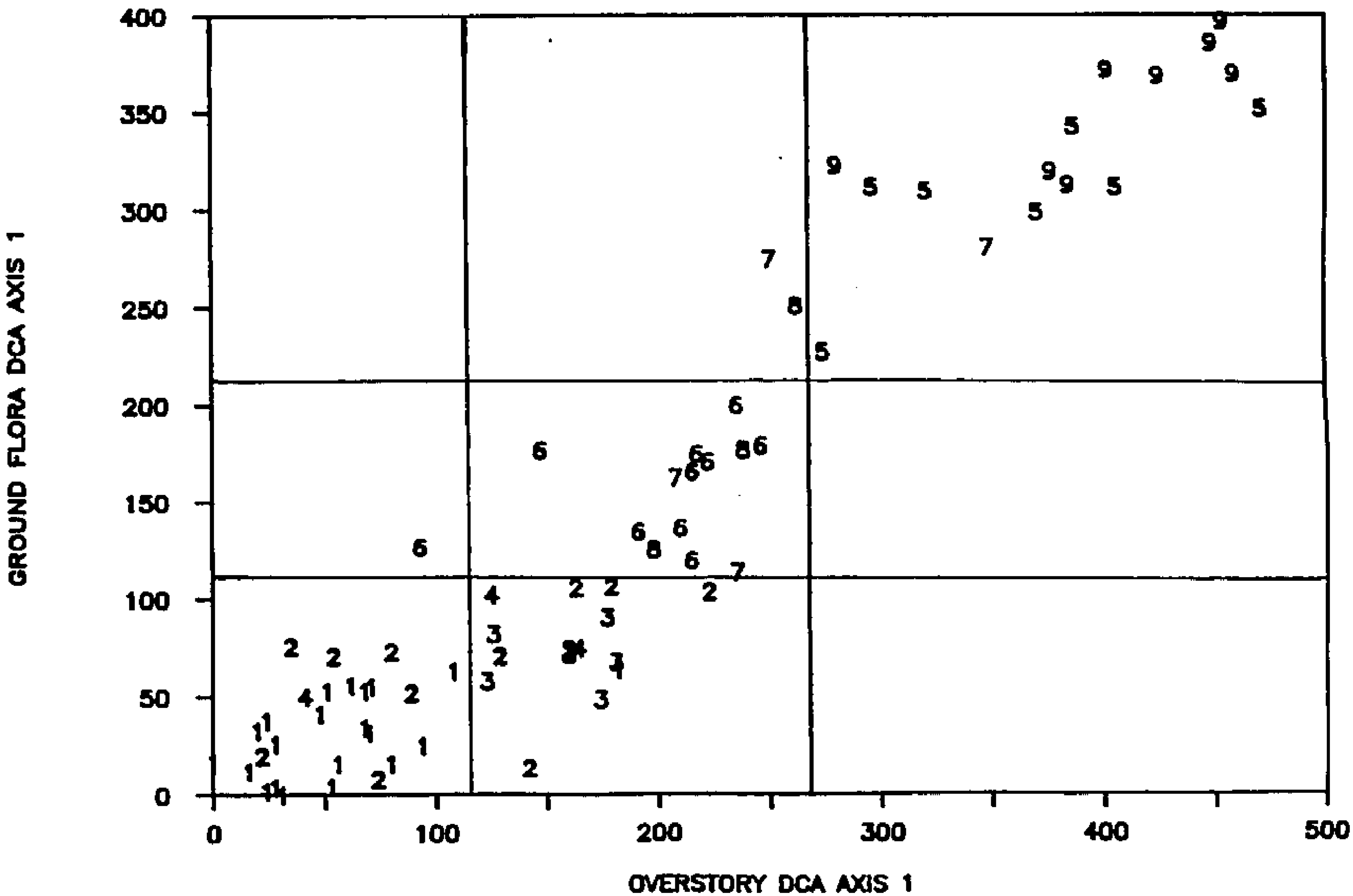
morainal hills with textural banding. Stands on outwash plains, unbanded moraines or unbanded kame complexes all received first axis scores < 100; these stands had high proportions of the Deschampsia and Vaccinium groups. Discrimination among the unbanded morainal and ice-contact hills by ground flora was poor. These dry sandy hills were very similar in relief, soil texture, and degree of soil development (Table 3.1), and it is likely that, while these features are of different ages and depositional environments, they are functionally similar in their effects on species composition.

The two-dimensional ordination of stands based on overstory data also separated stands by landform (Figure 3.5b). The first overstory DCA axis represented a compositional gradient from jack pine-black oak stands to stands dominated by sugar maple and basswood. Ordination along the second axis produced a gradient from stands with high proportions of red oak to stands with a significant component of red maple or white pine. The partitioning of variance was nearly identical to the partitioning of variance in the ground flora ordination; the first two overstory axes explained 71 and 14% of the summed eigenvalues, respectively. Again, stands on the Interlobate Moraine received the highest first axis scores ( > 250), stands on banded morainal or ice-contact hills occupied the central portion of the gradient (200-250), and stands on outwash plains received the lowest scores (< 100).

The overstory ordination scores were highly correlated with the ordination scores derived using ground flora data ($r^2$=0.89; $p < 0.05$). Species turnover within oak-dominated and sugar maple-dominated forests was gradual in both the overstory and ground flora layers (Figure 3.6), reflecting the continuous pattern of change characteristic of Wisconsin forests (Curtis 1957, Peet and Loucks 1977). Superimposing landform on the ordinations shows that the assemblages of overstory and ground flora covary as a function of landform (Figure 3.6). Partitioning the ordination space by species assemblages identified three distinct classes of landform 1) outwash plains and dry sand hills (lower left), 2) hills with loamy surface textures or subsurface banding (center) and 3) banded and unbanded hills of the Interlobate Moraine (upper right). Compositional differences among the first two classes of landforms were clearly related to differences in soil moisture-holding capacity; Spearman's rank order correlations of the ground flora and overstory DCA scores against the soil moisture index were both highly significant ($p < 0.01$). There was little difference in species composition among the ice contact hills and the Port Huron and Valparaiso-Charlotte moraines, either on banded or unbanded sites (Figure 3.6). Within the study area, these landforms differed primarily by age and geographic extent, rather than by topography or parent materials. In this glaciated landscape, it is not the landforms per se, but the ability of the landforms to retain

Figure 3.6 Scatterplot of stand scores from ordinations by ground flora and overstory. Values represent landform codes:

1 - Outwash plains
2 - Kame complexes - unbanded
3 - Port Huron Moraine - unbanded
4 - Valparaiso-Charlotte Moraine - unbanded
5 - Interlobate Moraine - unbanded
6 - Kame complexes - banded
7 - Port Huron Moraine - banded
8 - Valparaiso-Charlotte Moraine - banded
9 - Interlobate Moraine - banded


GROUND FLORA DCA AXIS 1
400
350
300
250
200
150
100
50
0
0
100
200
300
400
500
OVERSTORY DCA AXIS 1

moisture and nutrients that appears to be a primary factor influencing forest composition.

## DISCUSSION

The pattern imparted to this regional landscape as a result of its glacial and post-glacial history has directed the historical and recent development of soils and plant communities. Moisture availability, as related to the depositional environments which produced this landscape configuration, appears to be the primary factor responsible for the existing upland vegetation pattern. This is consistent with the results of Peet and Loucks (1977), who noted that the sand content of the $A_1$ horizon (interpreted as an index of soil moisture availability) was most closely correlated with an overstory ordination of Wisconsin forests. Similarly, in a canonical analysis of soil and physiographic variables against ecological species groups in the Upper Peninsula of Michigan, Spies and Barnes (1985a) found the relative proportions of coarse and medium sands and depth to mottling be highly correlated with the first canonical axis.

In our study area, the extensive outwash plains, formed predominately by low-gradient braided streams, have well-sorted, coarse-textured soils with low moisture holding capacity. Morainal and ice contact landforms tend to be more poorly sorted, with somewhat finer-textured soils and greater moisture availability. Finally, landforms in which sedimentation, flow till, or other geomorphic processes resulted in deposition of subsurface textural bands have a further enhanced moisture supply. All of these differences in soil moisture were reflected in the species composition of the overstory and understory, as evident in the BDA and the correlation of the soil moisture index with the ordination scores. Outwash plains support plant communities characteristic of xeric environments: black and white oak overstories, with the Deschampsia and Vaccinium species groups as the characteristic ground flora. More mesic landforms support species with greater moisture requirements: red oak and red maple overstories, with ground flora dominated by the Trientalis or Viburnum groups.

Relating moisture availability to depositional environment (or landform) allows us to apply our findings from gradient analysis to a regional landscape. The ability to describe landforms in terms of their depositional environments, and make subsequent inferences about their moisture and nutrient status, allows one to predict where in the landscape a given species or group of species is likely to occur. For example, sandy sites within the Interlobate Moraine which have been minimally disturbed have a high probability of supporting sugar maple - red oak overstories with members of the Maianthemum species group as the predominant ground flora. Banded ice-contact hills in northwestern Lower Michigan tend to support high basal areas of red oak and ground flora of the Viburnum or Desmodium species groups. While these relationships are regional in nature (Cleland et al. 1985, Spies and Barnes 1985a), and apply to stands which are relatively undisturbed, they allow us to map potential species composition. A related study has shown that not only present composition, but also potential successional pathways vary among landforms (Chapter 5). Landform is a major selective force in determining potential species composition in specific and definable portions of the landscape. The ability to map potential species composition by landform has important ramifications for land management, especially for silviculture and wildlife.

The problem of scale

The nature of environmental factors controlling vegetation pattern varies with the scale of observation (Damman 1979); at small scales, aspect, slope, and local disturbance are important, while at large scales, regional relief and climate are dominant factors. In the glaciated terrain of northwestern Lower Michigan, significant vegetation pattern exists at the scale of landform; in our case, the geomorphic maps were made at a scale of 1:62,500. The subsurface configuration of textural bands is poorly understood, but banded soil series have been mapped at a scale of 1:15,000. Within this regional landscape, variation in community composition can therefore be quantified at scales between 1:10,000 and 1:100,000. Moisture availability, and its concomitant influence on nitrogen availability and other nutrient cycling processes (Pastor et al. 1984, Pastor and Post 1986), appears to be the key environmental factor operating within this range of scales.

The correlation among forest structural layers is also a function of scale. The high correlation between the overstory and ground flora ordinations, and the repeated co-occurrence of specific overstory and ground flora species on similar landforms implies that there are particular assemblages of ground flora and overstory (plant associations *sensu* Daubenmire 1966) which occur as a response to environmental factors. This contrasts with results from montane forests in the western United States: McCune and Antos (1982) found a poor correlation among forest structural layers, and concluded that stand history, intraspecific genotypic variation, and other factors preclude close correlations among layers. They also note, however, that higher correlations may occur along longer ecological gradients (i.e. among sets of stands with higher beta-diversity). Their study was based on a restricted range of communities, specifically, those communities in which *Abies grandis* occurs. At this low level of beta-diversity, the influence of the physical environment was secondary to canopy and stochastic effects. Hence, correlations among layers were low.

DelMoral and Watson (1978) sampled montane forests at a larger scale (i.e. along a longer compositional gradient) and reported a high correlation between the overstory and herbaceous layers under dry forest conditions. They hypothesize that, under closed canopies, ground flora composition is largely controlled by the canopy, while under open canopy conditions, ground flora and overstory respond to the same factors. Beta diversity in our study was similar to delMoral and Watson's, representing a complete turnover in species (Hill 1979). Canopy closure in our study ranged from the relatively open canopies of the outwash plains to closed canopies on morainal hills. There was no apparent scatter of scores within the closed canopy portion of the gradient, as we would expect under DelMoral and Watson's hypothesis. The close association we observed between overstory and ground flora species appears to be closely related to landform, as illustrated by Figure 3.6. In Michigan, at the scale of the regional landscape, plant associations occurred repeatedly in predictable landscape positions. The variation in species composition which appears continuous and unpatterned at one scale may exhibit gradient-related structure at another.

Landform-mediated fire history

A major dichotomy in species composition exists between the northern hardwood-dominated Interlobate Moraine and the oak-dominated morainal or glaciofluvial landforms. These features are similar in soil texture and topography; they appear to differ, however, in their fire histories. The extensive outwash plains and ice-contact hills within them occupy fire-prone landscape positions, particularly if fires are driven inland by westerly winds from Lake Michigan. The Interlobate Moraine, on the other hand, is situated northeast of two major river systems, which provide natural firebreaks to fires advancing from the west. Grimm (1984) has attributed compositional differences between northern hardwood and oak dominated forests in Minnesota to landform-mediated differences in fire history. He further noted that, due to landform-controlled fire probability patterns, sites with virtually identical physical characteristics supported qualitatively different, stable vegetative communities. The presence of a well-developed Bhs horizon in soils of the Interlobate Moraine, contrasted with the more poorly developed Bs and Bw horizons encountered elsewhere, is an indication that the Interlobate may have been historically protected from fire, allowing a Bhs horizon to develop.

Actual vs. potential composition

Climate, fire history, and landform act to define and constrain potential species composition. The actual species composition of a site is a function of many biotic and abiotic factors, such as seed source and competition, as well as stochastic factors such as frequency and type of disturbance. The close association between overstory and ground flora is not due soley to independent responses of individual species to the predominant environmental factors, but also to interactions within and among life forms.

overstory species, by shading, allelopathy, chemical composition of litter, and other factors, create environmental conditions which select for particular sets of ground flora species. Zak et al. (1986) have shown that differences in litter quality have a strong influence on rates of nitrogen mineralization, which in turn may influence ground flora composition. Conversely, ground flora may affect establishment and growth of overstory species through competitive or allelopathic effects. Landform itself is an ultimate factor which imposes constraints on potential species composition, selecting for species capable of establishment and persistance in a site. Other, more proximal, factors determine the actual distribution of species. These factors act probabilistically (McNaughton 1984), so that models of species composition must necessarily be probabilistic rather than deterministic in nature (Pastor and Post 1986). Nonetheless, the actual species composition of this regional landscape, which was highly disturbed at the turn of the century (Mustard 1983), is strongly related to the geological processes that formed the face of this portion of earth.

Landform is the most stable morphological component of landscape ecosystems, certainly more stable than either soils or vegetation (Rowe 1984). In the glaciated terrain of northwestern Lower Michigan, I have shown that landform has directly and indirectly played an important role in determining the spatial distributions of plant communities.

Functional ecosystem processes tied to species composition, such as biomass production and nutrient turnover, must also be ultimately related to landform. Further work which attempts to quantify variation in these processes within and among landforms should allow us to understand ecosystem structure and function in the context of the three dimensional structure of the landscape rather than along two-dimensional gradients or at single points.

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## Chapter 4

# UPLAND FOREST ECOSYSTEMS OF NORTHWESTERN LOWER MICHIGAN


## ABSTRACT

Nine upland forest ecosystems were identified based on combinations of physiography, ground flora, and soils. Landform, defined as parent materials + surface configuration, provided the initial stratification of the landscape. Eighty sample stands were randomly located within landforms, and soil, floristic, and overstory data were collected at four points within each stand. Multivariate and tabular analyses were used to cluster stands with similar physiographic soil and floristic properties. Within landforms, variation in soils and ground flora composition were used to define upland ecosystems. Ground flora species were aggregated into ecological species groups to facilitate use of ground flora as a component of the classification. Sample stands were clustered by ground flora using a divisive classification algorithm. Soils were characterized using both solum and deep soil properties. Soil, floristic, and physiographic data were integrated to define landscape ecosystems. This paper describes the nine ecosystems and tabularizes salient ecosystem properties.

# INTRODUCTION

Intelligent forest management requires a thorough understanding of the land base: forest composition and structure, potential productivity, physical limitations, and the optimal silvicultural prescription for a site given specific management objectives. An effective means of categorizing or classifying a heterogeneous landscape is a prerequisite to developing an effective management strategy. Many classification systems have been developed for this purpose: cover types, habitat types, and soil surveys are but a few. Each system has strengths and weaknesses, proponents and critics. The European system of ecological land classification has recently been introduced to the United States (Barnes et al. 1982). The advantages and problems with ecosystem classification systems are reviewed in Bockheim (1984). Ecosystem classification involves integrating physiography, soils, and vegetation to define ecosystem units, or ecosystems. Ecosystems are units of relatively homogeneous composition and structure that occur in characteristic landscape positions. A working hypothesis of ecological land classification has been stated by Spies (1985): "...that strong relationships among physiography, soil and vegetation exist, enabling the recognition of ecosystem units (site units) which are characteristic combinations of these components."

The following study describes an ecological classification of the Manistee National Forest in northwestern Lower Michigan. The study developed as a cooperative agreement between the U. S. Forest Service and Michigan State University. The ecosystems described here represent one of the initial phases in the development of the classification, and will be successively refined as the project continues. Nonetheless, the ecosystems defined here represent spatial units which occur repeatedly in characteristic landscape positions. They may be identified using simple field criteria, and possess characteristic compositional, structural, and functional ecosystem properties.

Nine upland forest ecosystems were identified. The characteristic physiography, overstory, soils and ground flora of each ecosystem are described narratively in the following sections; and tabularized in Tables 4.1 to 4.4 (beginning page 108).

## ECOSYSTEM DESCRIPTIONS

### Ecosystem 1 - Pin oak-black oak/Deschampsia

The pin oak-black oak/Deschampsia ecosystem occurs on outwash plains. Physiography is level to slightly undulating, although kettleholes and low inland sand dunes may occur. Slopes are generally < 5%. The soils are excessively drained; coarse and medium sands account for 70% of the total particle weight at 50 cm. The typical horizon sequence is O-A-Bw-C. Because of low overstory basal areas, net inputs of litter are low. The A horizons range from 5-10 cm in thickness. Soil pH and organic carbon levels in the A horizon are low, averaging 4.0 and 2%, respectively. The profusion of fine roots of Carex pensylvanica and various grasses is a primary cause of A horizon development. E horizons are absent. B horizons are yellowish brown to brown coarse and medium sands about 50 cm in thickness. C horizons are very pale brown coarse and medium sands; depth to C horizon is about 60-65 cm. The sands show no evidence of textural stratification or banding in the top 4.5 m. The typical soil series is Grayling sand, a sandy, mixed, frigid Typic Udipsamment.

The overstory is dominated by upland pin and black oak, having a combined average basal area of 8.9 $m^2$/ha. White oak contributes approximately 7.7 $m^2$/ha. Red maple is extremely uncommon in the overstory. Stocking is low on these sites, presumably because of the xeric conditions. After fire, this ecosystem is commonly dominated by jack pine. The average basal area in pin oak-black oak/Deschampsia ecosystem is 17.5 $m^2$/ha, the average standing volume is 105 $m^3$/ha. Mean annual increment is 1.6 $m^3$/ha/yr; mean annual biomass increment is 1.3 t/ha/yr. The site indices for red and black oaks are 48 and 51, respectively. The site index for white oak is 44. The site indices and mean annual increment are the lowest of all ecosystems.

Stem densities in the 2-9 cm size classes are low, averaging 61 stems/ha. Jack and white pines are the most common species in this size class, averaging 11 and 12 stems/ha respectively. Black cherry and white oak frequently occur, but black cherry is usually infected with black knot disease (Dibotryon morbosum), and the white oaks are typically in a state of decline. There is little vigorous natural reproduction.

The ground flora consists of a near-continuous mat of Carex pensylvanica and Deschampsia flexuosa. Carex pensylvanica can be found in all of the ecosystems described, but attains its maximum coverage in pin oak-black oak/Deschampsia ecosystem, where it covers 50-100% of the forest floor. Arctostaphylos uva-ursi, Comptonia peregrina and Andropogon gerardii are common. Gaultheria procumbens and Vaccinium angustifolium are also common, but occur in other ecosystems as well. The predominant feature of the ground flora is the dense sedge and grass mat carpeting the forest floor.

The pin oak-black oak/Deschampsia plains are similar to the black oak-white oak/Vaccinium plains, but differ by having a more open canopy, a lawn-like sedge and grass layer, the presence of Comptonia peregrina and Arctostaphylos uva-ursi, and the lack of an E horizon.

Ecosystem 2 - Black oak-white oak/Vaccinium plains

The black oak-white oak/Vaccinium plains occur on outwash sands. Physiography is level to slightly undulating, although kettleholes and low inland sand dunes may occur. Slopes are generally < 3%. The soils are excessively drained; coarse and medium sands account for 70% of the total particle weight at 50 cm. The typical horizon sequence is O-A-E-Bs-C. A horizons average 5 cm in thickness. Soil pH and organic carbon levels in the A horizon are low, averaging 4.1 and 2%, respectively. Light gray E horizons are usually present but discontinuous and range from 0-5 cm in thickness. The brown Bs horizons average 26 cm in thickness. C horizons are very pale brown medium sands; depth to the C horizon is 60-70 cm. The soils exhibit little evidence of textural stratification or banding in the top 4.5 m. The Grayling and Rubicon sands (sandy, mixed, frigid Entic Haplorthods) are typical soil series.

Black and white oak dominate the overstory, averaging 9.7 and 9.0 $m^2$/ha basal area, respectively. Red maple is typically absent from the overstory. Red oak contributes 2.0 $m^2$/ha to the total basal area. The forest canopy is not completely closed, allowing moderate light penetration to the forest floor. Average basal area is 21.6 $m^2$/ha; average standing volume is 129 $m^3$/ha. Mean annual increment is 1.7 $m^3$/ha/yr; mean annual biomass increment is 1.7 t/ha/yr. The site indices for red, black, and white oaks are 53, 54, and 46, respectively.

The black oak-white oak/Vaccinium plains supports an understory averaging 100 stems/ha. White oak is the most frequent species, averaging 16 stems/ha. White pine and red maple average 24 and 20 stems/ha, respectively, but only occurred in 50% of the sample stands. Red maple in this ecosystem rarely occurs in the overstory, however, possibly due to xeric site conditions. Hamamelis virginiana is a common tall shrub, averaging 20 stems/ha.

The Vaccinium group typifies this ecosystem. Predominant species are Vaccinium angustifolium, Gaylussacia baccata, Gaultheria procumbens, Melampyrum lineare, and Dicranum polysetum. Trientalis borealis and Maianthemum canadense are usually absent from this ecosystem. The ground flora is similar to that of Ecosystem 1, except that Arctostaphylos uva-ursi and Comptonia peregrina are typically absent, Carex pensylvanica and Deschampsia flexuosa are less abundant, and red maple seedlings are present. Sassafras albidum , absent from Ecosystem 1, occurs here.

The black oak-white oak/Vaccinium plains is similar to Pin oak-black oak/Deschampsia and the black oak-white oak/Vaccinium hills ecosystems. The black oak-white oak/Vaccinium plains differ from the pin oak-black oak/Deschampsia ecosystem by having a more closed canopy, decreased cover of the Deschampsia group, increased cover of the Vaccinium group, and the presence of a discontinuous E horizon in the soil profile.

Ecosystem 3 - Black oak-white oak/Vaccinium hills

The black oak-white oak/Vaccinium hills ecosystem occurs on both ice contact hills and moraines. Physiography is variable, ranging from locally level to steep kame-kettle topography; slopes range from 2-30%. The soils are well-drained sands; coarse and medium sands account for 70% of the total particle weight. The typical horizon sequence is O-A-E-Bs-C. A horizons average 5 cm in thickness. Soil pH and organic carbon levels of the A horizon are low, averaging 3.9 and 2%, respectively. Light grey E horizons are usually present and range from 2-11 cm in thickness. Brown spodic horizons may be present and average 22 cm in thickness. Average depth to the C horizon is 66 cm. The typical soil series is Rubicon sand.

Black and white oak dominate the overstory, averaging 7.9 and 6.8 $m^2$/ha basal area, respectively. Red maple is uncommon in the overstory. Red oak is more abundant compared with Ecosystem 2, averaging 5.1 $m^2$/ha. The forest canopy is not completely closed, allowing moderate light penetration to the forest floor. Average basal area is 21.6 $m^2$/ha; average standing volume is 156 $m^3$/ha. Mean annual increment is 2.0 $m^3$/ha/yr; mean annual biomass increment is 1.7 t/ha/yr. The site indices for red, black, and white oaks are 61, 56, and 47, respectively.

Red maple is the most common species in the understory, averaging 60 stems/ha. Hamamelis virginiana is a common (16 stems/ha). White pine is uncommon, with an average density of 9 stems/ha.

The ground flora is characterized by the Vaccinium, Pteridium and Hamamelis groups. The Trientalis group is usually absent. Vaccinium angustifolium, Pteridium aquilinium, Sassafras albidum, and Carex pensylvanica are the most conspicuous ground flora elements.

Composition of all structural layers in the black oak-white oak/Vaccinium hills is virtually identical with black oak-white oak/Vaccinium plains; differences are primarily physiographic. The black oak-white oak/Vaccinium hills differ from the red oak-white oak/Trientalis ecosystem by absence of red oak and the Trientalis species group.

Ecosystem 4 - Red oak-white oak/Trientalis

The red oak-white oak/Trientalis ecosystem occurs on weakly banded sands of both ice contact hills and moraines. Physiography is variable, ranging from level to strongly undulating to kame-kettle topography. Slopes range from 0-12%. The soils are well drained sands; coarse and medium sands account for 66% of the total particle weight. The typical horizon sequence is O-A-E-Bs-C. A horizons average 4 cm in thickness. Soil pH and organic carbon levels of the A horizon are low, averaging 4.0 and 2%, respectively. Light grey E horizons are usually present and range from 2-12 cm in thickness. Brown spodic horizons may be present and range from 3-67 cm in thickness. Average depth to the C horizon is

66 cm. The red oak-white oak/Trientalis ecosystem is characterized by subsoil textural banding of sandy loam to sandy clay. The typical soil series is Rubicon, a sandy, mixed, frigid, Entic Haplorthod.

The overstory is dominated by red, white, and black oaks, averaging 10.6, 7.8, and 5.2 $m^2$/ha basal area, respectively. Red maple occurs in the overstory with a mean basal area of 2.4 $m^2$/ha. In the drier ecosystems (Ecosystems 1, 2, and 3), red maple is absent as an overstory species, even though it may be found in smaller size classes. The average standing volume of this ecosystem is 161 $m^3$/ha; the average basal area is 23.4 $m^2$/ha. Mean annual increment is 2.2 $m^3$/ha/yr; mean annual biomass increment is 2.0 t/ha/yr. The site indices for black, red, and white oaks are 62, 60, and 49, respectively.

Red maple and white pine dominate the advance regeneration, averaging 63 and 25 stems/ha, respectively. A strong understory layer of _Hamamelis_ _virginiana_ (32 stems/ha) is also common. This species forms large, spreading clumps of 7-14 stems, typically 3-5 m tall. There is virtually no oak reproduction in this ecosystem.

Species of the Trientalis group, including _Trientalis_ _borealis_, _Aralia_ _nudicaulis_ , _Viburnum_ _acerifolium_, and white pine are common in this ecosystem, and separate this ecosystem from the drier ecosystems. Members of the Vaccinium group also occur in this ecosystem, as does

*Maianthemum canadense*. Red maple and red oak seedlings are abundant.

The red oak-white oak/Trientalis ecosystem is similar to the black oak-white oak/Vaccinium and red oak-white oak/Viburnum ecosystems. This ecosystem differs from the black oak-white oak/Vaccinium hills by the presence of the Trientalis group, *Maianthemum canadense*, and by having more strongly developed eluvial (E) and spodic (Bs) soil horizons. Both of these systems may have *Hamamelis virginiana* as a tall shrub. Red maple is present in the overstory of the red oak-white oak/Trientalis ecosystem but absent in the black oak-white oak/Vaccinium hills. The red oak-white oak/Viburnum ecosystem has stronger banding and an increased cover of *Viburnum acerifolium* compared to the red oak-white oak/Trientalis ecosystem.

Ecosystem 5 - Red oak-white oak/Viburnum

The red oak-white oak/Viburnum ecosystem occurs on banded ice-contact or morainal hills. Local physiography ranges from level to highly dissected hills, slopes range from 0-20%. The soils are well-drained to moderately well-drained sands, occasionally loamy sands; silt and clay account for 8% of the total particle weight. The typical horizon sequence is O-A-E-Bs-C. A horizons average 3.5 cm in thickness. Soil pH and organic carbon levels of the A horizon are low, averaging 4.1 and 2%, respectively. Light grey E horizons are present and range from 5-14 cm in thickness. Brown spodic horizons average 34 cm in thickness; the dominant texture of the B horizon is sand. Average depth to the C horizon is 72 cm. Surface soils are underlain by sandy clay or sandy clay loam bands. The bands typically have a cumulative thickness over 15 cm within 4.5 m of the surface. The typical soil series is Rubicon sand, a sandy, mixed, frigid, Entic Haplorthod.

Red oak dominates the overstory of this ecosystem, averaging 17.4 $m^2$/ha basal area. Red maple and white oak are also important, averaging 3.4 and 3.9 $m^2$/ha, respectively. The red oak-white oak/Viburnum ecosystem supports one of the highest average timber volumes, 35.2 $m^3$/ha. Average basal area is 214 $m^2$/ha. Mean annual increment is 3.1 $m^3$/ha/yr; mean annual biomass increment is 3.0 t/ha/yr. The site indices for red and white oaks are 75 and 60, respectively.

Red maple is the most significant advanced regeneration, averaging 47 stems/ha. The understory also supports a high densities of Hamamelis virginiana (40 stems/ha). Red and white oaks and white pine are virtually absent from the understory. Beech and sugar maple occasionally occur in the understory.

Viburnum acerifolium is an important component of the ground flora. It is found as a medium-sized shrub (40-60 cm in height) forming large clonal patches. Viburnum acerifolium is also found in Ecosystem 4, but it is much less abundant and typically < 15 cm tall. Trientalis *borealis* , *Maianthemum canadense* and *Aralia nudicaulis* are common, as are elements of the Vaccinium group. Sugar maple and beech seedlings are occasionally observed.

The red oak-white oak/Viburnum ecosystem is similar to the red oak-white oak/Trientalis and red oak-red maple/Desmodium ecosystems. The red oak-white oak/Viburnum ecosystem has heavier substratum banding than the red oak-white oak/Trientalis ecosystem and supports large clones of *Viburnum acerifolium*. The red oak-white oak/Viburnum ecosystem also has a higher frequency of *Trientalis borealis* and *Trillium grandiflorum* than the red oak-white oak/Trientalis ecosystem. The red oak-white oak/Viburnum ecosystem has sandy subsurface horizons, as opposed to the loamy subsurface horizons of the red oak-red maple/Desmodium ecosystem.

Ecosystem 6 - Red oak - red maple/Desmodium

The red oak-red maple/Desmodium ecosystem occurs on moraines and ice contact features. Physiography is level to very steep, slopes ranging from 0-55%. The soils are well-drained fine sands to loams; silt and clay account for 25% of the total particle weight at 50 cm. The typical horizon sequence is O-A-E-Bs-C. The A horizons average 4 cm in thickness. Soil pH and organic carbon levels of the A horizon are low, averaging 4.3 and 2%, respectively. E horizons range from 3-7 cm in thickness. Dark brown Bs horizons range from 6-62 cm in thickness. Bhs horizons are absent. Average depth to the C horizon is 93 cm. The subsoil is typified by bands of sandy clay loam to sandy clay, with a cumulative thickness of 15 cm in the upper 1 to 4.5 m. Typical soil series are Blue Lake (sandy, mixed frigid Alfic Haplorthod), Montcalm (coarse-loamy mixed Eutric Glossoboralf), and Rosseau (sandy, mixed frigid Entic Haplorthod).

The overstory is quite similar to the red oak-white oak/Viburnum ecosystem, with red oak averaging 16.3 $m^2$/ha basal area. Basal area of red maple is higher here, averaging 5.5 $m^2$/ha. White oak is also common in the overstory, with an average of 5.3 $m^2$/ha. This ecosystem supports the greatest standing hardwood volumes found in the stands sampled to date, averaging 245 $m^3$/ha. The average basal area is 26.2 $m^2$/ha. Mean annual increment is 3.4 $m^3$/ha/yr; mean annual biomass increment is 3.1 t/ha/yr. The site indices for red and white oaks are 85 and 67, respectively. The overstory is seral and the late successional community will likely comprise northern hardwoods.

This ecosystem has a prominent understory layer of _Cornus florida_ and _Hamamelis virginiana_. These spreading tall shrubs form a distinctive structural layer in the understory. Tree regeneration is sparse, dominated by red maple at 17 stems/ha. Sugar maple and beech may be present as minor components (< 10 stems/ha).

_Desmodium spp._ are the dominant species of the ground flora. _Cornus florida_ is important as both a ground flora and understory species. The ground flora contains elements of both sugar maple and oak ecosystems: sugar maple seedlings, *Maianthemum canadense*, *Viola pubescens*, *Trientalis borealis*, and *Gaultheria procumbens*. This community represents a successional sere of an oak ecosystem progressing toward a northern hardwood climax community.

The red oak-red maple/Desmodium ecosystem is similar to the red oak-white oak/Viburnum ecosystem, but the former ecosystem has a distinctive ground flora containing *Cornus florida* and *Desmodium* spp. The red oak-red maple/Desmodium ecosystem has loamy subsoil textures, as opposed to the sandy subsoil textures of the red oak-white oak/Viburnum ecosystem.

Ecosystem 7 - Unbanded sugar maple-red oak/Maianthemum

The unbanded sugar maple-red oak/Maianthemum ecosystem occurs on unbanded moraines and sandy till plains. In the Manistee National Forest this system occurs primarily on the Interlobate Moraine in Wexford Co. The topography of this system is complex, characterized by level to moderately steep slopes formed in a mosaic of dendritic drainage patterns. Slopes range from 0-17%. The soils are well drained medium and loamy sands. The typical horizon sequence is O-A-E-Bhs-Bs-C. The presence of a Bhs horizon is diagnostic for all upland ecosystems of the Interlobate moraine. The O horizon consists of a heavy layer of oak and beech litter. Very dark brown A horizons average 6 cm in thickness. Soil pH and organic carbon levels of the A horizon are low, averaging 4.3

and 3%, respectively. Light gray E horizons range from 12-17 cm in thickness. Dark brown Bhs horizons range from 2-23 cm. Textures of the B horizons are sands or loamy sands. Average depth to the C horizon is 75 cm. Subsoil textural banding is absent. The typical soil series for this ecosystem is Kalkaska sand, unbanded phase, a sandy, mixed, frigid, Typic Haplorthod.

Sugar maple, and red oak are dominant members of the overstory, both contributing approximately 7.2 $m^2$/ha basal area. White ash, beech and basswood contribute 3.3, 1.9, and 1.7 $m^2$/ha basal area, respectively. Red maple and black cherry each contribute 1.2 $m^2$/ha basal area. The forest canopy of this ecosystem is closed, with little light penetration to the forest floor. The ecosystem carries the lowest standing volume of the three northern hardwood ecosystems, 190 $m^3$/ha. Average basal area of this ecosystem is 23.9 $m^2$/ha. Mean annual increment is 3.0 $m^3$/ha/yr; mean annual biomass increment is 2.7 t/ha/yr. The site indices for red oak, sugar maple, and black cherry are 76, 65, and 69, respectively.

This ecosystem has the highest understory stem density (153 stems/ha). Virtually all of this was sugar maple reproduction (131 stems/ha). Beech is also present in the understory, averaging 14 stems/ha. Red oak was absent from almost all stands in this ecosystem.

The unbanded sugar maple-red oak/Maianthemum ecosystem has a depauperate ground flora, in terms of both species abundance and coverage. In fact, the sparse nature of the ground flora is so characteristic that it is a distinguishing feature of the ecosystem. Species which are present belong to the Maianthemum group: Maianthemum canadense, Polygonatum biflorum, Lycopodium obscurum and L. lucidulum, and Carex deweyana. Species of the Osmorhiza group, including Osmorhiza claytonii, Viola canadense, and Carex plantaginea, may occur infrequently. In spring, prior to canopy closure, the forest floor is carpeted with the spring ephemerals Erythronium americanum and Claytonia virginiana. Pteridium aquilinium occupies open or gap areas in the forest.

The unbanded sugar maple-red oak/Maianthemum ecosystem lacks the subsurface banding found in the banded sugar maple-red oak/Maianthemum ecosystem, but is otherwise similar in terms of its ground flora and soil properties.

Ecosystem 8 - Banded sugar maple - red oak/Maianthemum

The banded sugar maple-red oak/Maianthemum ecosystem, occurs on banded morainal positions. In the Manistee National Forest this system occurs on the Interlobate Moraine in Wexford Co. The topography of this system is complex, characterized by level to moderately steep slopes formed in a mosaic of dendritic drainage patterns. Slopes range from 0-15%. The soils are well-drained medium and fine sands. The typical horizon sequence is O-A-E-Bhs-Bs-C. The presence of a Bhs horizon is diagnostic for all upland ecosystems of the Interlobate Moraine. A horizons average 7 cm in thickness. Soil pH and organic carbon levels of the A horizon are low, averaging 4.1 and 3%, respectively. Average thickness of the light gray E horizon ranges from 7-24 cm; average thickness of the dark brown Bhs horizon ranges from 5-8 cm. Average depth to the C horizon is 79 cm. The important discriminating factor is the presence of sandy loam to sandy clay loam bands below the control section (depths > 1.2 m). The typical soil series is Kalkaska sand, banded phase, a sandy, mixed, frigid Typic Haplorthod.

Red oak and sugar maple are dominant members of the overstory, accounting for 12.8 and 8.0 $m^2$/ha basal area, respectively. Beech contributes 3.8 $m^2$/ha basal area. Red maple and white ash are uncommon. The forest canopy of this ecosystem is closed, with little light penetration to the forest floor. Standing volume is substantially higher on banded sites than on the similar but unbanded sites of Ecosystem 7; the average volume is 250 $m^3$/ha. Average basal area is 28.2 $m^2$/ha. Mean annual increment is 3.7 $m^3$/ha/yr; mean annual biomass increment is 3.6 t/ha/yr. The site indices for red oak, sugar maple, and black cherry are 86, 72 and 78, respectively.

Like the unbanded sugar maple-red oak/Maianthemum ecosystem, the understory of the banded sugar maple-red oak/Maianthemum ecosystem is dominated by sugar maple and beech. Stem densities of these species are lower, however, 49 and 26 stems/ha, respectively. Red maple is uncommon in the understory; red oak, white ash and basswood are absent.

The ground flora of the banded sugar maple-red oak/Maianthemum ecosystem, as in the unbanded phase, is quite sparse, and typified by the Maianthemum group.

The banded sugar maple-red oak/Maianthemum ecosystem, is similar to the unbanded sugar maple-red oak/Maianthemum ecosystem, but is separated by the presence of sandy loam to sandy clay loam bands at depths > 1 m. The banded and unbanded sugar maple-red oak/Maianthemum ecosystems cannot be distinguished on the basis of ground flora. Subsoil textural features must be used to separate these ecosystems. The presence of the Osmorhiza species group in the sugar maple-basswood/Osmorhiza ecosystem separates this ecosystem from both the banded and unbanded sugar maple-red oak/Maianthemum ecosystems.

Ecosystem 9 - Sugar maple - basswood/Osmorhiza

The sugar maple-basswood/Osmorhiza ecosystem occurs on deep banded sites on moraines. In the Manistee National Forest this system occurs on the Interlobate Moraine in Wexford Co. The topography of this system is complex, characterized by level to steep slopes formed in a mosaic of dendritic drainage patterns. Slopes range from 0-33%. The soils are well-drained sands to sandy clay loams; silt and clay account for 10% of the total particle weight at 50 cm. The typical horizon sequence is O-A-E-Bhs-Bs-C. The presence of a Bhs horizon is diagnostic for all upland ecosystems of the Interlobate Moraine. The sugar maple-basswood/Osmorhiza ecosystem has a thick very dark greyish brown A horizon, averaging 9 cm in thickness. Average thickness of the E horizon is 9 cm; average Bhs horizon thickness is 5 cm. Average depth to the C horizon is 79 cm. Soil pH and organic carbon levels are relatively high in this ecosystem, averaging 5.4 and 4%, respectively. Thick sandy clay loam to clay loam bands are present at depths > 1 m. The typical soil series is Kalkaska sand, banded phase, a sandy, mixed, frigid, Typic Haplorthod.

The overstory is dominated by sugar maple and basswood, averaging 11.9 and 6.5 $m^2$/ha basal area, respectively. White ash and red oak contribute 3.4 and 2.9 $m^2$/ha basal area, respectively. Beech, black cherry and red maple collectively contribute about 1.9 $m^2$/ha basal area. Overstory diversity is high. This ecosystem also carries the highest standing volume of the northern hardwoods ecosystems, averaging 264 $m^3$/ha. Average basal area is 28.4 $m^2$/ha. Mean annual increment is 4.2 $m^3$/ha/yr; mean annual biomass increment is 4.2 t/ha/yr. The site indices for red oak, sugar maple, and black cherry are 86, 75, and 81, respectively.

Sugar maple dominates the advance regeneration, with 83 stems/ha. Ostrya virginiana is usually present, with an average of 10 stems/ha. Beech occurs at low densities (10 stems/ha).

The sugar maple-basswood/Osmorhiza ecosystem is characterized by a diverse and abundant ground flora. Many of the species are specific to the ecosystem and rarely occur outside it. The Osmorhiza species comprises a diverse group of ephemeroids and herbaceous perennials, including Osmorhiza claytonii, Viola canadense , Allium tricoccum, Mitella diphylla, and Carex plantaginea. Of these species, Osmorhiza claytonii is the most prominent, having a high coverage and uniform distribution throughout the stand. In spring, the forest floor is a near-continuous carpet of Allium tricoccum, Dicentra spp., Erythronium americanum, and many other spring wildflower species. The ground flora is unique, and one of the more readily-identified groups in the forest.

The sugar maple-basswood/Osmorhiza ecosystem is similar to the banded and unbanded sugar maple-red oak/Maianthemum ecosystems, but has a distinctive ground flora typified by species of the Osmorhiza group. A thick (9 cm) A horizon is also characteristic of this ecosystem.

Table 4.1 Selected overstory characteristics of upland forest ecosystems in northwestern lower Michigan.

| Variable | Ecosystem 1 (n = 10) | 2 (n = 12) | 3 (n = 10) | 4 (n = 11) | 5 (n = 7) | 6 (n = 7) | 7 (n = 7) | 8 (n = 6) | 9 (n = 6) |
|---|---|---|---|---|---|---|---|---|---|
| Age | 69 (2) | 77 (3) | 79 (3) | 75 (3) | 70 (2) | 73 (3) | 63 (2) | 69 (3) | 64 (3) |
| Basal area (sq m/ha) | 17.5 (3.1) | 21.6 (2.4) | 21.6 (2.9) | 23.4 (2.4) | 26.4 (3.4) | 26.2 (2.6) | 23.9 (4.5) | 28.2 (2) | 28.4 (2.5) |
| # trees/ha | 100 (27) | 114 (30) | 98 (26) | 125 (40) | 104 (33) | 82 (33) | 126 (35) | 117 (36) | 115 (19) |
| Volume (cu m/ha) | 105 (25) | 129 (38) | 156 (25) | 161 (40) | 214 (39) | 245 (51) | 190 (35) | 250 (33) | 264 (40) |
| MAI (cu m/ha/yr) | 1.6 (0.3) | 1.7 (0.6) | 2 (0.4) | 2.2 (0.4) | 3.1 (0.6) | 3.4 (0.5) | 3 (0.4) | 3.7 (0.6) | 4.2 (0.6) |
| Biomass (t/ha) | 85 (6) | 122 (7) | 133 (9) | 151 (8) | 208 (8) | 225 (13) | 172 (14) | 249 (7) | 210 (11) |
| MABI (t/ha/yr) | 1.3 (0.1) | 1.7 (0.1) | 1.7 (0.2) | 2 (0.1) | 3 (0.2) | 3.1 (0.1) | 2.7 (0.2) | 3.6 (0.2) | 3.3 (0.2) |
| Species basal area (sq m/ha) | | | | | | | | | |
| Quercus velutina | 8.9 (1.5) | 9.7 (1.8) | 7.9 (2.0) | 5.2 (1.3) | | | | | |
| Q. alba | 7.7 (1.7) | 9 (0.9) | 6.8 (1.3) | 7.8 (0.9) | 3.9 (0.8) | 5.3 (2.3) | | | |
| Q. rubra | | | 5.1 (2.3) | 10.6 (1.8) | 17.4 (2.2) | 16.3 (3.3) | 7.2 (3.5) | 12.8 (3.8) | |
| Acer rubrum | | | | 2.4 (0.7) | 3.4 (0.7) | 5.5 (0.9) | 1.2 (0.6) | | |
| A. saccharum | | | | | | | 7.1 (2.4) | 8.0 (2.7) | 11.9 (1.6) |
| Tilia americana | | | | | | | 1.7 (0.8) | 1.1 (0.9) | 6.5 (2.0) |
| Fraxinus americana | | | | | | | 3.3 (1.1) | 0.2 (0.2) | 3.4 (1.5) |
| Site indices | | | | | | | | | |
| Quercus velutina | 51 (6) | 54 (5) | 56 (5) | 62 (8) | | | | | |
| Q. alba | 44 (6) | 46 (5) | 47 (8) | 49 (7) | 60 (8) | 67 (8) | | | |
| Q. rubra | | 53 (4) | 61 (7) | 60 (6) | 75 (8) | 85 (7)* | 76 (4)* | 86 (8)* | 86 (7)* |
| Acer saccharum | | | | | | | 65 (6) | 72 (1) | 75 (6) |

Note: All values are means (standard error)

* Site indices may be overestimated due to stump sprouting.

Table 4.2 Selected understory (stems 1-9 cm dbh) stem densities of upland forest ecosystems in northwestern Lower Michigan.

| Variable | Ecosystem 1 (n = 10) | 2 (n = 12) | 3 (n = 10) | 4 (n = 11) | 5 (n = 7) | 6 (n = 7) | 7 (n = 7) | 8 (n = 6) | 9 (n = 6) |
|---|---|---|---|---|---|---|---|---|---|
| Total # stems/ha | 61 (9) | 94 (17) | 111 (19) | 138 (19) | 111 (24) | 102 (20) | 153 (35) | 82 (17) | 109 (33) |
| # stems/ha by species | | | | | | | | | |
| Acer rubrum | 2 (1) | 20 (10) | 59 (17) | 63 (11) | 47 (11) | 17 (4) | 1 (1) | 3 (2) | 1 (1) |
| A. saccharum | | | | | 1 (1) | | 131 (40) | 49 (14) | 83 (24) |
| Amelanchier spp. | 3 (2) | | 1 (0) | 4 (2) | 9 (4) | 1 (1) | | | |
| Cornus florida | | | | | | 11 (5) | | | |
| Fagus grandifolia | | | 1 (1) | | | 2 (1) | 14 (5) | 26 (10) | 7 (3) |
| Hamamelis virginiana | 1 (1) | 20 (9) | 16 (4) | 32 (10) | 39 (23) | 38 (12) | | | |
| Ostrya virginiana | | | | | 4 (4) | 1 (0) | 3 (1) | 5 (5) | 13 (5) |
| Pinus banksiana | 11 (4) | | | | | | | | |
| P. strobus | 12 (11) | 24 (11) | 9 (6) | 25 (18) | | 22 (17) | | | |
| Prunus serotina | 11 (2) | 5 (2) | | 1 (1) | 2 (1) | 4 (4) | | | |
| Quercus alba | 14 (5) | 16 (4) | 7 (3) | 3 (2) | | | | | |
| Q. ellipsoidalis | 3 (1) | 1 (1) | | | | | | | |
| Q. rubra | | 1 (0) | 2 (1) | 5 (4) | 1 (1) | | 3 (3) | | |
| Q. velutina | 2 (1) | 2 (1) | 4 (2) | | | | | | |
| Sassafras albidum | | 4 (2) | 7 (3) | 5 (3) | 4 (2) | 1 (1) | | | |
| Tilia americana | | | | | | | 1 (1) | | |

Note: All values are means (standard error)

Table 4.3 Mean rank abundance of ground flora species in ecological species groups.

| Species | Ecosystem 1 (n = 10) | 2 (n = 12) | 3 (n = 10) | 4 (n = 11) | 5 (n = 7) | 6 (n = 7) | 7 (n = 7) | 8 (n = 6) | 9 (n = 6) |
|---|---|---|---|---|---|---|---|---|---|
| Deschampsia group | | | | | | | | | |
| Deschampsia flexuosa | - | 0.2 (0.1) | - | 0.1 (0.1) | - | - | - | - | - |
| Arctostaphylos uva-ursi | 1.0 (0.4) | - | - | - | - | - | - | - | - |
| Andropogon gerardii | 0.6 (0.2) | - | - | - | - | - | - | - | - |
| Comptonia peregrina | 1.9 (0.4) | 0.4 (0.1) | 0.3 (0.1) | - | - | - | - | - | - |
| Cladina rangiferina | 0.2 (0.1) | 0.2 (0.1) | 0.3 (0.1) | - | - | - | - | - | - |
| Dicranum polysetum | 1.2 (0.3) | 0.8 (0.2) | 0.6 (0.2) | 0.8 (0.2) | 0.1 (0.1) | - | - | - | - |
| Vaccinium group | | | | | | | | | |
| Melampyrum lineare | 0.9 (0.2) | 1.0 (0.2) | 0.7 (0.2) | 0.6 (0.1) | 0.1 (0.1) | 0.1 (0.1) | - | - | - |
| Gaylussacia baccata | 0.6 (0.4) | 1.0 (0.4) | 1.7 (0.5) | 1.2 (0.4) | 0.3 (0.3) | - | - | - | - |
| Epigaea repens | 0.3 (0.2) | 0.1 (0.0) | 0.3 (0.1) | 0.6 (0.2) | 0.1 (0.1) | - | 0.1 (0.1) | - | - |
| Vaccinium angustifolium | 3.7 (0.3) | 3.1 (0.3) | 2.9 (0.3) | 3.6 (0.2) | 2.2 (0.4) | 1.1 (0.4) | - | - | - |
| Gaultheria procumbens | 0.9 (0.3) | 1.2 (0.3) | 1.1 (0.2) | 1.8 (0.3) | 1.3 (0.3) | 1.0 (0.3) | - | - | - |
| Leucobryum glaucum | - | 0.2 (0.1) | 0.1 (0.1) | 0.1 (0.1) | 0.1 (0.1) | 0.1 (0.0) | - | - | - |
| Hamamelis group | | | | | | | | | |
| Hamamelis virginiana | 0.2 (0.2) | 1.2 (0.4) | 1.6 (0.3) | 2.3 (0.4) | 1.9 (0.4) | 2.7 (0.3) | - | - | 0.1 (0.1) |
| Sassafras albidum | - | 2.2 (0.4) | 2.5 (0.4) | 3.3 (0.1) | 2.5 (0.3) | 2.1 (0.4) | - | - | - |
| Pteridium group | | | | | | | | | |
| Pteridium aquilinium | 2.9 (0.4) | 3.9 (0.5) | 3.5 (0.2) | 3.4 (0.3) | 3.6 (0.6) | 2.9 (0.3) | 0.7 (0.5) | 0.4 (0.2) | 0.2 (0.2) |
| Amelanchier spp. | 1.4 (0.3) | 1.3 (0.1) | 1.5 (0.2) | 2.0 (0.3) | 2.4 (0.3) | 1.3 (0.3) | 0.4 (0.2) | 0.3 (0.1) | - |
| Carex pensylvanica | 6.1 (0.2) | 5.6 (0.3) | 4.2 (0.5) | 3.3 (0.2) | 3.3 (0.7) | 2.2 (0.5) | 0.1 (0.1) | 1.3 (0.4) | 0.7 (0.4) |
| Trientalis group | | | | | | | | | |
| Trientalis borealis | - | - | - | 0.6 (0.2) | 0.9 (0.4) | 0.6 (0.2) | - | 0.3 (0.3) | 0.1 (0.1) |
| Aster macrophyllum | - | 0.2 (0.1) | 0.1 (0.1) | 0.4 (0.1) | 0.8 (0.2) | 0.7 (0.2) | 0.1 (0.1) | - | 0.1 (0.1) |
| Desmodium group | | | | | | | | | |
| Desmodium spp. | - | 0.1 (0.1) | 0.1 (0.1) | - | 0.9 (0.7) | 1.4 (0.5) | - | 0.1 (0.1) | - |
| Viola pubescens | - | - | - | - | - | 0.8 (0.3) | - | - | 0.4 (0.2) |
| Cornus florida | - | - | 0.1 (0.1) | - | - | 3.2 (1.1) | - | - | 0.4 (0.2) |
| Viburnum group | | | | | | | | | |
| Viburnum acerifolium | - | 0.1 (0.0) | 0.9 (0.2) | 1.6 (0.3) | 2.5 (0.6) | 3.3 (0.4) | 0.3 (0.3) | 1.1 (0.5) | 0.8 (0.3) |
| Aralia nudicaulis | - | - | - | 0.3 (0.1) | 1.0 (0.4) | 0.9 (0.3) | 0.5 (0.2) | 0.2 (0.1) | 1.3 (0.3) |
| Medeola virginiana | - | - | - | - | - | 0.4 (0.2) | - | 0.1 (0.1) | - |
| Mitchella repens | - | - | 0.1 (0.1) | - | 0.2 (0.1) | 0.6 (0.3) | 0.3 (0.1) | 0.3 (0.1) | 0.1 (0.1) |

Note: All values are means (standard error). Ranks $< 2.0$ represent trace percent coverage ( <1%).
Ranks $\geq 2.0$ can be converted to percent coverage by the formula: % coverage = $(rank*(-19.0))+(rank^2*3.9)+24$.

Table 4.3 - continued page 2

| Species | Ecosystem 1 (n = 10) | 2 (n = 12) | 3 (n = 10) | 4 (n = 11) | 5 (n = 7) | 6 (n = 7) | 7 (n = 7) | 8 (n = 6) | 9 (n = 6) |
|---|---|---|---|---|---|---|---|---|---|
| Maianthemum group | | | | | | | | | |
| Maianthemum canadense | - | - | - | 0.3 (0.1) | 1.2 (0.2) | 0.9 (0.4) | 1.7 (0.3) | 1.2 (0.2) | 1.6 (0.3) |
| Epifagus virginiana | - | - | - | - | - | - | 0.1 (0.1) | 0.2 (0.1) | - |
| Polygonatum biflorum | - | - | - | 0.1 (0.1) | 0.1 (0.1) | 0.4 (0.2) | 1.0 (0.3) | 0.7 (0.3) | 0.9 (0.3) |
| Lycopodium lucidulum | - | - | - | - | - | - | - | 0.3 (0.1) | - |
| Carex deweyana | - | - | - | - | - | - | 0.5 (0.2) | - | - |
| Lycopodium obscurum | - | - | - | - | 0.1 (0.1) | - | 0.3 (0.3) | 0.4 (0.2) | - |
| Carex pedunculata | - | - | - | - | - | - | 0.5 (0.2) | 0.1 (0.1) | - |
| Solidago caesia | - | - | - | - | 0.1 (0.1) | 0.1 (0.0) | 0.4 (0.3) | 0.2 (0.1) | 0.6 (0.4) |
| Dryopteris spinulosa | - | - | - | - | - | 0.1 (0.1) | 0.3 (0.2) | 0.1 (0.1) | 0.4 (0.2) |
| Osmorhiza group | | | | | | | | | |
| Osmorhiza claytonii | - | - | - | - | - | 0.1 (0.1) | 0.3 (0.2) | 0.4 (0.2) | 3.0 (0.6) |
| Adiantum pedatum | - | - | - | - | - | - | - | - | 0.6 (0.2) |
| Mitella diphylla | - | - | - | - | - | - | 0.2 (0.1) | - | 1.0 (0.4) |
| Tiarella cordifolia | - | - | - | - | - | - | - | - | 0.9 (0.3) |
| Allium tricoccum | - | - | - | - | - | - | 0.1 (0.1) | - | 1.4 (0.6) |
| Hepatica acutiloba | - | - | - | - | - | - | - | - | 0.4 (0.2) |
| Uvularia perfoliata | - | - | - | - | - | - | 0.2 (0.1) | - | 1.1 (0.4) |
| Actaea alba | - | - | - | - | - | 0.1 (0.0) | - | - | 0.4 (0.2) |
| Botrychium virginiana | - | - | - | - | - | - | 0.1 (0.1) | - | 0.8 (0.2) |
| Caulophyllum thalictroides | - | - | - | - | - | - | 0.1 (0.1) | - | 0.9 (0.3) |
| Carex plantaginea | - | - | - | - | - | - | 0.3 (0.1) | 0.2 (0.1) | 1.2 (0.3) |
| Viola canadense | - | - | - | - | - | 0.2 (0.1) | 0.1 (0.1) | 0.2 (0.1) | 1.3 (0.3) |

Note: All values are means (standard error). Ranks $< 2.0$ represent trace percent coverage ( <1%).
Ranks $\geq 2.0$ can be converted to percent coverage by the formula: % coverage = $(rank*(-19.0))+(rank^2*3.9)+24$.

Table 4.4 Selected soil characteristics of upland forest ecosystems in northwestern lower Michigan.

| Variable | Ecosystem 1 (n = 10) | 2 (n = 12) | 3 (n = 10) | 4 (n = 11) | 5 (n = 7) | 6 (n = 7) | 7 (n = 7) | 8 (n = 6) | 9 (n = 6) |
|---|---|---|---|---|---|---|---|---|---|
| Horizon thickness (cm) | | | | | | | | | |
| A1 | 7 (2) | 5 (2) | 5 (2) | 4 (1) | 4 (1) | 4 (2) | 6 (2) | 7 (3) | 9 (4) |
| E | 0 (0) | 3 (1) | 6 (2) | 6 (2) | 7 (3) | 5 (2) | 14 (6) | 13 (6) | 9 (4) |
| Bhs | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 10 (4) | 5 (2) | 5 (2) |
| Bs | 14 (5) | 26 (8) | 23 (8) | 26 (8) | 34 (14) | 28 (11) | 42 (17) | 49 (22) | 28 (13) |
| Laboratory analyses | | | | | | | | | |
| % Organic carbon (0-10 cm) | 2.1 (0.1) | 1.8 (0.2) | 1.8 (0.1) | 2.1 (0.2) | 1.7 (0.2) | 2.4 (0.2) | 2.6 (0.3) | 1.8 (0.2) | 4.1 (0.6) |
| pH (0 - 10 cm) | 4.0 (0.1) | 4.1 (0.1) | 3.9 (0.1) | 4.0 (0) | 4.2 (0.1) | 4.3 (0.1) | 4.2 (0.1) | 4.2 (0.2) | 5.4 (0.1) |
| % cs + ms (45 - 55 cm) | 72 (5) | 70 (2) | 67 (3) | 63 (2) | 55 (7) | 41 (6) | 61 (6) | 56 (3) | 55 (6) |
| % si + cl (45 - 55 cm) | 5 (0.5) | 6 (0.5) | 4 (0.5) | 5 (0.5) | 9 (2) | 24 (6) | 8 (2) | 6 (1) | 9 (1.5) |
| Mean weighted diameter (mm) (45 - 55 cm) | 0.37 (0.02) | 0.35 (0.1) | 0.34 (0.1) | 0.32 (0.01) | 0.31 (0.03) | 0.24 (0.03) | 0.31 (0.02) | 0.30 (0.01) | 0.30 (0.01) |

Note: All values are means (standard error)

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Chapter 5

# LANDFORM-MEDIATED DIFFERENCES IN SUCCESSIONAL PATHWAYS AMONG UPLAND FOREST ECOSYSTEMS IN NORTHWESTERN LOWER MICHIGAN

## ABSTRACT

Seedling and sapling densities were compared with current overstory composition in 30 upland forest stands in northwestern lower Michigan to study potential successional pathways. The patterns of compositional change were strongly related to topographic and edaphic differences among glacial landforms. Glaciofluvial landforms, currently dominated by oak, have relatively high densities of oak seedlings (4913 stems/ha) that seldom move into the sapling layer (10 stems/ha). Oak-dominated ecosystems on hilly ice-contact stratified drift exhibited relatively high densities of red maple saplings (48 stems/ha). Oak-dominated ecosystems on extremely well drained outwash plains exhibited sparse sapling regeneration of any species; red maple was typically absent, and oak saplings were usually in an apparent state of decline. Differences in the potential for recruitment of saplings into the overstory among these ecosystems may be attributable to differences in fire history or site-dependent effects on the competitive abilities of species. Morainal landforms, currently supporting relatively diverse northern hardwood overstories, showed little potential recruitment of any species other than sugar maple.

Glacial landforms in northwestern Lower Michigan direct compositional change by influencing soil moisture and nutrient availability, and historical patterns of disturbance and species establishment.

# INTRODUCTION

Many oak forests of the eastern United States are developing understories of red maple (Acer rubrum L.) and other shade-tolerant species (Johnson 1976, Lorimer 1984, McCune and Cottam 1985). Hypotheses proposed to explain this change in composition include dominance of red maple as a result of decreased fire frequency and site-dependent differences in the competitive relationships among these species (Lorimer 1984). We lack a clear understanding, however, of how differences in site characteristics or fire frequencies relate to patterns of compositional change across the landscape. Lorimer (1984) and McCune and Cottam (1985) used long term data to document change in composition over time. Their studies were point-specific: the composition of individual stands was followed over time. Still to be explained is variation in spatial patterns of forest composition. For example, is the conversion of existing oak forests to more tolerant communities impending everywhere - across all oak cover types? Or does variation in topography or parent material play a role in directing compositional change? McNaughton (1984) and Rowe (1984) contend that geology, topography, and climate are the primary environmental factors which define and constrain soil formation and ecosystem development. If so, spatial patterns of community dynamics should therefore be related, at least partially, to the dominant environmental factors acting as selective forces. Our objective was to relate landscape features to the apparent direction of compositional change in upland oak ecosystems of northwestern Lower Michigan.

Landform, defined as parent materials and surficial topography, plays a critical role in controlling local patterns of insolation and drainage, and thereby exerts a strong influence on soil development and species composition (Rowe 1969, 1984). In the upland landscape of northwestern Lower Michigan, the predominant landforms are level outwash plains, hilly ice-contact stratified drift (kame and kettle topography), and moraines. Outwash plains are typically formed of highly-sorted medium sand with low moisture-holding capacity. The ice-contact and morainal hills have higher proportions of fine sands, silt and clay, more highly developed soil profiles, and greater moisture holding capacity. These hills are sometimes underlain by "bands" of finer-textured sediment - either flowtill (Flint 1971) or glaciofluvial sediment deposited as the velocity of meltwater varied. The bands occur with varying thickness and depth from the soil surface. Hannah and Zahner (1970) discuss the importance of deep nonpedogenic textural bands to forest growth. Variation in parent material composition and topography may exert a significant influence on species establishment and growth. Parent material and topography may also influence patterns of disturbance, such as fire (Grimm 1984).

It was expected that overstory composition and successional trends would vary among landforms. Within individual landforms, however, variation in physiography and soils may further influence forest composition and the recruitment of understory trees to the overstory. By identifying characteristic combinations of landform, soil, and ground flora, we were able to define "landscape ecosystems" (Rowe 1969): land classification units derived by integrating ecologically important factors (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985a). Using this ecological approach, we were able to further explain variation in forest structure and composition across an upland landscape. We hypothesized that seedling and sapling densities would vary significantly at both the landform and ecosystem levels, and that this variation could be used to better understand potential recruitment patterns and direction of compositional change across northwestern Lower Michigan.

## MATERIALS AND METHODS

Stratified random sampling was used to sample the overstory, understory, ground flora and soils of 120 plots distributed in 30 upland forest stands in the Manistee National Forest, northwestern Lower Michigan. The study area included Manistee, Wexford, Lake and Newaygo counties, and ranged from 44°22'N, 86°15'W to 43°30'N, 85°30'W. The sample stratification was based on upland landforms (landforms not influenced by a permanent or seasonal water table), and included outwash plains, ice-contact hills, and moraines. Only well-stocked stands, at least 1 ha in area and with minimal evidence of recent disturbance (i.e. thinning, firewood cutting, windthrow) were selected for sampling. Stands with greater than 7 $m^2$ basal area/ha in aspen (Populus grandidentata Michx. and P. tremuloides Michx.) were excluded from sampling. Most of this part of Michigan was heavily logged near the turn of the century (Mustard 1983), and stand ages ranged from 60 to 90 years. Stands were even-aged and most probably originated after clearcutting and some after burning. The selection criteria we used allowed us to study potential recruitment in stands with similar histories and ages distributed across a regional landscape.

In each stand, four 5 x 30 m plots were randomly located for overstory, sapling, seedling/ground flora, and soil sampling. Seedling abundance was determined by stem counts in six 1 $m^2$ frames systematically located along the long axis of each plot (24 $m^2$ per stand). Seedlings were separated into two size classes: < 30 cm in height, and $\geq$ 30 cm in height but < 1.2 cm dbh. Saplings, defined as stems 1.2 - 9.0 cm dbh, were sampled using stem counts in the 5 x 30 m plot (600 $m^2$ per stand). This sample area is consistent with the area recommended for evaluating oak advance reproduction suggested by Sander et al. (1984). Relative frequency was calculated by species as the percentage of stands in which a species occurred relative to the total number of stands in an ecosystem. The overstory was sampled using a 10 BAF (English) point sample at the center of each plot. Dbh and total and merchantable height (to a 10 cm top diameter) were recorded for each tally tree. Merchantable volume was calculated according to Beers and Miller (1966). USFS cover types (Eyre 1980) were determined for each stand. Nomenclature follows Little (1979), with the exception that, because of similarities in appearance, black oak (Quercus velutina Lam.) and northern pin oak (Q. ellipsoidalis E. J. Hill) were recorded as black oak. Soil morphological properties were described in soil pits dug to 150 cm on each plot (Soil Survey Staff 1975). In addition, bucket auger samples were excavated to 450 cm to record the depth and texture of bands.

Sample stands were classified into ecosystems based on combinations of landform, soil, and ground flora (Pregitzer and Barnes 1984; Spies and Barnes 1985a). Diagnostic characteristics of each ecosystem are presented in Table 5.1. For brevity, the five ecosystems are named for their existing overstory and characteristic ecological species group (Pregitzer and Barnes 1982; Spies and Barnes 1985b). Ecosystem names differ from those in Chapter 4 because this manuscript was written and submitted during an earlier version of the classification (February 1986). Also since

Table 5.1. Landform, soil, and vegetational properties of five upland forest ecosystems common in northwestern Lower Michigan.

| Overstory/ Species Group | n (plots) | Characteristic Ground Flora | Landform | Soil: Texture | Soil: Drainage | Soil: Banding[a] |
|---|---|---|---|---|---|---|
| Black oak-white oak/ <u>Vaccinium</u> | 32 | <u>Vaccinium angustifolium</u><br><u>Gaultheria procumbens</u><br><u>Carex pensylvanica</u> | level outwash plains slopes < 5% | medium sand | extremely well | - |
| Mixed oak/ <u>Trientalis</u> | 32 | <u>Trientalis borealis</u><br><u>Aster macrophyllum</u> | ice-contact drift slopes 5 - 30% | medium sand to loamy fine sand | well | - |
| Mixed oak/ <u>Viburnum</u> | 24 | <u>Viburnum acerifolium</u><br><u>Aralia nudicaulis</u><br><u>Cornus florida</u> | ice-contact drift slopes 5 - 15% | medium sand to sandy loam | well | +/- |
| Sugar maple-red oak/ <u>Maianthemum</u> | 16 | <u>Maianthemum canadense</u><br><u>Polygonatum biflorum</u><br><u>Lycopodium lucidulum</u> | moraines slopes 5 - 20% | medium sand | well | +/- |
| Sugar maple-basswood/ <u>Osmorhiza</u> | 16 | <u>Osmorhiza claytonii</u><br><u>Viola canadense</u><br><u>Allium tricoccum</u> | moraines slopes 5 - 35% | medium sand to sandy loam | well | + |

[a] - no textural strata have textures finer than fine sand.
+ textural strata of sandy loam or finer present in the upper 450 cm.
+/- textural strata of sandy loam or finer may be present or absent.

this study used a subset of the 80 stands for seedling counts, summary statistics for overstory and understory may vary slightly.

Seedling and sapling densities and overstory characteristics were analyzed at the ecosystem level using t-tests or analysis of variance. Ecosystems on glaciofluvial landforms (outwash plains and hilly ice contact drift) were analyzed independently from ecosystems on morainal landforms because of extreme differences in species composition between these landforms. Because seedlings in the second size class ($\geq$ 30 cm in height but < 1.2 cm dbh) were rarely encountered in the 1 $m^2$ sample frame, the two size classes of seedlings were combined in all statistical analyses. Non-zero means were compared using a protected Fisher's LSD procedure (Steel and Torrie 1980).

## RESULTS AND DISCUSSION

### Overstory

The three ecosystems that occurred on outwash and ice-contact landforms currently support oak overstories, and would be classified as White oak-black oak-northern red oak or Northern red oak cover types (Eyre 1980). Within the white oak-black oak-northern red oak cover type, there was considerable variation in relative dominance among overstory species (Table 5.2). On outwash plains, black and white oaks (Quercus alba L.) were the dominant species, and red oak

Table 5.2. Overstory composition of five upland forest ecosystems common in northwestern Lower Michigan. Ecosystems are ordered along an increasing moisture gradient, based on soil texture. Morainal landforms treated separately in statistical analyses.

| Ecosystem | Mean age | Mean basal area ($m^2$/ha) | Mean dbh (cm) | Mean merchantable volume[a] ($m^3$/ha) | Basal area ($m^2$/ha) by species | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Black oak | White oak | Red oak | Red maple | Sugar maple | Bass-wood | White ash | Beech |
| I. Glaciofluvial landforms[b] | | | | | | | | | | | | |
| Black oak-white oak/*Vaccinium* | 75 a | 21.1 a | 20 a | 106.2 a | 11.2 a | 7.8 a | 0.5 a | 0.5 a | 0 | 0 | 0 | 0 |
| Mixed oak/*Trientalis* | 71 a | 23.0 ab | 19 a | 138.4 ab | 4.6 b | 6.0 a | 9.6 b | 1.6 a | 0 | 0 | 0 | 0 |
| Mixed oak/*Viburnum* | 73 a | 25.7 b | 24 a | 181.2 b | 3.4 b | 6.9 a | 11.9 b | 3.0 b | 0 | 0 | 0 | 0.7 |
| II. Morainal landforms[c] | | | | | | | | | | | | |
| Sugar maple-red oak/*Maianthemum* | 65 y | 25.5 y | 20 y | 202.6 y | 0 | 0 | 11.5 y | 0.9 | 8.0 y | 0.7 y | 1.8 y | 1.4 y |
| Sugar maple-basswood/*Osmorhiza* | 64 y | 29.6 z | 22 y | 265.9 z | 0 | 0 | 3.2 y | 0 | 10.1 y | 9.4 z | 1.4 y | 1.4 y |

[a] volume to a 10.2 cm top.
[b] Column means followed by a different letter (a,b) significantly different (alpha=0.05).
[c] Column means followed by a different letter (y,z) significantly different (alpha=0.05).

(*Quercus rubra* L.) and red maple were rare. The relative proportions of red oak and red maple increased and proportions of black oak decreased as site conditions became more mesic. Curtis (1959) reported similar patterns of species replacement along moisture gradients in Wisconsin. Red oak dominated the mixed oak/*Trientalis* and mixed oak/*Viburnum* ecosystems which occurred on ice-contact hills (Table 5.2). Total basal area, standing merchantable volume, and total basal area of red oak were highest in the mixed oak/*Viburnum* ecosystem, which occurs on finer textured or deep banded soils.

The sugar maple-red oak/*Maianthemum* and sugar maple-basswood/*Osmorhiza* ecosystems that occurred on moraines would be classified as Northern red oak, Sugar maple or Sugar maple-basswood cover types (Eyre 1980). The sugar maple-basswood/*Osmorhiza* ecosystem occurred exclusively on sites with nonpedogenic textural bands of sandy clay loam, generally below 150 cm. The sugar maple-red oak/*Maianthemum* ecosystem occurred on both banded sites and deep sands; in this study only sugar maple-red oak/*Maianthemum* stands on unbanded sites were considered. The sugar maple-basswood/*Osmorhiza* ecosystem had a significantly higher proportion of basswood in the overstory and greater standing volume (Table 5.2). A related study has shown that rates of nitrogen turnover are more rapid in this ecosystem (Zak et al. 1986).

Natural Regeneration on Glaciofluvial Landforms

Within ecosystems found on glaciofluvial landforms, the numbers of seedlings of black oak, red oak and red maple differed significantly (Table 5.3). The differences in number corresponded to differences in soil texture, an indirect index of available soil moisture. Black oak seedlings were most numerous on outwash plains, while numbers of red oak and red maple seedlings increased as conditions became more mesic. Most of the oak "seedlings" were actually sprouts from the root collars of older, well-established root systems. These oaks may be analogous to the oak "grubs" described by Cottam (1949), which were able to persist in the oak openings of the Wisconsin Prairie Peninsula for many years. Numbers of white oak seedlings did not significantly differ among landforms. Red oak seedling densities were significantly higher in the mixed oak/Viburnum ecosystem. In most stands, the densities of natural oak seedlings approached or exceeded artificial planting densities (Johnson 1984).

Mean densities of oak saplings, however, were extremely low. On outwash plains, black oak, the dominant species in the overstory, represented only 5% of all saplings (Table 5.4). White oak was one of the most abundant saplings, averaging 16 stems/ha, but these individuals were typically old and in an apparent state of decline. Likewise, black cherry (Prunus serotina Ehrl.) saplings were severely infected with black knot (Dibotryon morbosum) and apparently

Table 5.3. Mean seedling densities for five upland forest ecosystems common in northwestern Lower Michigan. Ecosystems are ordered along an increasing moisture gradient, based on soil texture. Morainal landforms treated separately in statistical analyses.

| | number of stems/ha | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Ecosystem | Black oak | White oak | Red oak | Red maple | Sugar maple | Beech | White ash | Black cherry | White pine |
| I. Glaciofluvial landforms[a] | | | | | | | | | |
| Black oak-white oak/<u>Vaccinium</u> | 5217 a | 2820 a | 274 a | 4911 a | 0 | 0 | 0 | 2045 a | 260 a |
| Mixed oak/<u>Trientalis</u> | 1159 b | 1476 a | 506 a | ·10438 a | 0 | 21 | 0 | 1539 a | 625 a |
| Mixed oak/<u>Viburnum</u> | 309 b | 1686 a | 1293 b | 29650 b | 478 | 0 | 253 | 447 a | 468 a |
| II. Morainal landforms[b] | | | | | | | | | |
| Sugar maple-red oak/<u>Maianthemum</u> | 0 | 0 | 153 y | 1535 | 9315 y | 461 y | 1979 y | 1365 y | 0 |
| Sugar maple-basswood/<u>Osmorhiza</u> | 0 | 0 | 170 y | 0 | 9161 y | 546 y | 20976 z | 1194 y | 0 |

[a] Column means followed by a different letter (a,b) significantly different (alpha=0.05; red oak alpha=0.1).
[b] Column means followed by a different letter (y,z) significantly different (alpha=0.05).

Table 5.4. Mean sapling densities for five upland forest ecosystems common in northwestern Lower Michigan. Ecosystems are ordered along an increasing moisture gradient, based on soil texture. Morainal landforms treated separately in statistical analyses.

| Ecosystem | number of stems/ha | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Black oak | White oak | Red oak | Red maple | Sugar maple | Beech | White ash | White pine | Bass-wood | Iron-wood | Witch-hazel |
| I. Glaciofluvial landforms[a] | | | | | | | | | | | |
| Black oak-white oak/*Vaccinium* | 4 | 16 a | 1 a | 14 a | 0 | 0 | 0 | 18 a | 0 | 0 | 13 a |
| Mixed oak/*Trientalis* | 0 | 4 b | 3 a | 66 b | 0 | 0 | 0 | 26 a | 0 | 0 | 25 a |
| Mixed oak/*Viburnum* | 0 | 1 b | 1 a | 31 ab | 3 | 11 | 0 | 5 a | 0 | 4 | 16 a |
| II. Morainal landforms[b] | | | | | | | | | | | |
| Sugar maple-red oak/*Maianthemum* | 0 | 0 | 4 | 2 y | 110 y | 15 y | 0 | 0 | 1 | 1 y | 0 |
| Sugar maple-basswood/*Osmorhiza* | 0 | 0 | 0 | 3 y | 98 y | 4 y | 0 | 0 | 0 | 11 y | 7 |

[a] Column means followed by a different letter (a,b) significantly different (alpha=0.05).
[b] Column means followed by a different letter (y,z) significantly different (alpha=0.05).

incapable of reaching the overstory. Red maple, common in the seedling layer, was typically absent from the sapling layer (25% relative frequency). Half of the sample stands on outwash plains had white pine (Pinus strobus L.) in the sapling layer; the white pine were 20-30 years old. In general, the advance reproduction on outwash plains was quite sparse.

Higher stem densities and greater species diversity were observed on the relatively more mesic ice-contact landforms. In the mixed oak/Trientalis ecosystem, red maple was the dominant understory species, averaging 66 stems/ha or 50% of the total number of saplings. White pine averaged 26 stems/ha (21% relative density), but had a relative frequency of only 25%. White pine was not found in the overstory in any sample stands, and it is likely that the patchy distribution of white pine saplings is related to the lack of seed sources. A well-developed tall shrub/small tree layer composed of witch-hazel (Hamamelis virginiana L.), sassafras (Sassafras albidum Nees.), and serviceberry (Amelanchier spp. Medic.) accounted for 45% relative density. White and red oaks, the dominant overstory species, accounted for less than 5% of the saplings. It is in the mixed oak/Trientalis ecosystem that the compositional shift toward dominance by red maple and other shade-tolerant species reported by Lorimer (1984) and McCune and Cottam (1985) is evident. As the stands on these glaciofluvial landforms are of similar ages, it is likely that red maple saplings and larger stems are excluded from the outwash plains due to inadequate soil moisture, increased competition from more xerophilic species, or increased fire frequency.

The more productive mixed oak/*Viburnum* ecosystem found on finer-textured or banded soils had high oak seedling densities (3222 trees/ha; Table 5.3), but essentially no oak saplings (Table 5.4). Red maple was again the most common sapling in the understory (31 stems/ha). Beech (*Fagus grandifolia* Ehrl.), ironwood (*Ostrya virginiana* K, Koch), and sugar maple (*Acer saccharum* Marsh.) were present as seedlings and occasionally as saplings. While red maple dominated the sapling layer, the presence of beech and sugar maple suggests that in the absence of disturbance, mixed oak/*Viburnum* forests may eventually support northern hardwoods.

Natural Regeneration on Morainal Landforms

On the morainal landforms, the ecosystems that occurred on banded sites had significantly higher numbers of seedlings due to the high numbers of first-year white ash (*Fraxinus americana* L.) seedlings (Table 5.3). Red maple was absent from the seedling layer in the sugar maple-basswood/*Osmorhiza* ecosystem, but was abundant in the unbanded sugar maple-red oak/*Maianthemum* ecosystem. This may be related to seed source, as red maple was a minor component of the overstory of the sugar maple-red oak/*Maianthemum* ecosystem but absent from the sugar maple-basswood/*Osmorhiza* ecosystem (Table 5.2). Competition and low light levels at the forest floor may also exclude red maple from the more mesic sugar maple-basswood/*Osmorhiza* ecosystem. First-year sugar maple seedlings were very abundant in both sugar maple ecosystems (Table 5.3).

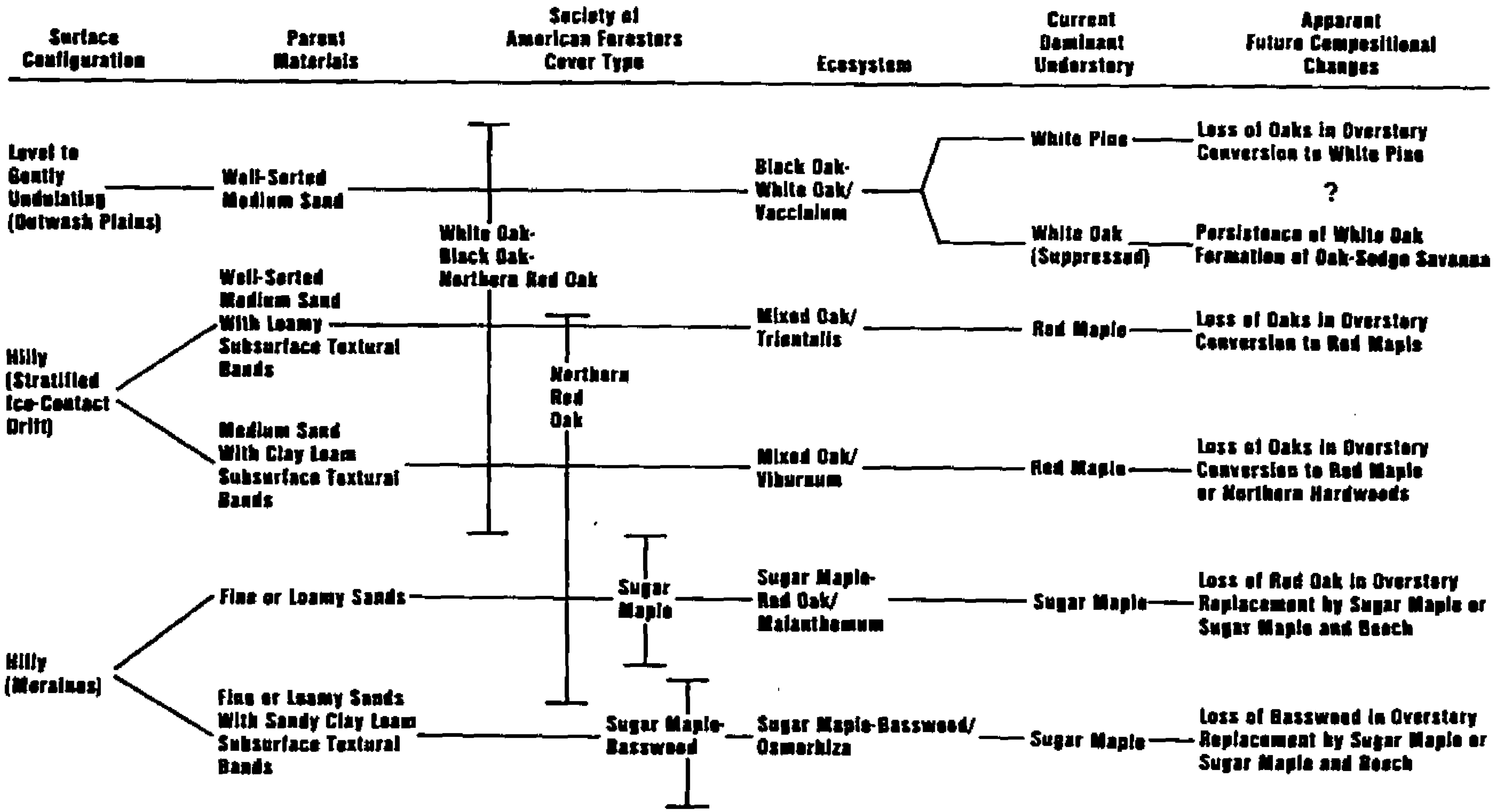
Sapling densities were much higher on morainal landforms in comparison to glaciofluvial landforms, with sugar maple predominating (80% relative density). Beech, red oak, ironwood, and witch-hazel were minor components of the understory; red maple was uncommon (Table 5.4). White ash, a major component of the seedling layer, was not found in the sapling layer. Basswood (*Tilia americana* L.), a major overstory component of the sugar maple-basswood/*Osmorhiza* ecosystem, was virtually absent from both the seedling and sapling layers. The total numbers of saplings and individual numbers of species did not differ significantly between the two sugar maple ecosystems.

Potential Successional Patterns Among Ecosystems

Differences in stem densities among diameter classes have been used to study rates of succession and the direction of compositional change (Peet and Loucks 1977). While windthrow, disease, and other stochastic factors influence the growth of saplings into the overstory, the existing sapling layer expresses the potential future stand composition. Several landform-mediated patterns of compositional change were present among the ecosystems studied. A schematic diagram of these patterns is presented in Figure 5.1. The extremely well-drained outwash plains currently support the black oak-white oak/Vaccinium ecosystem, but exhibit little potential oak recruitment. We do not know if white oak saplings, common but apparently in decline, will persist on these sites. Likewise, we do not understand what factors preclude oak seedlings from moving into larger size classes. As a result, the future composition of forests in this landscape position is unclear. Some stands appear to be reverting to white pine, the dominant species of the presettlement forest (Mustard 1983). Other stands have little or no potential recruitment in the sapling layer; these may become meadows or savannas dominated by Carex pensylvanica Lam., such as those described by Abrams et al. (1985). Red maple saplings were absent from 75% of the stands sampled on this landform.

In northwestern Lower Michigan, the compositional change toward red maple described by Lorimer (1984) and McCune and Cottam (1985) occurred on hilly ice-contact landforms. Here, red maple was the dominant species of the sapling layer. The difference in red maple abundance between level sand plains and ice-contact hills is perhaps a result of differences in fire frequency among these landforms. Grimm (1984) has shown that variation in topography, soil texture, and the presence of firebreaks has a strong influence on fire history, and therefore on species composition. Topography has also been shown to influence both rates of succession and

Figure 5.1. Understory composition and patterns of compositional change related to landform, SAF cover type (Eyre 1980) and ecosystem. The figure should not be interpreted as indicative of linear and deterministic successional pathways; rather, it depicts existing landscape patterns.


Surface Configuration
Parent Materials
Society of American Foresters Cover Type
Ecosystem
Current Dominant Understory
Apparent Future Compositional Changes
Level to Gently Undulating (Outwash Plains)
Well-Sorted Medium Sand
Black Oak-White Oak/Vaccinium
White Pine
Loss of Oaks in Overstory Conversion to White Pine
?
White Oak (Suppressed)
Persistence of White Oak Formation of Oak-Sedge Savanna
White Oak-Black Oak-Northern Red Oak
Hilly (Stratified Ice-Contact Drift)
Well-Sorted Medium Sand With Loamy Subsurface Textural Bands
Mixed Oak/Trientalis
Red Maple
Loss of Oaks in Overstory Conversion to Red Maple
Northern Red Oak
Medium Sand With Clay Loam Subsurface Textural Bands
Mixed Oak/Viburnum
Red Maple
Loss of Oaks in Overstory Conversion to Red Maple or Northern Hardwoods
Hilly (Moraines)
Fine or Loamy Sands
Sugar Maple
Sugar Maple-Red Oak/Maianthemum
Sugar Maple
Loss of Red Oak in Overstory Replacement by Sugar Maple or Sugar Maple and Beech
Fine or Loamy Sands With Sandy Clay Loam Subsurface Textural Bands
Sugar Maple-Basswood
Sugar Maple-Basswood/Osmorhiza
Sugar Maple
Loss of Basswood in Overstory Replacement by Sugar Maple or Sugar Maple and Beech

fire frequency in Rocky Mountain subalpine forests (Romme and Knight 1981). The outwash plains in the study area may have historically burned more frequently than the surrounding uplands, resulting in different patterns of species recruitment. It is also possible that differences in red maple distribution may be due to differences in site moisture status; red maple may be a poor competitor on the more xeric outwash plains. If this is true, then red maple may simply not have the potential to reach the overstory on xeric landforms.

The mixed oak/Viburnum ecosystem found on ice-contact landforms with subsurface textural discontinuities had well-developed red maple understories, but also exhibited some recruitment of sugar maple, beech, ironwood, and other species characteristic of northern hardwoods. It is likely that northern hardwoods are the dominant late successional species in this landscape position.

The morainal landforms which support the sugar maple-red oak/Maianthemum ecosystem appear to be losing the red oak component of the overstory, with sugar maple being the primary replacement species. Red oak currently has the greatest basal area (11.5 $m^2$/ha) of any overstory species in these forests. A similar trend is evident in the sugar maple-basswood/Osmorhiza ecosystems, with loss of basswood from the overstory and probable replacement by sugar maple. On morainal landforms in northern Lower Michigan, red oak and basswood appear to be seral responses to the cutting and burning of the early 1900s. These species are currently being replaced by sugar maple and beech, following a classical successional pattern of shade-tolerant species replacing less tolerant species. The future overstory composition of these two ecosystems may be quite similar.

The differences in composition and potential recruitment among ecosystems suggest that successional pathways vary within cover types (Figure 5.1). White oak-black oak-northern red oak forests may become forests with significant components of either white pine or red maple depending on landform and ecosystem type. Northern red oak cover types seem to be trending toward red maple or sugar maple dominance, again depending on landform and soil characteristics. Differences in existing recruitment patterns are related to ecosystem type. Landform, soil and plant indicators were important factors in accounting for some of the successional variation among the upland oak forests in northwestern Lower Michigan. Certainly other factors, such as fire history, are related to the patterns of recruitment observable in the field.

McCune and Cottam (1985) have raised questions as to the applicability of classical successional theory in the face of changes in natural disturbance regimes, such as the suppression of fire, and chance events. We have shown that deviations in classical successional patterns can be explained in part by understanding landscape factors which control the growth and distribution of species. Of particular importance are landform and soil factors which influence moisture and nutrient availability and possibly fire history. Future work on landform and soil-mediated patterns of disturbance and succession may help understand impending wide-spread changes in community composition in the Lake States.

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Chapter 6

# THE BIOMASS RESPONSE OF GLACIAL LANDFORMS AND LANDSCAPE ECOSYSTEMS IN UPLAND FORESTS OF NORTHWESTERN LOWER MICHIGAN

## ABSTRACT

Total aboveground biomass and mean annual biomass increment (MABI) were estimated for 75 upland forest stands in northwestern lower Michigan. Biomass estimates were based on allometric regressions equations using height and diameter. Ground flora, soils and physiography were used to develop ecological classification units (ecosystems). Analysis of variance was used to study patterns of total biomass and biomass increment among glacial landforms and ecosystems. Differences in biomass were strongly correlated with landscape position: landform accounted for 40% of the total variation in biomass. The ecosystem classification accounted for a higher proportion of variation, approximately 60% of the total. Total biomass ranged from 84 t/ha (MABI=1.3 t/ha/yr) in stands on xeric outwash plains to almost 250 t/ha (MABI=3.6 t/ha/yr) in mesic morainal positions. Variation in biomass appeared to be strongly related to available soil moisture, as evidenced by differences in soil texture and the presence or absence of deep-lying textural bands.

Ground flora exhibited patterned variation related to soil moisture availability. Detrended correspondence

analysis was used to ordinate ground flora species, the ordination being an indirect reflection of moisture availability. Stand ordination scores were regressed against total biomass and MABI to determine if predictive relationships exist between ground flora composition and site productivity. The regression accounted for more of the variation in biomass ($r^2$=0.76) than either the landform or ecosystem classification. In this regional glaciated landscape, ground flora composition appears to be related to the same factors which control site productivity.

## INTRODUCTION

Recent process-oriented models of landscape behavior treat the landscape as a mosaic of relatively homogeneous patches (Risser et al. 1984). Patch dynamics collectively define landscape dynamics. Bormann and Likens (1979) proposed that northern hardwood forests reach a steady state equilibrium in total aboveground biomass at a regional scale, even though the component patches may be in various successional states at a given time. Regional-scale disturbance theoretically causes biomass to rise to an overshoot, and eventually settle to a quasi-equilibrium value. Shugart (1984) observed a similar pattern of biomass accumulation using gap models of a monospecies forest in a homogeneous environment.

To model temporal dynamics of a forest, one must choose a scale at which to observe and describe patch behavior. In temporal models of biomass equilibrium, patch size is closely related to the scale of disturbance: patches or gaps are much smaller in an area characteristically disturbed by windthrow than in areas disturbed by fire (Shugart 1984). A similar question arises in the development of spatial models of landscapes: what scale of observation will most accurately quantify the variable of interest? Landscapes exhibit variation in regional climate and hydrology, in local microclimate and physiography, and in edaphic and floristic properties at the site level. The spatial biomass response of landscapes is further confounded by historical disturbance, which operates stocastically at all scales. Our objective was to examine spatial differences in biomass and biomass increment among upland oak and northern hardwood forests within a regional landscape of northwestern lower Michigan.

Northwestern lower Michigan was heavily logged at the turn of the century; in most areas, logging was followed by fire. The oldest forests generally do not exceed 90 years. Present-day forests represent a pulse response to this large-scale regional disturbance. We believe that this response should exhibit patterned spatial variation; specifically that variation in biomass accumulation should be related primarily to landform, and secondarily to variation in environmental factors within landforms.

We studied the landscape at two scales:the scale of glacial landforms, which can be readily mapped at 1:60,000, and at the scale of local ecosystems, typically mapped at 1:15,000 to 1:20,000. This study entailed mapping the glacial landforms of the area and developing an ecological classification system to define land classification units. The degree to which the two classifications account for variability in biomass should indicate the scale of resolution required to develop spatially explicit models of biomass accumulation.

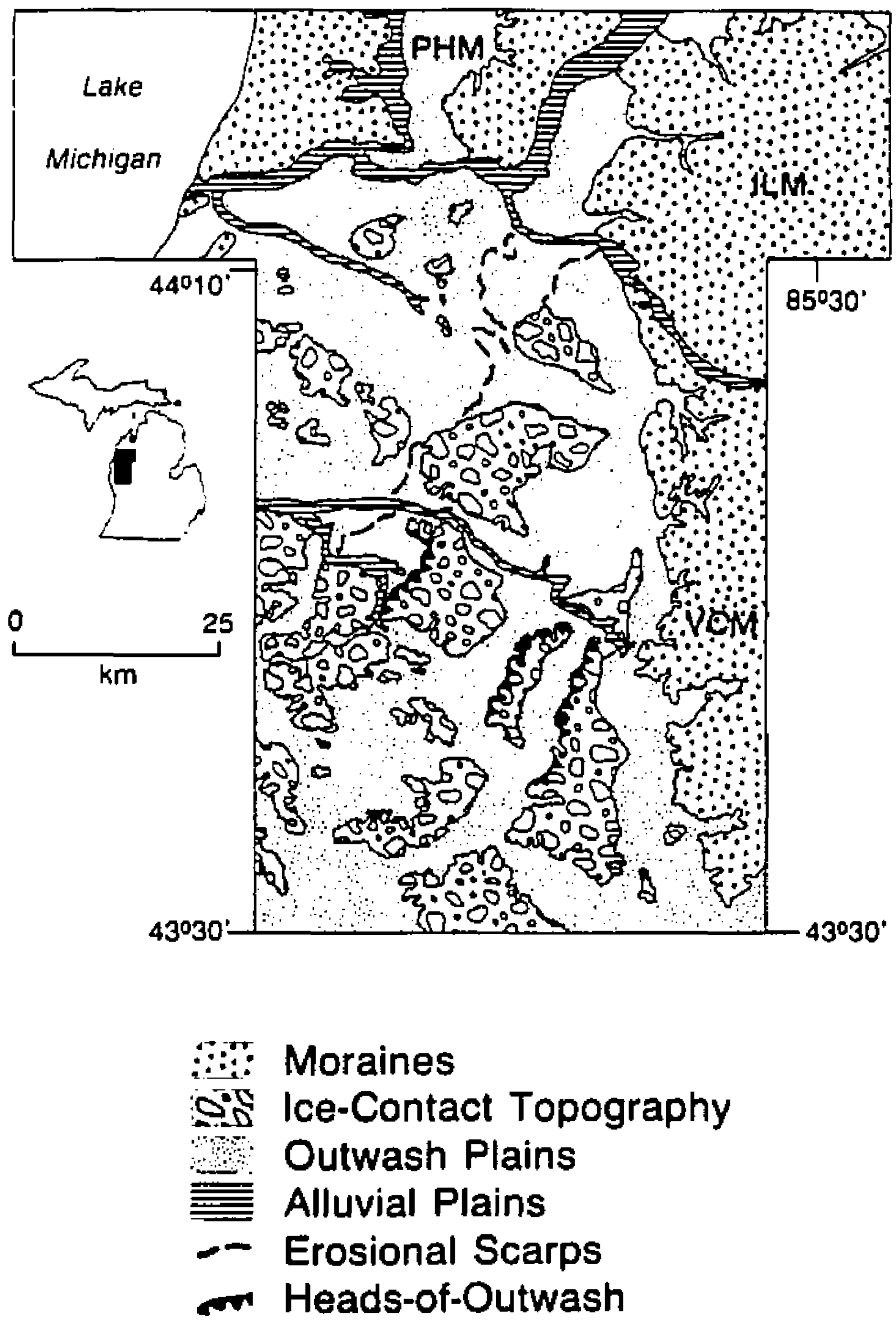
# MATERIALS AND METHODS

## Study area and sample design

Eighty upland forest stands were sampled as part of the development of an ecosystem classification system for the Huron-Manistee National Forest. Sample stands were located on upland sites throughout the Manistee National Forest (44°22'N, 86°15'W to 43°30N, 85°30'W) in Manistee, Wexford, Mason, Lake, and Newaygo counties, Michigan (Figure 6.1). A stratified random sampling design was used, with landform as the basis for stratification. Three major types of landforms occur within the study area. Outwash plains form an extensive network throughout the study area; the plains occur as terraces, with elevations ranging from 207 to 290 m above sea level. They are composed of well-sorted, extremely well-drained sands and were deposited by braided streams during glacial ablation. The second major landform, ice-contact hills, resulted from disintegration of stagnant ice. Ice contact topography is generally hilly, characterized by the presence of closed depressions, and generally has a finer texture and higher degree of soil development than soils of outwash plains. Moraines, the third major landform, are geographically extensive features characterized by complex dendritic drainage systems. Three morainal systems occur within the study area: the Interlobate, Valparaiso-Charlotte, and Port Huron moraines. The Interlobate and Valparaiso-Charlotte moraines were deposited penecontemporaneously,

Figure 6.1. Map of study area, showing predominant glacial landforms.

PHM - Port Huron Moraine
ILM - Interlobate Moraine
VCM - Valparaiso-Chalotte Moraine



Lake
Michigan
PHM
ILM
VCM
44°10'
85°30'
43°30'
43°30'
0
25
km
Moraines
Ice-Contact Topography
Outwash Plains
Alluvial Plains
Erosional Scarps
Heads-of-Outwash

approximately 14,500 ybp, while the Port Huron Moraine was deposited approximately 13,000 ybp (Lusch 1982). Soil textures and degree of development are similar to those of ice-contact topography, with the exception of the Interlobate Moraine. The Interlobate has the highest degree of soil development and finest texture of the landforms we sampled. Each moraine was considered a separate landform, resulting in five classes of landform in the statistical analysis. The important distinctive characteristics of each landform are summarized in Table 6.1.

Only well-stocked stands with minimal evidence of recent disturbance (windthrow, firewood cutting, etc.) were selected for sampling. Stands with greater than 7 $m^2$ basal area/ha in aspen (Populus grandidentata Michx. and P. tremuloides Michx.) were excluded from sampling. Four sample points were randomly located in each stand; these points served as loci for sampling the overstory, soil and vegetation.

Field methods

At each point, the overstory was sampled using a 10 BAF (English) wedge prism. The species, dbh, total height and merchantable height (to a 10 cm top), were recorded for all live tally trees > 9 cm dbh. Increment cores were taken from two dominant species at each point to determine average age at breast height (1.37 m). Common names of overstory species follow Little (1979).

Table 6.1. Forest composition and soil properties among glacial landforms of northwestern Lower Michigan.

| | Landform | | | | |
|---|---|---|---|---|---|
| | Outwash Plains | Ice-contact Hills | Port Huron Moraine | Valparaiso-Charlotte Moraine | Interlobate Moraine |
| Overstory | (n = 22) | (n = 22) | (n = 10) | (n = 6) | (n = 16) |
| Density (stems/ha) | 659 (39) | 605 (52) | 699 (84) | 723 (41) | 764 (46) |
| Total basal area (sq m/ha) | 19.7 (0.7) | 23.9 (0.8) | 24.3 (1.1) | 26.2 (1.2) | 27.4 (1.3) |
| Species basal area (sq m/ha) | | | | | |
| Quercus velutina | 9.3 (1.2) | 4.9 (1.2) | 1.5 (0.5) | 4.6 (2.9) | 0.0 (0.0) |
| Quercus alba | 8.4 (0.9) | 5.9 (0.8) | 6.2 (1.6) | 4.8 (1.4) | 0.0 (0.0) |
| Quercus rubra | 1.1 (0.7) | 11.7 (1.9) | 13.0 (2.0) | 10.6 (3.2) | 5.5 (2.0) |
| Acer rubrum | 0.3 (0.2) | 2.6 (0.8) | 2.5 (0.8) | 3.6 (0.9) | 1.1 (0.6) |
| Acer saccharum | 0.0 (0.0) | 0.0 (0.0) | 1.4 (1.2) | 0.6 (0.4) | 9.2 (1.5) |
| Tilia americana | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 3.6 (1.0) |
| Fraxinus americana | 0.0 (0.0) | 0.0 (0.0) | 0.1 (0.1) | 0.0 (0.0) | 2.6 (0.8) |
| Prunus serotina | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 2.2 (1.0) |
| Fagus grandifolia | 0.0 (0.0) | 0.0 (0.0) | 0.7 (0.7) | 1.1 (0.8) | 2.3 (0.6) |
| Soils | | | | | |
| Mean weighted particle diameter (mm) (100 cm depth) | 0.366 (0.01) | 0.307 (0.018) | 0.309 (0.014) | 0.315 (0.021) | 0.300 (0.015) |
| % cs+ms (100 cm depth) | 76 (2.9) | 58 (4.6) | 57 (4.7) | 63 (5.4) | 56 (4.8) |
| % si+cl (100 cm depth) | 2 (0.37) | 10 (2.5) | 5 (1.4) | 8 (3.3) | 7 (1.8) |

Note: All values are means (standard error)

Ground flora vegetation was sampled using a 5 x 30 m rectangular plot centered over each of the four sample points. The average percent ground cover was determined using a modified Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974). Relative frequencies for ground flora species were determined by recording species presence/absencu in six 1 $m^2$ frequency frames located at 5 m intervals along the long axis of the plot.

Soil profiles for each subplot were described to 1 m using standard descriptive procedures (Soil Survey Staff 1975). The subplots were also evaluated to a depth of 4.5 m using a bucket auger to record changes in soil texture. Within the soil pits, samples were taken at 50 and 100 cm for particle size analysis. The percent slope, slope shape and position, and aspect were recorded for each plot, and local topography was described. Sand size fractions and silt+clay content from the 50 and 100 cm samples were determined in the laboratory by wet sieving; samples were shaken for two hours in a 5% sodium hexametaphosphate solution prior to sieving.

Ecosystem classification

Ecosystems were defined based on combinations of physiography, soils and ground flora (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985a). The independent assignment of stands to ecosystems insured that the ecosystem analysis was not merely a further division of the original landform units. Important characteristics of each ecosystem are presented in Table 6.2. Some aspects of the classification, however, require special consideration.

The soils of all landforms we sampled were extremely sandy, generally with a sand content of 90% or more (Table 6.1). The moraines and ice-contact features, however, sometimes contained layers or bands of fine-textured materials, generally sandy clay loam or finer, within 4 or 5 meters of the soil surface. The presence of these textural bands has been shown to have a significant influence on tree growth and species composition (Hannah and Zahner 1977, Cleland et al., 1985, Chapter 3). The presence or absence of deep-lying textural bands was an important discriminating factor in the ecosystem classification.

Ground flora composition is a fundamental component of ecological classification systems. Individual ground flora species are usually aggregated into ecological species groups (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985b) using tabular or numerical methods. Ecological species groups are more effective than individual species for field classification work (Spies and Barnes 1985a). Descriptions of the ecological species groups used in this study are presented elsewhere (Chapter 2).

Statistical methods

Stand, landform, and ecosystem-level biomass estimates were obtained using species-specific biomass equations (Table

Table 6.2. Selected landform, overstory, ground flora and soil properties of upland forest ecosystems in northwestern Lower Michigan.

| Ecosystem | n (plots) | Dominant landform | Dominant overstory | | | Dominant ecological species group | Dominant soils | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Species | Basal area (sq m/ha) | SE | | Subgroup | Drainage | Banding |
| 1 | 40 | Outwash plains | Quercus velutina<br>Quercus alba | 8.9<br>7.7 | (1.5)<br>(1.7) | Deschampsia | Typic Udipsamments | Extremely well | absent |
| 2 | 52 | Outwash plains | Quercus velutina<br>Quercus alba | 9.7<br>9 | (1.8)<br>(0.9) | Vaccinium | Typic Udipsamments | Extremely well | absent |
| 3 | 40 | Kame complexes and moraines | Quercus velutina<br>Quercus alba<br>Quercus rubra | 7.9<br>6.8<br>5.1 | (2.0)<br>(1.3)<br>(2.3) | Vaccinium | Entic Haplorthods | Well | absent |
| 4 | 44 | Kame complexes and moraines | Quercus rubra<br>Quercus alba<br>Quercus velutina | 10.6<br>7.8<br>5.2 | (1.8)<br>(0.9)<br>(1.3) | Trientalis | Entic Haplorthods | Well | present |
| 5 | 28 | Kame complexes and moraines | Quercus rubra<br>Quercus alba | 17.4<br>3.9 | (2.2)<br>(0.8) | Viburnum | Entic Haplorthods | Well | present |
| 6 | 32 | Kame complexes and moraines | Quercus rubra<br>Acer rubrum | 16.3<br>5.5 | (3.3)<br>(0.9) | Desmodium | Alfic Haplorthods | | present |
| 7 | 30 | Interlobate Moraine | Acer saccharum<br>Quercus rubra | 7.1<br>7.2 | (2.3)<br>(3.5) | Maianthemum | Typic Haplorthods | Well | absent |
| 8 | 24 | Interlobate Moraine | Acer saccharum<br>Quercus rubra | 8<br>12.8 | (2.7)<br>(3.8) | Maianthemum | Typic Haplorthods | Well | present |
| 9 | 28 | Interlobate Moraine | Acer saccharum<br>Tilia americana<br>Fraxinus americana | 11.9<br>6.5<br>3.4 | (1.6)<br>(2.0)<br>(1.5) | Osmorhiza | Typic Haplorthods | Well | present |

Table 6.3. Regression equations used to calculate above ground dry weight for upland species in northwestern Lower Michigan.

| Species | Regression equation | $r^2$ | Range (dbh) | Locality | Units (Y-D-H) | Source |
|---|---|---|---|---|---|---|
| Pinus banksiana | Y = .0726*D^2.091*H^.435 | .99 | 2.8 - 32.8 cm | Lake Sts. | kg-cm-m | Green and Grigal 1978 |
| Pinus resinosa | Y = .03556*D^1.8869*H^.8693 | .99 | 10.4- 27.2 cm | MN MI WI | kg-cm-m | Alban and Laidly 1982 |
| Pinus strobus | Y = .5209+.07434*D-.5439*H +.0001516*D^2*H | .98 | 2.5 - 55 cm | NY | kg-mm-m | Monteith & Jacobs 1979 |
| Tsuga canadensis | Y = 1.4081+.1824*D+1.4563*H+ .0001842*D^2*H | .99 | 2.5 - 55 cm | NY | kg-mm-m | Monteith & Jacobs 1979 |
| Acer rubrum | ln Y = -1.545+.923*ln D^2*H | .97 | 10 - 52.2 cm | Lake Sts. | lb-in-ft | Crow and Erdmann 1983 |
| Tilia americana | Y = 1.4416*D^2.5328 | .96 | 5 - 50 cm | WV | kg-cm | Brenneman et al. 1978 |
| Acer saccharum | Y = .06116+.1752*D-.8988*H+ .0002761*D^2*H | .99 | 2.5 - 55 cm | NY | kg-mm-m | Monteith & Jacobs 1979 |
| Fraxinus americana | Y = -4.17764+.21947*D-.44212*H+ .000204*D^2*H | .99 | 2.5 - 55 cm | NY | kg-mm-m | Monteith & Jacobs 1979 |
| Quercus alba | Y = .08782*(D^2*H)^1.0206 | .99 | 5 - 40 cm | WV | lb-in-ft | Wiant et al. 1979 |
| Quercus rubra | Y = 9.68288+.42137*D-4.16579*H+ .000265*D^2*H | .99 | 2.5 - 55 cm | NY | kg-mm-m | Monteith & Jacobs 1979 |
| Quercus velutina | Y = .14206*(D^2*H)^.97268 | .99 | 5 - 40 cm | WV | lb-in-ft | Wiant et al. 1979 |
| Prunus serotina | Y = .12968*(D^2*H)^.97028 | .99 | 5 - 40 cm | WV | lb-in-ft | Wiant et al. 1979 |
| Populus tremuloides | log Y = -.685+2.249*log D | .99 | 14.7- 39.7 cm | WI | kg-cm | Pastor & Bockheim 1981 |
| Fagus grandifolia | Y = .78331+.08899*D-.529705*H+ .0002996*D^2*H | .97 | 2.5 - 55 cm | NY | kg-mm-m | Monteith & Jacobs 1979 |
| General hardwoods | Y = .31666+.04666*D-.2082455*H+ .0002549*D^2*H | .96 | 2.5 - 55 cm | NY | kg-mm-m | Monteith & Jacobs 1979 |
| General softwoods | Y = 1.57734+.13039*D-1.21916*H+ .0001774*D^2*H | .90 | 2.5 - 55 cm | NY | kg-mm-m | Monteith & Jacobs 1979 |

Y = oven-dry mass, D = diameter at breast height, H = total height.

6.3.) The equations predicted total aboveground oven-dry weights of all live tally trees recorded in the point sample; these values were expanded to an areal basis. The equations were taken from published literature of studies done in the Lake States area, and used both height and diameter to account for differences in site (Ker and van Raalte 1981). Mean annual biomass increment was calculated as total plot biomass divided by plot age.

Differences among the biomass levels of ecosystems and landforms were tested using analysis of variance and Fisher's Protected LSD (Steele and Torrie 1980). Non-normal data were normalized using logarithmic transformations. Cover-abundance data of herbaceous and woody ground flora species were subjected to detrended correspondence analysis, an ordination technique (DECORANA; Hill 1979). Stand-level ordination scores were related to mean annual biomass increment using regression analysis. Results of the analyses of variance and regression were corroborated using the Kruskal-Wallis test and Spearman's rank order correlation, respectively.

## RESULTS

### Analysis by Landform

Biomass levels showed significant variation among landforms (Table 6.4). There was almost a twofold difference in standing aboveground biomass between the outwash plains

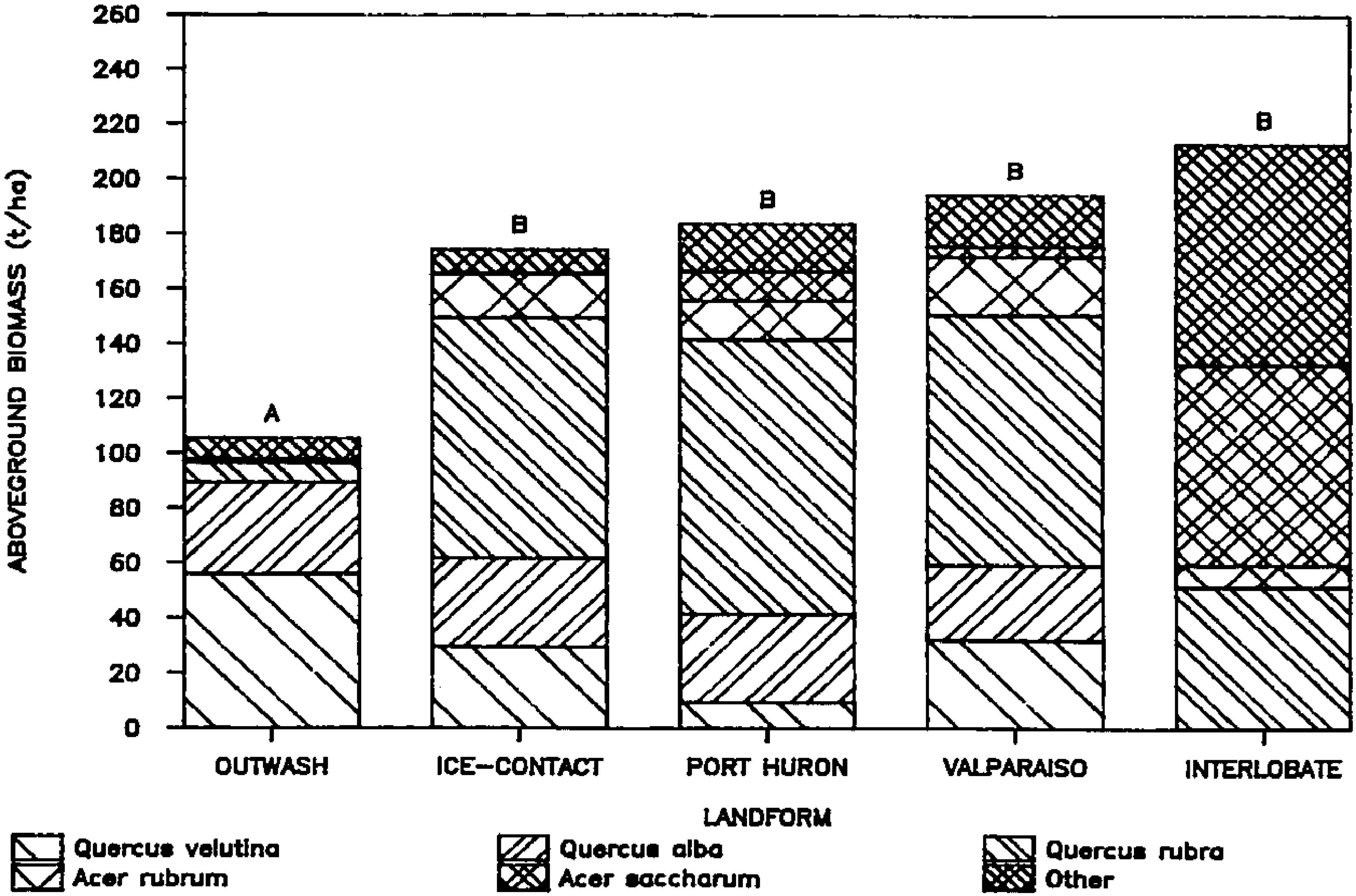
Table 6.4. Total aboveground biomass, mean annual biomass increment, and stand age summarized by landform. Means followed by the same letter not different at alpha=0.05.

| Landform | Mean Total Aboveground Biomass (t/ha) | (SE) | Mean Annual Biomass Increment (t/ha/yr) | (SE) | Mean Stand Age (years) | (SE) |
|---|---|---|---|---|---|---|
| Outwash plains | 105.2 a | (6.0) | 1.5 a | (0.1) | 74 a | (2) |
| Ice-contact hills | 172.6 b | (10.6) | 2.4 b | (0.2) | 75 a | (2) |
| Port Huron Moraine | 180.8 b | (16.2) | 2.5 b | (0.3) | 75 a | (4) |
| Valparaiso-Charlotte Moraine | 190.4 b | (18.0) | 2.6 bc | (0.3) | 73 a | (3) |
| Interlobate Moraine | 206.3 b | (12.3) | 3.2 c | (0.2) | 68 b | (1) |

(105 t/ha) and deep banded kamic or morainal hills (173-206 t/ha), even though stands on morainal landforms were often younger. These estimates of total aboveground biomass are comparable with estimates from other forest types in the northeastern United States (Tritton and Hornbeck 1982). Outwash plains were dominated by black and white oak (56 and 33 t/ha, respectively), while the Interlobate Moraine was dominated by northern hardwoods: sugar maple (73 t/ha), beech (19 t/ha), white ash (18 t/ha), and basswood (17 t/ha; Figure 6.2). Red oak occurred in half the sample stands on the Interlobate Moraine, and was the dominant species on all other ice-contact or morainal landforms, averaging between 88 and 100 t/ha. The ice-contact hills and the Port Huron and Valparaiso-Charlotte moraines were dominated primarily by red, white and black oak; these landforms did not exhibit significant differences in total biomass levels. Landform accounted for 40% of the total variance in biomass. Within-landform variability, however, was also significant, accounting for almost 30% of the total variability.

The mean annual biomass increment (MABI) showed a similar pattern. There was a twofold difference in MABI between the outwash plains and the kamic or morainal hills (Table 6.4). The outwash landforms exhibited the lowest MABI, 1.5 t/ha/yr, while the Interlobate Moraine accumulated an average of 3.2 t/ha/yr. The differences in biomass increment were more pronounced than differences in total biomass levels; stands with low total biomass were in many

Figure 6.2 Aboveground biomass among landforms summarized by species. Landforms with the same letter do not differ in total aboveground biomass.


ABOVEGROUND BIOMASS (t/ha)
0
20
40
60
80
100
120
140
160
180
200
220
240
260
A
B
B
B
B
OUTWASH
ICE-CONTACT
PORT HURON
VALPARAISO
INTERLOBATE
LANDFORM
Quercus velutina
Acer rubrum
Quercus alba
Acer saccharum
Quercus rubra
Other

cases significantly older than sites with higher biomass levels. The average age of stands on outwash plains was 74 years, while stands on the Interlobate Moraine averaged 68 years. Differences in age may be due to differences in cutting history, with the more accessible stands having been logged earlier than stands located in steeper terrain.

An interesting pattern in both biomass and biomass increment was that landforms which were similar in local physiography and soil textures did not show significant variation in total biomass or MABI. Stands on the Port Huron and Valparaiso-Charlotte moraines and the ice-contact hills were very similar in physiography and soils (Table 6.1); they were also similar in species composition, total biomass levels, and mean annual biomass increment (Table 6.4). The fact that the landforms themselves are of very different ages appears to be of little consequence compared to the more immediate factors influencing tree growth.

Of further importance is that ground flora also exhibited patterned variation among and within landforms: a related study showed that there are significant associations between ground flora and landform (Chapter 3). The Deschampsia group, for example, occurs almost exclusively on deep outwash sands, while the Viburnum group was restricted to mesic portions of banded hills. The fact that associations of overstory and ground flora species repeatedly occur in characteristic landscape positions is an indication that the ecosystem approach may provide more accurate estimates of site productivity than estimates based on single factors, such as landform, soils, or vegetation alone.

Analysis by Ecosystem

Analysis by ecosystem explained more of the variation in total biomass, accounting for 59% of the total variation. The ecosystem analysis incorporated much of the within-landform variation, reducing this value from 28% to 8%. The inclusion of ground flora and soils in the identification of site units tended to subdivide some landform units, but combine others. In many cases, stands on the Port Huron and Valparaiso-Charlotte moraines and ice-contact hills did not exhibit overall differences in soil texture or topography, and were therefore included in the same ecosystem type. When moisture availability within landforms was enhanced due to finer soil textures or the presence of banding, such as in Ecosystems 4, 5, 6, 8, and 9, biomass levels and MABI were significantly higher (Table 6.5). Differences in biomass did not appear to be related to the kamic or morainal origin of the landforms, but rather were related to site level differences in moisture availability. For site classification purposes, these landforms are functionally similar in terms of the composition and structure of the forests they support.

The ecosystem classification provided a finer scale of resolution to account for variation in biomass. For example, the average biomass for all outwash plains was 105 t/ha

Table 6.5. Total aboveground biomass, mean annual biomass increment, and stand age summarized by ecosystem. Means followed by the same letter not significantly different at alpha=0.05.

| Ecosystem | Mean Total Aboveground Biomass (t/ha) | (SE) | Mean Annual Biomass Increment (t/ha/yr) | (SE) | Mean Stand Age (years) | (SE) |
|---|---|---|---|---|---|---|
| 1 | 84.7 a | (6.2) | 1.3 a | (0.1) | 69 abc | (2) |
| 2 | 122.2 b | (6.6) | 1.7 b | (0.1) | 77 cd | (3) |
| 3 | 132.8 b | (8.7) | 1.7 b | (0.2) | 79 d | (3) |
| 4 | 151.3 bc | (7.9) | 2.0 b | (0.1) | 75 cd | (3) |
| 5 | 207.9 d | (8.4) | 3.0 cd | (0.2) | 70 abcd | (2) |
| 6 | 225.1 de | (13.2) | 3.1 cd | (0.1) | 73 bcd | (3) |
| 7 | 172.2 c | (14.5) | 2.7 c | (0.2) | 63 a | (2) |
| 8 | 248.6 e | (7.9) | 3.6 d | (0.2) | 69 abc | (3) |
| 9 | 210.1 d | (11.3) | 3.3 d | (0.2) | 64 ab | (3) |

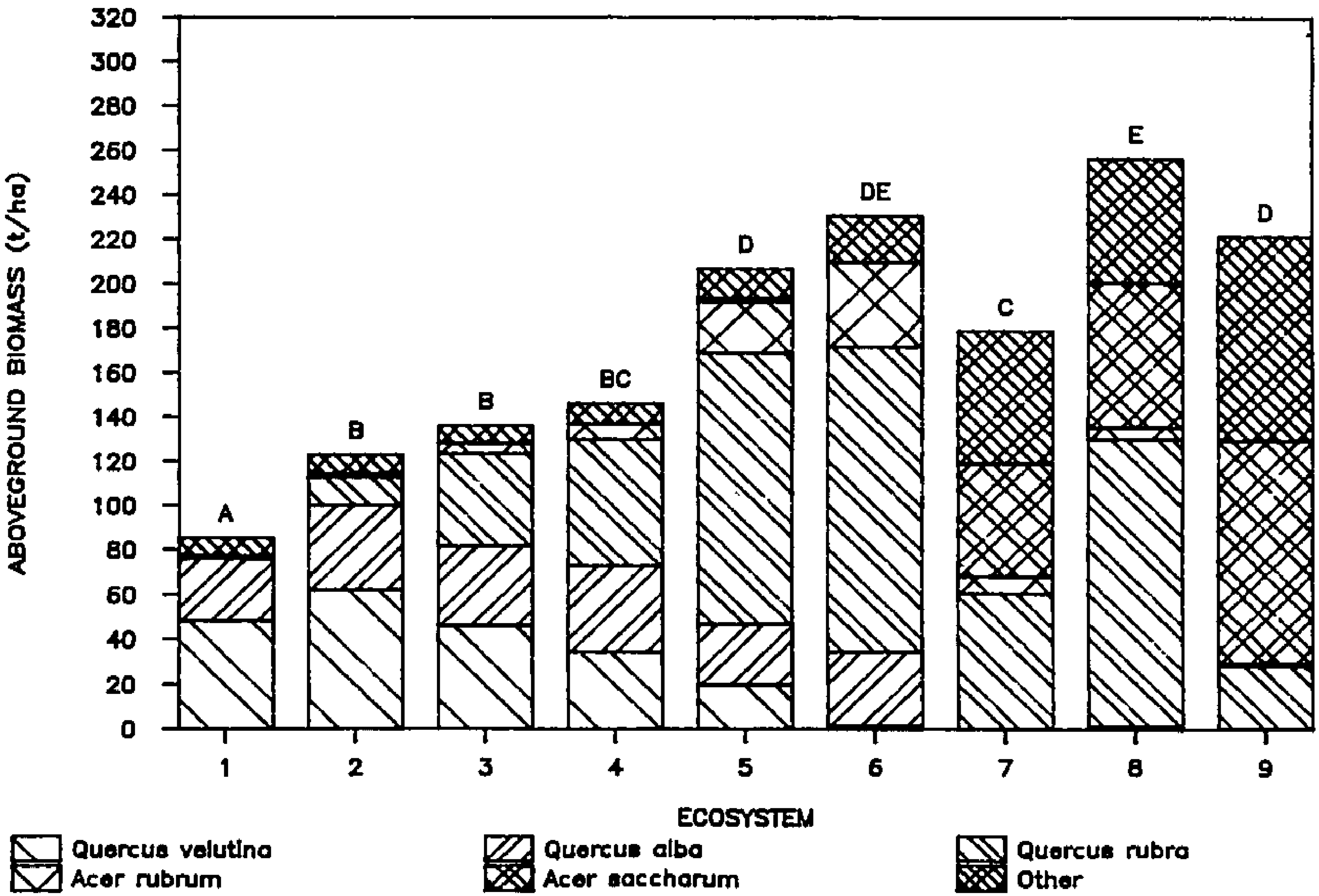
(Table 6.4). The outwash plains, however, support two distinct ecological species groups: the Deschampsia and Vaccinium groups. When stands on outwash plains were classified using ground flora, the stands supporting the Deschampsia species group averaged 85 t/ha (MABI=1.3 t/ha/yr), while those supporting the Vaccinium species group averaged 122 t/ha (MABI=1.7 t/ha/yr); these differences were statistically significant. Likewise, inclusion of ground flora and deep soil properties in the characterization of stands on the Interlobate Moraine brought out significant differences in site productivity. Two unique ecological species groups occurred on the Interlobate Moraine; the Osmorhiza group occurred on banded sites in association with a sugar maple-basswood overstory, whereas the Maianthemum group occurred on both banded and unbanded sites in association with sugar maple-red oak overstories. Both total biomass and MABI were significantly different between the banded and unbanded sites (Ecosystems 8 and 9 vs. Ecosystem 7; Table 6.5), the unbanded sites averaging less than 180 t/ha (MABI=2.7 t/ha/yr). Total biomass levels and MABI were also significantly different between the two banded sites; banded sites characterized by the Maianthemum group averaged 249 t/ha, (MABI=3.6 t/ha/yr), while those characterized by the Osmorhiza group averaged 210 t/ha, (MABI=3.3 t/ha/yr). Thus, the inclusion of ground flora and soils accounted for significant proportions of within-landform variation in productivity.

The distribution of biomass among species showed significant variation among ecosystems, paralleling the patterns observed among landforms (Figure 6.3). Black oak was the predominant component of biomass on the outwash plains (Ecosystems 1 and 2), but was progressively replaced by red oak as site conditions became more mesic. Differences in red oak biomass were a primary source of variation. Ecosystems with greater soil moisture availability, either due to finer surface textures or the presence of banding, had higher proportions of red oak. Red maple was an important biomass component in ecosystems 5 and 6, which were among the most productive ecosystems (MABI=3.0 and 3.1 t/ha/yr, respectively). Ecosystem 6 occurs in landscape positions with loamy surface horizons; while this ecosystem is currently dominated by red oak and red maple, regeneration data suggest that these stands may succeed to northern hardwoods (Chapter 5). Ecosystem 9 was dominated primarily by sugar maple and basswood; red oak was uncommon. The lack of red oak in these ecosystems may be a result of competitive exclusion from other northern hardwoods.

## Ground flora - Overstory Relationships

Certain ecological species groups have been shown to be strongly related to particular edaphic conditions (Pregitzer et al. 1982). In this study, the Desmodium and Viburnum groups were characteristic of banded or fine-textured soils, and can therefore be considered indicators of highly

Figure 6.3. Aboveground biomass among ecosystems summarized by species. Ecosystems with the same letter do not differ in total aboveground biomass.



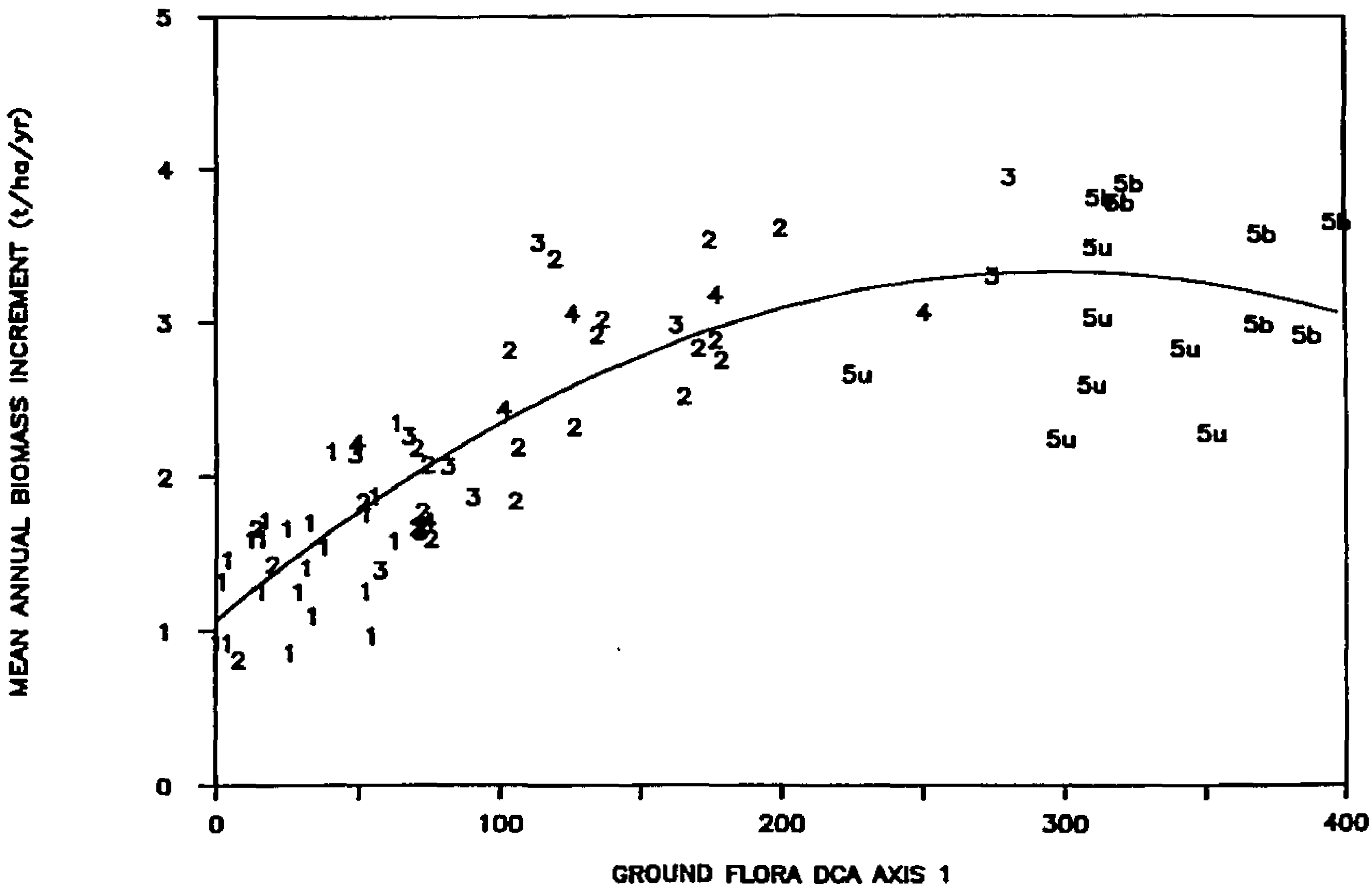
ABOVEGROUND BIOMASS (t/ha)
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
A
B
B
BC
D
DE
C
E
D
1
2
3
4
5
6
7
8
9
ECOSYSTEM
Quercus velutina
Quercus alba
Quercus rubra
Acer rubrum
Acer saccharum
Other

productive sites. Variation in biomass is strongly related to ground flora composition, because many of the factors which affect biomass production also affect species distribution patterns. These relationships were studied further using ordination techniques, which allow comparison of ground flora-overstory relationships on a stand-by-stand basis.

The ordination of stands by ground flora appeared to rank stands predominantly along an underlying moisture gradient. Species receiving large positive coefficients on the first axis were species of the Maianthemum and Osmorhiza groups, such as Osmorhiza claytonii, Adiantum pedatum and Mitella diphylla. These species were characteristic of northern hardwood stands on relatively fine-textured soils with underlying textural bands. Species receiving high negative coefficients were members of the Deschampsia group, which is found on the extremely well-drained soils of outwash plains; example members are Andropogon gerardii, Deschampsia flexuosa, Comptonia peregrina, and Arctostaphylos uva-ursi.

Since soil moisture appears to have a strong influence on productivity, we expected to find a correlation between the stand ordination scores and biomass increment. Along the vegetation gradient, biomass increment increased from xeric oak sites to mesic oak sites, but decreased in sites dominated by northern hardwoods (Figure 6.4). Stands in Figure 6.4 have been coded by landform to show the relationship between ground flora composition and landform.

Figure 6.4. Scatterplot of aboveground biomass increment with stand ordination scores. Ordination scores were derived from a detrended correspondence analysis based on ground flora abundance. Numbers represent landform codes: 1 - Outwash plains, 2 - Ice-contact hills, 3 - Port Huron Moraine, 4 - Valparaiso-Charlotte Moraine, 5b - banded Interlobate Moraine, 5u - unbanded Interlobate Moraine.


MEAN ANNUAL BIOMASS INCREMENT (t/ha/yr)
GROUND FLORA DCA AXIS 1
0
1
2
3
4
5
0
100
200
300
400

The relationship between ground flora ordination scores and biomass increment was best fit by a second-order polynomial; the $r^2$ of 0.76 was significant at p=0.05 (Figure 6.4). The decreased biomass increment observed in the northern hardwoods stands appeared to be a function of overstory composition; the shade-tolerant northern hardwoods tend to grow more slowly than the less tolerant oak species (Spurr and Barnes 1980). Figure 6.4 also shows that stands on banded sites on the Interlobate Moraine tend to have higher biomass increments compared with those on unbanded sites.

## DISCUSSION

### Landscape patterns of biomass accumulation

The glaciated landscape of northwestern Lower Michigan shows patterned spatial variation in biomass production. These patterns are fundamentally related to geologic history: depositional environments which produce extremely well-sorted and well-drained sandy parent materials show minimal development of the soil profile and low productivity. Depositional environments resulting in less-sorted, more finely-textured parent materials exhibit a greater degree of soil development and a concomitant increase in productivity. Rowe (1984) describes a close relationship between the nature of glacial landforms and the long-term development of soils and vegetation. The proximal reasons for these differences in productivity appear to be most related to differences in soil texture, an indirect index of soil moisture holding capacity. Biomass studies in Maine (Ferwerda and Young 1981, Young 1981) showed that forest productivity bore a significant relationship to soil drainage classes. Peet and Loucks (1977) observed that differences in species composition in Wisconsin oak forests were strongly related to variation in the sand content of the A horizon.

The differences in overstory species composition along the moisture gradient may also have contributed to the observed differences in biomass increment. The most productive stands had large components of red oak (Table 6.2; Figure 6.3). Red oak, which normally acts as a gap phase member of northern hardwood communities (Spurr and Barnes 1980), may have proliferated in more mesic landscape positions because of logging and subsequent fires at the turn of the century. Horn (1971, 1974) has suggested that species characteristic of early successional stages are more efficient at maximizing photosynthesis compared to late successional species. Ratios of sapwood per unit leaf area also suggest that relatively intolerant species are often more effecient at producing wood (Waring and Sleschinger 1985). Red oak is absent from the extremely xeric end of the gradient, as well as from some of the mesic northern hardwoods stands; site conditions, either through environmental limitations or competitive exclusion, affect composition. The observed biomass increment is therefore a function of both spatial (effects of site) and temporal (site-mediated responses to disturbance) factors. Since these factors interact, it is difficult to precisely factor out spatial and temporal effects. Nonetheless, spatially-explicit patterns of biomass production were evident in spite of the confounding temporal and stochastic events.

A previous study has shown that the patterned variation observed in ground flora composition was primarily related to soil moisture availability, as evidenced by differences in soil texture (Chapter 3). If ground flora and overstory are responding to the same environmental gradient, we would expect to find a high correlation between productivity and the ordination scores. Significant correlations were observed, although these relationships were confounded somewhat by temporal effects. Biomass increment increased with increasing ordination scores in the oak-dominated ecosystems, but stands dominated by northern hardwoods had high ordination scores and reduced biomass increments (Figure 6.4). While site conditions between the mesic oak and northern hardwood ecosystems were similar, dominance by late successional species in the latter ecosystem appeared to influence biomass increment. This again points to the fact that rates of production are closely related to successional status as well as environmental factors.

Red oak is currently not regenerating in any of the ecosystems we studied; these ecosystems appear to be succeeding to red maple and other shade-tolerant species

(Chapter 5). This pattern has been observed in many of the oak forests throughout the eastern United States (Lorimer 1984, McCune and Cottam 1985). The present dominance of red oak in mesic landscape positions may represent a pulse response to a regional-scale disturbance; the narrow range of stand ages (60 to 90 years) is further evidence of this response. The current problems with oak regeneration may actually be an attempt to maintain red oak stocking at densities which are not characteristic under "normal" disturbance regimes. Bormann and Likens' (1979) model of biomass aggradation following catastrophic disturbance predicts a drop in productivity as stands lose their even-aged character and composition shifts toward late successional species. As species composition changes to slower growing, more tolerant species and patch synchrony is lost due to disturbance and stochastic mortality, productivity levels will likely decline.

Ecosystems as functional landscape units

While glacial landforms mapped at a scale of 1:60,000 accounted for statistically significant portions of variation in biomass, within-landform variation in soil properties, species composition and biomass production was substantial. This is not unexpected, as there is considerable heterogeneity in physiography and soils within the broad areas delimited by landform boundaries. The Interlobate Moraine, for example, occupies about 560 $km^2$ of northwestern

Lower Michigan. The ecosystem approach, i.e. the combined use of landform, ground flora, and soils, essentially partitions this heterogeneity by identifying units which occur repeatedly in characteristic landscape positions. The approach is not new; several other mapping systems, such as soil surveys (Soil Survey Staff 1975), habitat types (Daubenmire 1952, Steele et al. 1981, Coffmann et al. 1982), and many European systems (Spurr and Barnes 1980), are based on the same principles. The combined use of landform, vegetation and soils simply represents a different means of categorizing the landscape into homogeneous units, but it capitalizes on the ecological relationships among these factors. As such, ecosystem classification offers a high degree of spatial resolution in the quantification of ecosystem functional processes, such as biomass production.

Ecosystems are three-dimensional volumetric segments of the regional landscape (Rowe 1984). The regional landscape exhibits variation in ecosystem processes which are related to ecosystem distribution patterns. An ecosystem-based map therefore provides information not only on spatial patterns of vegetation and soil, but also on the functional ecosystem processes associated with these patterns; biomass increment is but one example. Since land management requires information on process as well as pattern, the delineation of ecosystems is an effective tool for interpretation and land use planning. The rates of biomass production vary widely across the regional landscape. By considering the regional landscape as an ecosystem mosaic, these differences in productivity can be related to discrete and identifiable portions of the landscape.

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## Chapter 7

## CONCLUSIONS

1) Nine ecological species groups were formed, using 48 of the 192 ground flora species encountered in the study. Species in the groups bore significant associations with specific geologic features. The groups can therefore be used as indicators of site conditions, and as a useful part of an ecological land classification system.

2) A geomorphic map was created for the study area. Of particular interest were several landforms previously mapped as moraines (Leverett and Taylor 1913, Martin 1955, Farrand 1984) that have surface configurations and parent materials characteristic of the outwash morphosequences described in New England (Koteff and Pessl 1982). While this particular genetic aspect does not appear to influence forest composition, structure, or productivity per se, it may be of interest in the reconstruction of the Pleistocene history of this area.

3) Overstory composition exhibited patterned variation related to glacial landform. Compositional variation was strongly related to soil moisture availability, as evidenced by differences in solum textures and the presence of subsurface banding.

4) Ground flora composition exhibited patterned variation related to both overstory composition and landform. The close correlations of overstory and ground flora with solum textures and deep soil properties, coupled with the relationships of soil properties to Pleistocene and recent depositional-erosional events, allows the delineation of relatively homogenous plant-soil units which recur in characteristic landscape positions. These units, or ecosystems, provide the basis for an ecosystem classification of the regional landscape.

5) Nine landscape ecosystems were defined for upland areas of northwestern Lower Michigan. The ecosystems differ in physiography, soils, ground flora, and overstory. They can be identified in the field using simple floristic and edaphic criteria, and provide a means to extrapolate processes studied on a point-specific basis to the regional landscape.

6) Advance regeneration varies among landscape ecosystems. Red maple is uncommon or absent from the xeric outwash plains, but is abundant in the more mesic ecosystems. Oaks, currently overstory dominants on eight of the nine ecosystems, are very poorly represented in the smaller diameter classes. Red maple and white pine appear to be replacing oak in dry-mesic landscape positions, while red oak is being replaced by sugar maple in ecosystems currently dominated by northern hardwoods.

7) Total biomass and mean annual biomass increment vary among landforms and landscape ecosystems. The ecosystem classification accounted for more of the variation in biomass than the landform classification. Variation in biomass production was closely related to soil moisture availability, with more mesic sites being generally more productive than xeric sites. Variation was also related to species composition: stands with high basal areas of red oak had high total biomass levels, as well as high biomass increments. This is significant for two reasons:

    a) Red oak is a relatively fast-growing gap phase species. Its growth is particularly high on sites with relatively large quantities of available moisture. Ecosystems with high proportions of red oak and good moisture status are the most productive ecosystems observed.

    b) Red oak does not show significant advance regeneration in any portion of the landscape. It is being replaced by more shade tolerant species: red maple on dry sites, and sugar maple on more mesic sites. Because of species replacement, the current high levels of productivity are not likely to carry into the next rotation. Silvicultural practices which promote red oak regeneration or coppice management could counteract this trend.

These conclusions are significant, not only from the forest management standpoint, but also for the development of temporal biomass accumulation models. Most of the current models use logistic lagged functions to simulate biomass accumulation over time (Peet 1981). After a large scale disturbance, such as the early logging history of Michigan, the models predict a biomass overshoot followed by a decline to a quasi-equilibrium state. The rational for the overshoot is that landscape patches are synchronized, and biomass accumulation of patches occurs in a "lockstep" fashion.

Over time, stochastic disturbance and mortality disrupt patch synchrony. This study shows that compositional change to more slowly growing, shade tolerant species may be another factor which contributes to a decrease in biomass production following the overshoot. The inclusion of landscape spatial variation and successional status of component species may increase the precision of biomass accumulation models.

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# APPENDICES

# APPENDIX A

Table A.1. Legal descriptions of stand locations, USFS Ranger Districts and Compartments.

| Stand Number | Township | Range | Section | Stand location | Ranger District | USFS Stand Number | USFS Compartment Number |
|---|---|---|---|---|---|---|---|
| 1 | 22N | 14W | 30 | S 1/2, NW 1/4 | MANISTEE | 60/599 | 118 |
| 2 | 22N | 14W | 10 | NE 1/4, NW 1/4 | MANISTEE | 6/846 | 119 |
| 3 | 22N | 15W | 31 | NE 1/4, SE 1/4 | MANISTEE | 1/536 | 127 |
| 4 | 17N | 15W | 18 | SE 1/4, SW 1/4 | BALDWIN | 3/596 | 95 |
| 5 | 17N | 15W | 18 | SE 1/4, NW 1/4 | BALDWIN | 3/596 | 95 |
| 6 | 21N | 11W | 17 | NE 1/4, NW 1/4 | CADILLAC | 8/816 | 83 |
| 7 | 21N | 11W | 29 | N 1/2, NW 1/4 | CADILLAC | 1/K6 | 99 |
| 8 | 22N | 13W | 28 | N 1/2, NW 1/4 | MANISTEE | 19/599 | 104 |
| 9 | 22N | 14W | 11 | SE 1/4, SW 1/4 | MANISTEE | 9/546 | 119 |
| 10 | 21N | 15W | 27 | NE 1/4, SE 1/4 | MANISTEE | 20/K9 | 87 |
| 11 | 20N | 15W | 18 | NE 1/4, SW 1/4 | MANISTEE | 38/546 | 32 |
| 12 | 22N | 13W | 16 | NW 1/4, NE 1/4 | MANISTEE | 35/599 | 110 |
| 13 | 20N | 18W | 35 | SW 1/4, SE 1/4 | MANISTEE | 17/816 | 57 |
| 14 | 22N | 13W | 10 | SW 1/4, SE 1/4 | MANISTEE | 18/896 | 108 |
| 15 | 22N | 13W | 16 | NE 1/4, NW 1/4 | MANISTEE | 5/596 | 110 |
| 16 | 22N | 13W | 3 | E 1/2, NE 1/4 | MANISTEE | 31/596 | 108 |
| 17 | 17N | 15W | 19 | S 1/2, S 1/2 | BALDWIN | 48/596 | 96 |
| 18 | 17N | 15W | 28 | NE 1/4, NW 1/4 | BALDWIN | 14/599 | 97 |
| 19 | 18N | 15W | 25 | N 1/2, NW 1/4 | BALDWIN | 26/599 | 47 |
| 20 | 21N | 15W | 23 | NE 1/4, NW 1/4 | MANISTEE | 18/K6 | 86 |
| 21 | 23N | 13W | 24 | SW 1/4, NW 1/4 | MANISTEE | 27/896 | 60 |
| 22 | 23N | 12W | 24 | SE 1/4, SW 1/4 | CADILLAC | 123/826 | 54 |
| 23 | 22N | 11W | 34 | NW 1/4, SW 1/4 | CADILLAC | 1/816 | 84 |
| 24 | 21N | 12W | 10 | SW 1/4, SE 1/4 | CADILLAC | 1/M6 | 15 |
| 25 | 21N | 12W | 4 | NE 1/4, NE 1/4 | CADILLAC | 33/816 | 28 |
| 26 | 21N | 11W | 29 | SW 1/4, NW 1/4 | CADILLAC | 1/559 | 98 |
| 27 | 21N | 12W | 2 | N 1/2 | CADILLAC | 21/829 | 16 |
| 28 | 19N | 15W | 25 | NE 1/4, SW 1/4 | BALDWIN | 10/596 | 152 |
| 29 | 17N | 15W | 1 | W 1/2, NW 1/4 | BALDWIN | 21/K6 | 95 |
| 30 | 22N | 14W | 16 | NW 1/4,SE 1/4,NW 1/4 | MANISTEE | na | 120 |
| 31 | 22N | 14W | 26 | SW 1/4, NW 1/4 | MANISTEE | 27/559 | 114 |
| 32 | 16N | 16W | 4 | SW 1/4, NW 1/4 | BALDWIN | 39/819 | 145 |
| 33 | 20N | 15W | 17 | SE 1/4, NW 1/4 | MANISTEE | 12/546 | 32 |
| 34 | 21N | 15W | 27 | N 1/2, NW 1/4 | MANISTEE | 18/K6 | 87 |
| 35 | 23N | 13W | 32 | Center of section | MANISTEE | 27/559 | 112 |

Table A.1 (continued page 2)

| Stand Number | Township | Range | Section | Stand location | Ranger District | USFS Stand Number | USFS Compartment Number |
|---|---|---|---|---|---|---|---|
| 38 | 22N | 15W | 36 | SW 1/4, SW 1/4 | MANISTEE | 1/536 | 80 |
| 39 | 22N | 13W | 21 | NE 1/4, SE 1/4, NE 1/4 | MANISTEE | 18/536 | 103 |
| 40 | 23N | 10W | 25 | SW 1/4,SW 1/4 | CADILLAC | 24/816 | 142 |
| 41 | 23N | 10W | 35 | NE 1/4, SE 1/4 | CADILLAC | 1/816 | 69 |
| 42 | 23N | 10W | 22 | NW 1/4, SW 1/4 | CADILLAC | 7/816 | 150 |
| 43 | 23N | 11W | 29 | S 1/2 | CADILLAC | 1/826 | 59 |
| 44 | 17N | 15W | 18 | N 1/2, SE 1/4 | BALDWIN | 3/596 | 95 |
| 45 | 17N | 15W | 29 | NW 1/4, NW 1/4 | BALDWIN | 55/596 | 96 |
| 46 | 19N | 14W | 33 | NW 1/4, NW 1/4 | BALDWIN | 13/596 | 18 |
| 47 | 18N | 14W | 4 | W 1/2, NE 1/4,SE 1/4 | BALDWIN | 54/546 | 19 |
| 48 | 21N | 12W | 30 | NW 1/4, SW 1/4 | CADILLAC | 14/596 | 1 |
| 49 | 21N | 13W | 7 | NW 1/4, NW 1/4 | MANISTEE | 11/536 | 130 |
| 50 | 21N | 16W | 14 | E 1/2, NW 1/4 | MANISTEE | 1/536 | 98 |
| 51 | 19N | 14W | 13 | NW 1/4, NE 1/4 | BALDWIN | 10/536 | 10 |
| 52 | 20N | 13W | 20 | SE 1/4 | MANISTEE | 39/596 | 4 |
| 53 | 19N | 13W | 9 | SW 1/4, SE 1/4 | BALDWIN | 54/535 | 1 |
| 54 | 17N | 15W | 4 | NW 1/4, NW 1/4 | BALDWIN | 1/596 | 93 |
| 55 | 18N | 15W | 28 | NW 1/4, SW 1/4 | BALDWIN | 3/486 | 49 |
| 56 | 22N | 12W | 25 | NW 1/4, NE 1/4 | CADILLAC | 24/816 | 31 |
| 57 | 21N | 12W | 1 | SW 1/4 | CADILLAC | 38/556 | 81 |
| 58 | 22N | 13W | 16 | NE 1/4, NW 1/4 | MANISTEE | 33/596 | 110 |
| 59 | 21N | 14W | 1 | SE 1/4, SW 1/4 | MANISTEE | 14/536 | 76 |
| 60 | 21N | 12W | 18 | SE 1/4, NE 1/4 | CADILLAC | 2/M6 | 11 |
| 61 | 18N | 14W | 2 | NE 1/4, SE 1/4 | BALDWIN | 25/536 | 29 |
| 62 | 22N | 14W | 12 | N 1/2, SW 1/4 | MANISTEE | 9/556 | 113 |
| 63 | 15N | 13W | 27 | SW 1/4, SE 1/4 | WHITE CLOUD | 6/596 | 87 |
| 64 | 16N | 14W | 1 | NE 1/4, NW 1/4 | BALDWIN | 76/896 | 76 |
| 65 | 16N | 14W | 9 | SW 1/4, SE 1/4 | BALDWIN | 17/556 | 126 |
| 66 | 13N | 10W | 28 | N 1/2, SW 1/4 | WHITE CLOUD | 3/596 | 188 |
| 67 | 14N | 13W | 15 | W 1/2, SW 1/4 | WHITE CLOUD | 47/599 | 81 |
| 68 | 16N | 14W | 6 | NE 1/4, NE 1/4 | BALDWIN | 1/599 | 127 |
| 69 | 14N | 12W | 13 | E 1/2, SE 1/4 | WHITE CLOUD | 3/559 | 131 |
| 70 | 15N | 11W | 17 | S 1/2, NW 1/4 | WHITE CLOUD | 2/556 | 146 |
| 71 | 16N | 13W | 36 | SW 1/4 | BALDWIN | 27/K6 | 111 |
| 72 | 16N | 13W | 24 | NE 1/4 | BALDWIN | 5/556 | 108 |
| 73 | 15N | 11W | 24 | NW 1/4 | WHITE CLOUD | 10/596 | 150 |
| 74 | 16N | 11W | 21 | SW 1/4, NW 1/4 | BALDWIN | 78/896 | 155 |
| 75 | 16N | 14W | 11 | NW 1/4, NE 1/4 | BALDWIN | 13/K6 | 110 |
| 76 | 14N | 11W | 11 | SE 1/4, NW 1/4 | WHITE CLOUD | 11/K6 | 156 |
| 77 | 13N | 12W | 31 | NE 1/4 | WHITE CLOUD | 16/595 | 112 |
| 78 | 13N | 12W | 32 | NW 1/4, NW 1/4 | WHITE CLOUD | 14/595 | 112 |
| 79 | 12N | 12W | 26 | E 1/2, SW 1/4 | WHITE CLOUD | 10/539 | 117 |
| 80 | 14N | 11W | 29 | NE 1/4 | WHITE CLOUD | 11/596 | 165 |

# APPENDIX B

Table B.1. Rank order and detrended correspondence analysis scores used to create synthesis table (Table B.2). Key to synthesis table page format shown below.

| Rank Order | DCA Score | Stand | Rank Order | DCA Score | Stand | Rank Order | DCA Score | Stand |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 49 | 27 | 73 | 12 | 54 | 184 | 44 |
| 2 | 6 | 59 | 28 | 74 | 11 | 55 | 189 | 5 |
| 3 | 11 | 55 | 29 | 78 | 3 | 56 | 192 | 60 |
| 4 | 13 | 51 | 30 | 80 | 61 | 57 | 197 | 10 |
| 5 | 15 | 33 | 31 | 81 | 75 | 58 | 197 | 4 |
| 6 | 17 | 54 | 32 | 81 | 76 | 59 | 206 | 74 |
| 7 | 19 | 29 | 33 | 85 | 39 | 60 | 222 | 7 |
| 8 | 21 | 34 | 34 | 88 | 45 | 61 | 234 | 2 |
| 9 | 26 | 79 | 35 | 88 | 68 | 62 | 244 | 21 |
| 10 | 33 | 38 | 36 | 90 | 73 | 63 | 245 | 35 |
| 11 | 33 | 65 | 37 | 95 | 15 | 64 | 249 | 31 |
| 12 | 35 | 48 | 38 | 100 | 18 | 65 | 265 | 41 |
| 13 | 36 | 28 | 39 | 101 | 70 | 66 | 282 | 40 |
| 14 | 39 | 50 | 40 | 109 | 8 | 67 | 282 | 56 |
| 15 | 39 | 53 | 41 | 113 | 67 | 68 | 284 | 57 |
| 16 | 47 | 71 | 42 | 114 | 62 | 69 | 285 | 23 |
| 17 | 48 | 78 | 43 | 120 | 16 | 70 | 295 | 32 |
| 18 | 53 | 46 | 44 | 126 | 47 | 71 | 295 | 26 |
| 19 | 56 | 1 | 45 | 130 | 77 | 72 | 297 | 42 |
| 20 | 57 | 9 | 46 | 132 | 80 | 73 | 305 | 25 |
| 21 | 59 | 66 | 47 | 139 | 20 | 74 | 321 | 6 |
| 22 | 60 | 30 | 48 | 141 | 17 | 75 | 321 | 36 |
| 23 | 63 | 19 | 49 | 141 | 13 | 76 | 329 | 24 |
| 24 | 64 | 63 | 50 | 144 | 64 | 77 | 335 | 27 |
| 25 | 67 | 52 | 51 | 164 | 14 | 78 | 336 | 43 |
| 26 | 70 | 58 | 52 | 177 | 69 | 79 | 347 | 22 |
| | | | 53 | 183 | 72 | 80 | 365 | 37 |

Synthesis table page format; values are page numbers.

<-------------------------- Stands -------------------------->

| | | | | | | |
|---|---|---|---|---|---|---|
| Species | 183 | 186 | 189 | 192 | 195 | 198 |
| | 184 | 187 | 190 | 193 | 196 | 199 |
| | 185 | 188 | 191 | 194 | 197 | 200 |

APPENDIX B

Table B.2. Synthesis table for all woody and herbaceous ground flora with stand level frequencies of 5% or greater. Stands and species are ranked by detrended correspondence analysis scores. Values are mean rank abundance. Ranks < 2.0 represent trace coverage (<1%); ranks > 2.0 converted to % coverage by: (rank*(-19.97)+(rank^2*3.86)+24.11).

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rank order | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| DCA score | 0 | 5 | 11 | 13 | 15 | 17 | 19 | 21 | 26 | 33 | 33 | 35 | 36 | 39 | 39 |
| Species | Stand | | | | | | | | | | | | | | |
| | 49 | 59 | 55 | 51 | 33 | 54 | 29 | 34 | 79 | 38 | 65 | 48 | 28 | 50 | 53 |
| Andropogon gerardii | 0.5 | - | 1.5 | 0.5 | - | 0.3 | - | - | - | - | - | 2.0 | - | 1.3 | - |
| Pinus banksiana | 0.5 | 0.5 | 2.8 | 0.8 | - | 0.8 | - | - | - | - | - | - | - | 1.0 | - |
| Arctostaphylos uva-ursi | 2.0 | 0.8 | - | - | - | 1.0 | - | - | - | - | 0.5 | 1.0 | - | 3.9 | 1.3 |
| Lycopodium tristachyum | - | 0.9 | 0.3 | - | 1.0 | - | - | - | - | 0.3 | - | - | 0.3 | - | - |
| Cladina spp. | 0.9 | 0.5 | 0.5 | - | 0.8 | - | 0.3 | 1.0 | - | 0.5 | - | - | 0.5 | - | - |
| Quercus ellipsoidalis | 3.0 | 3.0 | - | 1.3 | - | 2.5 | - | - | 1.3 | - | 2.8 | - | - | - | 2.5 |
| Rubus hispidus | 0.5 | 0.5 | 1.3 | - | - | - | 0.3 | - | - | - | - | 1.3 | 0.3 | - | 1.0 |
| Rudbeckia spp. | 0.5 | - | - | 0.3 | - | - | - | - | - | - | - | - | - | 0.8 | 0.5 |
| Cladonia spp. | 1.3 | 0.5 | 1.8 | 0.3 | 0.5 | 1.0 | 0.5 | 0.5 | - | 0.8 | 0.8 | 1.3 | 1.0 | 0.3 | 1.0 |
| Lupinus perennis | - | - | 0.3 | 0.3 | - | - | 0.3 | - | - | - | - | - | 1.0 | - | - |
| Crataegus spp. | 0.5 | - | - | 0.3 | 0.3 | - | 0.3 | - | 0.8 | - | 0.3 | 0.8 | - | 1.3 | 1.8 |
| Comptonia peregrina | 3.5 | 3.0 | 0.3 | 1.3 | 0.5 | - | 0.3 | 1.0 | - | - | 1.5 | 2.0 | - | 3.3 | 3.5 |
| Pleurozium schreberi | 0.9 | 0.3 | 0.8 | 0.5 | - | 0.8 | - | - | - | 0.3 | 0.8 | - | - | - | - |
| Polytrichum juniperinum | - | - | 0.3 | 0.3 | 0.5 | 0.3 | 0.8 | 0.8 | - | 0.5 | - | - | 0.3 | - | - |
| Comandra umbellata | 0.5 | 0.5 | - | 0.5 | 0.5 | - | 0.5 | - | 0.5 | 0.3 | 0.5 | 0.5 | - | - | - |
| Deschampsia flexuosa | - | - | - | - | - | - | - | - | - | - | 0.5 | - | - | - | - |
| Hieracium venosum | - | 0.3 | - | 0.3 | - | - | 0.3 | - | - | 0.5 | 0.3 | 0.3 | - | - | 0.3 |
| Galium circaezans | - | - | - | 1.0 | 0.3 | - | - | - | - | - | - | 0.3 | - | - | 0.8 |
| Polytrichum piliferum | - | - | - | - | 0.3 | - | 0.3 | - | - | 0.3 | - | - | 0.8 | - | - |
| Chimaphila umbellata | - | - | 0.8 | - | - | - | 0.3 | - | 1.0 | - | - | - | - | - | 0.3 |
| Melampyrum lineare | 0.5 | 1.0 | 0.8 | 0.3 | 2.0 | 1.0 | 1.5 | 1.0 | 1.3 | 2.0 | - | 0.8 | 1.8 | 2.3 | 1.0 |
| Dicranum polysetum | 1.9 | 2.3 | 2.8 | 1.3 | 1.3 | 1.5 | 1.0 | 1.3 | - | 2.3 | 1.5 | - | 0.8 | - | 1.3 |
| Pinus resinosa | - | - | - | - | 1.0 | - | - | - | - | - | 0.8 | - | - | - | - |
| Gaylussacia baccata | - | - | 0.9 | 1.0 | 3.8 | - | 0.5 | 3.3 | 2.3 | - | - | - | 3.0 | - | - |
| Thuidium recognitum | - | - | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - |
| Dicranum scoparium | - | 0.3 | 0.3 | 0.3 | 0.3 | 0.5 | 0.3 | 0.5 | - | 1.3 | - | - | 0.3 | - | - |
| Quercus velutina | 1.5 | 2.5 | 3.0 | 1.3 | 2.8 | 2.8 | 2.8 | 2.0 | 1.8 | 3.0 | 0.8 | 2.0 | 2.8 | 3.3 | 0.3 |
| Cypripedium acaule | - | - | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - |
| Rosa spp. | 0.5 | - | - | 0.5 | - | 1.0 | - | - | - | - | 0.5 | - | - | - | 0.3 |
| Pinus strobus | 0.8 | 0.3 | 0.5 | - | 2.5 | - | 0.5 | 1.8 | 3.9 | 1.0 | 0.5 | - | - | - | - |
| Leucobryum glaucum | - | - | - | - | 0.3 | - | 0.3 | 0.8 | - | 0.5 | - | - | - | - | - |
| Vaccinium angustifolium | 3.0 | 4.0 | 4.0 | 2.5 | 2.8 | 5.0 | 4.3 | 3.0 | - | 2.3 | 2.9 | 2.5 | 3.8 | 4.5 | 3.5 |
| Quercus alba | 3.5 | 3.8 | 3.8 | 4.3 | 3.5 | 3.8 | 2.3 | 1.8 | 2.8 | 4.3 | 3.0 | 3.0 | 3.0 | 2.8 | 3.8 |
| Potentilla simplex | - | - | - | 1.0 | - | - | - | - | 1.0 | - | 0.3 | - | - | 1.5 | 1.3 |

Table B.2. (cont.)

| Rank order | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 0 | 6 | 11 | 13 | 15 | 17 | 19 | 21 | 26 | 33 | 33 | 35 | 36 | 39 | 39 |
| Species | Stand | | | | | | | | | | | | | | |
| | 49 | 59 | 55 | 51 | 33 | 54 | 29 | 34 | 79 | 38 | 65 | 48 | 28 | 58 | 53 |
| Eurhynchium hians | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | 0.3 |
| Gaultheria procumbens | - | 1.5 | 1.0 | - | 1.0 | - | 2.3 | 1.0 | - | 2.0 | 0.3 | 1.0 | 0.5 | 1.3 | 2.3 |
| Epigaea repens | - | 0.5 | - | - | 1.0 | - | - | - | - | 0.3 | - | - | - | 0.8 | 1.5 |
| Pedicularis canadensis | - | - | - | 0.6 | - | - | - | - | - | - | - | - | - | - | - |
| Sassafras albidum | - | - | - | - | 3.8 | - | 1.8 | 2.8 | - | 3.0 | 3.0 | - | 3.3 | - | - |
| Pteridium aquilinium | 2.3 | 4.5 | 1.8 | 3.3 | 3.5 | 0.8 | 5.0 | 3.0 | 1.0 | 2.3 | 2.3 | 2.0 | 4.8 | 2.5 | 3.3 |
| Monotropa hypopithys | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - |
| Hamamelis virginiana | - | - | - | 1.8 | - | - | - | 1.5 | - | - | - | - | 0.5 | - | - |
| Callicladium haldanianum | - | - | 0.3 | - | 0.5 | - | 1.0 | 0.5 | - | 1.3 | - | 0.3 | - | - | - |
| Smilicina stellata | - | - | - | - | 0.3 | - | - | - | - | - | - | 0.3 | - | - | - |
| Amelanchier spp. | 1.3 | 2.5 | 1.0 | 0.5 | 1.5 | 0.3 | 1.0 | 0.3 | 0.8 | 1.0 | 1.3 | 0.3 | 1.3 | 1.5 | 2.0 |
| Polytrichum commune | - | - | - | - | - | - | - | - | - | 0.8 | - | - | 0.3 | - | - |
| Vitis aestivalis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex pensylvanica | 7.0 | 6.0 | 5.3 | 6.5 | 5.5 | 6.3 | 6.3 | 3.3 | 5.8 | 5.8 | 6.8 | 7.0 | 5.3 | 6.0 | 6.0 |
| Pyrola rotundifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Acer rubrum | 0.3 | 0.8 | - | 1.5 | 1.3 | 0.5 | 1.5 | 2.3 | - | 1.8 | 0.5 | - | 1.5 | 0.8 | 1.0 |
| Desmodium spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Populus grandidentata | - | - | - | - | - | - | - | - | - | - | 0.5 | 0.5 | - | 0.5 | - |
| Apocynum androsaemefolium | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.8 | 0.3 |
| Smilacina racemosa | 0.3 | 0.8 | 0.3 | 0.3 | - | 0.3 | 0.5 | - | - | 0.5 | 0.3 | - | - | 0.3 | 0.8 |
| Aster macrophyllus | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Trientalis borealis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Desmodium nudiflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Monotropa uniflora | 0.3 | 0.5 | - | 0.3 | - | - | 0.3 | - | - | - | - | - | - | - | - |
| Oryzopsis asperifolia | - | - | 0.3 | - | - | - | - | - | - | 0.8 | - | - | 3.3 | 0.3 | 3.0 |
| Rubus allegheniensis | - | - | 0.5 | - | - | 0.3 | - | - | - | - | - | 1.0 | - | 1.3 | 1.5 |
| Rubus idaeus | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polygala paucifolia | - | - | - | - | - | - | - | - | - | - | - | - | 3.3 | - | - |
| Prunus serotina | 2.8 | 2.8 | 3.5 | 1.0 | 0.5 | 3.3 | 2.8 | - | 2.5 | 2.0 | 2.0 | 3.8 | 1.0 | 4.0 | 3.5 |
| Viburnum acerifolium | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Panicum latifolium | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.5 |
| Conopholis americana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Quercus rubra | - | - | - | - | - | - | - | - | - | 0.8 | 0.5 | 0.5 | - | - | - |
| Populus tremuloides | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 | 0.3 |
| Lonicera canadense | 0.8 | 0.3 | 1.0 | 0.3 | 0.5 | 3.5 | - | - | - | - | 0.3 | 0.3 | - | - | - |
| Mnium spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Prenanthes alba | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Geranium maculatum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hystrix patula | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - |
| Aralia nudicaulis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Solidago caesia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

Table B.2. (cont.)

| Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 0 | 5 | 11 | 13 | 15 | 17 | 19 | 21 | 26 | 33 | 33 | 35 | 36 | 39 | 39 |
| Stand | 49 | 59 | 55 | 51 | 33 | 54 | 29 | 34 | 79 | 38 | 65 | 48 | 28 | 50 | 53 |
| Fagus grandifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Viola pubescens | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mitchella repens | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Maiantheaum canadense | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Panicum latifolia | - | - | - | - | - | - | - | - | - | 0.5 | - | - | 0.3 | - | - |
| Cornus florida | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Viola sororia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Medeola virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Campanula rotundifolia | - | - | - | 0.5 | - | - | - | - | - | - | - | 0.5 | - | - | 0.5 |
| Fraxinus americana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polygonatum biflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Galium boreale | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Epifagus virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium lucidulum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ostrya virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Galium triflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium obscurum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Acer saccharum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carpinus caroliniana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Trillium grandiflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Sambucus pubens | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Viola canadense | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex pedunculata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ribes cynosbati | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Actaea alba | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Osmorhiza claytonii | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex deweyana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hepatica acutiloba | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dryopteris spinulosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Tilia americana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Epipactis helleborine | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex plantaginea | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Adiantum pedatum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Uvularia perfoliata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Botrychium virginianum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Caulophyllum thalictroides | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mitella diphylla | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Allium tricoccum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dicentra canadensis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Tiarella cordifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

Table 8.2. (cont.)

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rank order | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
| DCA score | 47 | 48 | 53 | 56 | 57 | 59 | 60 | 63 | 64 | 67 | 70 | 73 | 74 | 79 | 80 |
| Species | Stand | | | | | | | | | | | | | | |
| | 71 | 79 | 46 | 1 | 9 | 66 | 30 | 19 | 63 | 52 | 58 | 12 | 11 | 3 | 61 |
| Andropogon gerardii | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pinus banksiana | - | - | - | - | - | - | - | 1.0 | - | - | - | - | - | - | - |
| Arctostaphylos uva-ursi | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium tristachyum | 0.3 | - | - | 1.2 | - | - | - | - | - | - | - | - | - | - | - |
| Cladina spp. | - | 1.0 | - | 0.2 | - | - | - | 0.5 | - | - | - | 0.3 | - | - | - |
| Quercus ellipsoidalis | - | 2.3 | - | - | - | 3.0 | - | - | - | - | - | - | - | - | - |
| Rubus hispidus | - | - | - | - | - | - | - | 0.5 | - | - | - | - | - | - | - |
| Rudbeckia spp. | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cladonia spp. | - | - | 0.3 | 0.3 | 0.3 | - | - | - | - | 0.8 | 0.8 | - | - | - | - |
| Lupinus perennis | 0.8 | 0.3 | - | - | - | - | - | 0.8 | - | - | - | - | - | - | - |
| Crataegus spp. | 0.3 | - | - | - | - | - | - | - | 0.3 | - | - | - | 0.3 | - | - |
| Comptonia peregrina | 0.3 | - | - | 0.5 | 1.3 | 0.5 | 0.3 | 2.0 | 0.3 | - | - | 0.5 | 0.5 | 0.7 | 0.3 |
| Pleurozium schreberi | - | - | - | - | - | - | - | - | 0.5 | 0.5 | 0.8 | - | - | 0.2 | - |
| Polytrichum juniperinum | - | - | - | - | - | 0.5 | - | - | - | 0.3 | - | 0.3 | 0.5 | - | - |
| Comandra umbellata | 0.3 | - | 0.5 | 0.5 | 1.0 | 0.8 | - | - | 0.3 | - | - | - | 1.3 | 0.2 | 0.3 |
| Deschampsia flexuosa | 0.8 | 1.3 | - | - | - | - | - | - | - | - | - | - | - | - | 0.8 |
| Hieracium venosum | 0.8 | - | - | - | 0.5 | - | - | - | - | - | - | - | - | 0.2 | - |
| Galium circaezans | 0.3 | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Polytrichum piliferum | - | 0.8 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Chimaphila umbellata | 1.3 | 0.5 | - | - | - | 0.5 | - | - | 0.5 | - | - | - | - | - | - |
| Melampyrum lineare | 2.0 | 0.8 | 0.5 | - | 0.8 | - | 1.3 | 1.8 | - | - | 0.8 | 0.5 | 0.5 | 0.8 | - |
| Dicranum polysetum | - | 1.0 | 0.5 | 1.5 | 1.0 | 0.3 | 0.5 | 1.0 | 0.3 | 1.0 | 1.0 | 0.3 | 0.5 | 1.2 | - |
| Pinus resinosa | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - |
| Gaylussacia baccata | 0.5 | 3.8 | 0.5 | 0.7 | - | 3.0 | 1.0 | - | 3.3 | 1.0 | - | 0.8 | - | 0.5 | - |
| Thuidium recognitum | - | - | 0.3 | - | - | - | 0.3 | - | - | - | - | - | - | - | - |
| Dicranum scoparium | - | - | 0.3 | 0.2 | 1.0 | - | - | - | - | 0.3 | 0.3 | 0.5 | 0.3 | 0.3 | - |
| Quercus velutina | 2.3 | 2.3 | 2.0 | 3.0 | 1.5 | 1.3 | 2.0 | 2.3 | 3.5 | 1.0 | 1.0 | 0.8 | 1.3 | 1.0 | 0.9 |
| Cypripedium acaule | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Rosa spp. | - | - | - | - | - | 0.3 | - | 0.5 | 0.3 | 0.5 | - | - | - | - | - |
| Pinus strobus | - | - | 3.0 | 1.8 | 1.0 | - | 2.5 | 3.3 | - | - | 2.3 | - | 0.5 | 0.2 | - |
| Leucobryum glaucum | - | 0.5 | 0.3 | 0.3 | - | - | - | - | - | - | 0.3 | - | - | 1.0 | - |
| Vaccinium angustifolium | 4.0 | 3.8 | 4.0 | 3.0 | 3.3 | 3.8 | 3.5 | 4.0 | 3.3 | 3.8 | 4.3 | 2.5 | 1.3 | 3.7 | 4.5 |
| Quercus alba | 2.5 | 3.5 | 2.8 | 3.7 | 3.8 | 1.5 | 2.8 | 2.0 | 2.5 | 2.0 | 3.3 | 2.0 | 1.5 | 3.0 | 2.2 |
| Potentilla simplex | 0.8 | - | - | - | - | - | 0.3 | 0.5 | 0.8 | - | - | - | - | - | - |
| Eurhynchium hians | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - |
| Gaultheria procumbens | 1.0 | - | 0.5 | 0.5 | 2.3 | 1.3 | 1.0 | 0.3 | 2.3 | 0.3 | 3.3 | 2.0 | 1.5 | 1.7 | 0.8 |
| Epigaea repens | - | - | 0.3 | - | 0.3 | - | - | 0.3 | - | 0.5 | 0.5 | 1.0 | - | 0.2 | 1.3 |
| Pedicularis canadensis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Sassafras albidum | 3.0 | 2.0 | 3.5 | 0.5 | 3.5 | - | - | 0.3 | 3.8 | 4.0 | 3.5 | 1.5 | 3.0 | 2.5 | 3.8 |
| Pteridium aquilinium | 6.0 | 2.0 | 2.8 | 3.8 | 3.3 | 4.3 | 4.3 | 4.5 | 6.0 | 3.3 | 3.3 | 2.8 | 3.5 | 4.2 | 4.3 |
| Monotropa hypopithys | - | - | 0.5 | - | - | 0.3 | - | - | - | 0.3 | - | - | - | - | - |

Table B.2. (cont.)

| Species | 71 | 78 | 46 | 1 | 9 | 66 | 30 | 19 | 63 | 52 | 58 | 12 | 11 | 3 | 61 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rank order | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
| DCA score | 47 | 46 | 53 | 56 | 57 | 59 | 60 | 63 | 64 | 67 | 70 | 73 | 74 | 78 | 80 |
| Hamamelis virginiana | 1.3 | - | 2.0 | 2.5 | 1.0 | - | 2.0 | - | 3.5 | 3.8 | 0.8 | 0.3 | 1.6 | 2.2 | 3.3 |
| Callicladium haldanianum | - | - | 0.3 | - | 1.0 | - | 0.5 | 0.8 | - | 0.3 | 0.3 | 0.6 | 1.0 | 0.5 | - |
| Smilicina stellata | - | - | - | 0.3 | - | - | - | - | - | - | - | - | 0.3 | - | - |
| Amelanchier spp. | 1.3 | 1.5 | 1.0 | 1.0 | 1.5 | 2.8 | 2.0 | 2.0 | 0.8 | 1.0 | 3.0 | 1.5 | 1.3 | 1.0 | 0.3 |
| Polytrichum commune | 0.3 | - | - | 0.3 | - | - | - | - | - | - | - | - | - | 0.7 | - |
| Vitis aestivalis | - | - | 0.8 | - | - | - | - | - | - | 1.5 | - | - | - | - | - |
| Carex pensylvanica | 6.3 | 5.0 | 3.0 | 4.8 | 5.8 | 5.8 | 4.0 | 5.0 | 6.5 | 3.0 | 4.5 | 2.5 | 3.3 | 3.0 | 3.3 |
| Pyrola rotundifolia | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Acer rubrum | 2.5 | 1.0 | 2.0 | 1.2 | 1.5 | 2.8 | 2.0 | 1.3 | 2.5 | 2.5 | 2.3 | 1.5 | 1.5 | 1.2 | 1.5 |
| Desmodium spp. | 0.8 | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Populus grandidentata | 0.3 | 0.5 | 0.3 | - | - | - | - | - | - | 0.3 | - | - | - | 0.2 | - |
| Apocynum androsaemefolium | - | - | - | 0.2 | - | - | - | 0.5 | - | - | - | - | - | - | - |
| Smilacina racemosa | - | - | - | - | 0.3 | 1.0 | 0.8 | - | 0.3 | 1.0 | - | - | 1.0 | 0.5 | 0.8 |
| Aster macrophyllus | 0.8 | - | - | - | 0.3 | - | - | - | 0.3 | 0.8 | - | 0.5 | - | 0.3 | 0.3 |
| Trientalis borealis | - | - | - | - | - | - | - | - | - | - | 1.3 | 0.3 | - | 0.2 | 0.3 |
| Desmodium nudiflorum | - | - | - | - | - | - | - | - | - | 0.5 | - | - | - | - | - |
| Monotropa uniflora | - | - | 0.3 | - | - | - | - | 0.3 | - | 0.5 | 0.8 | - | - | - | - |
| Oryzopsis asperifolia | 0.3 | - | 1.3 | 0.2 | - | - | 0.5 | 0.5 | 0.5 | 1.5 | 0.5 | - | 1.3 | 0.8 | 1.8 |
| Rubus allegheniensis | - | 0.3 | - | 0.2 | - | 0.8 | - | 0.3 | - | - | - | - | 0.8 | - | - |
| Rubus idaeus | - | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - |
| Polygala paucifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Prunus serotina | 2.0 | 1.0 | 0.5 | 0.5 | 1.3 | 3.0 | 2.0 | 2.3 | 1.0 | - | 1.8 | 0.5 | 1.0 | 1.2 | - |
| Viburnum acerifolium | - | 0.3 | 1.5 | 0.2 | - | 0.3 | - | - | - | 1.3 | 2.3 | 1.0 | 0.8 | - | 0.8 |
| Panicum latifolium | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Conopholis americana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Quercus rubra | 1.3 | - | - | - | 1.0 | 0.5 | - | - | 0.8 | 2.8 | 2.3 | 0.5 | 0.8 | 2.0 | 1.0 |
| Populus tremuloides | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lonicera canadense | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - |
| Mnium spp. | - | - | - | - | 0.3 | - | - | - | - | - | - | 0.5 | 0.5 | - | - |
| Prenanthes alba | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 | - | - |
| Geranium maculatum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hystrix patula | - | - | - | - | - | - | - | 1.0 | - | - | - | - | - | - | - |
| Aralia nudicaulis | - | - | - | - | - | - | - | - | 0.3 | - | 0.3 | - | - | - | - |
| Solidago caesia | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.2 | - |
| Fagus grandifolia | - | 0.5 | - | 0.5 | - | - | 0.3 | - | - | - | - | - | - | 0.3 | - |
| Viola pubescens | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mitchella repens | - | - | - | - | - | - | - | - | - | - | - | 0.5 | - | - | - |
| Maiantheaum canadense | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | 0.3 | - |
| Panicum latifolia | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Cornus florida | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Viola sororia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

Table B.2. (cont.)

| Rank order | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 47 | 48 | 53 | 56 | 57 | 59 | 60 | 63 | 64 | 67 | 70 | 73 | 74 | 78 | 80 |
| Species | Stand | | | | | | | | | | | | | | |
| | 71 | 79 | 46 | 1 | 9 | 66 | 38 | 19 | 63 | 52 | 58 | 12 | 11 | 3 | 61 |
| Medeola virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Campanula rotundifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Fraxinus americana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polygonatum biflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Galium boreale | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Epifagus virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium lucidulum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ostrya virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Galium triflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium obscurum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Acer saccharum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carpinus caroliniana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Trillium grandiflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Sambucus pubens | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Viola canadense | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex pedunculata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ribes cynosbati | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Actaea alba | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Osmorhiza claytonii | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex deweyana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hepatica acutiloba | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dryopteris spinulosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Tilia americana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Epipactis helleborine | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex plantaginea | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Adiantum pedatum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Uvularia perfoliata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Botrychium virginianum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Caulophyllum thalictroides | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mitella diphylla | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Allium tricoccum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dicentra canadensis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Tiarella cordifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

Table B.2. (cont.)

| Rank order | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 81 | 81 | 85 | 88 | 88 | 90 | 95 | 100 | 101 | 109 | 113 | 114 | 120 | 126 | 130 |
| Species | Stand | | | | | | | | | | | | | | |
| | 75 | 76 | 39 | 45 | 68 | 73 | 15 | 18 | 70 | 8 | 67 | 62 | 16 | 47 | 77 |
| Andropogon gerardii | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pinus banksiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Arctostaphylos uva-ursi | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium tristachyum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cladina spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Quercus ellipsoidalis | 3.0 | 0.5 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Rubus hispidus | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Rudbeckia spp. | 0.5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cladonia spp. | - | - | 1.0 | - | 0.3 | - | - | - | - | - | - | - | - | - | - |
| Lupinus perennis | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Crataegus spp. | 0.8 | - | - | - | - | - | - | 0.5 | - | - | 0.5 | - | - | - | 0.8 |
| Comptonia peregrina | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pleurozium schreberi | - | - | - | - | - | - | - | - | - | - | - | 0.5 | - | - | - |
| Polytrichum juniperinum | - | - | 0.3 | 0.3 | - | - | 0.5 | - | - | - | - | - | - | - | - |
| Comandra umbellata | 0.5 | - | 0.5 | - | - | - | - | - | - | - | 0.0 | - | - | - | - |
| Deschampsia flexuosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hieracium venosum | - | - | - | - | - | - | - | 0.3 | - | - | - | 0.3 | - | - | - |
| Galium circaezans | 0.3 | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Polytrichum piliferum | - | - | - | - | - | - | - | 0.3 | - | - | - | 0.3 | - | - | - |
| Chimaphila umbellata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.0 |
| Melampyrum lineare | 1.8 | 0.3 | 1.0 | 0.5 | 0.5 | 0.3 | 1.3 | 0.3 | 1.3 | 1.0 | - | 0.8 | - | 0.3 | - |
| Dicranum polysetum | - | - | 1.0 | 1.3 | 0.3 | 0.8 | 1.0 | 0.3 | 0.5 | 0.8 | - | 1.3 | 0.5 | - | - |
| Pinus resinosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Gaylussacia baccata | - | 3.3 | 1.3 | 0.3 | 2.5 | 2.0 | 3.3 | - | 0.5 | 0.5 | 1.8 | - | - | 0.3 | 2.0 |
| Thuidium recognitum | - | - | 0.8 | - | - | - | - | - | - | 0.3 | - | - | - | - | - |
| Dicranum scoparium | - | - | 0.5 | 0.5 | - | - | 0.3 | 0.5 | - | - | - | - | 0.5 | - | - |
| Quercus velutina | 1.8 | 2.0 | 0.5 | 2.5 | 2.3 | 2.3 | 0.3 | 1.8 | 0.8 | - | 1.0 | 0.5 | - | 1.0 | 2.0 |
| Cypripedium acaule | - | - | - | - | - | 0.5 | - | - | 0.3 | - | - | 0.3 | - | - | - |
| Rosa spp. | 0.5 | - | - | - | - | 0.5 | - | - | - | - | - | - | - | - | 0.8 |
| Pinus strobus | 2.0 | - | 3.0 | 2.0 | 0.5 | - | 3.5 | 0.3 | - | 0.3 | - | - | - | - | - |
| Leucobryum glaucum | 0.3 | - | 0.5 | - | - | - | 0.5 | - | - | - | - | 0.3 | - | - | - |
| Vaccinium angustifolium | 3.3 | 3.8 | 3.5 | 3.3 | 4.3 | 4.0 | 3.8 | 1.9 | 2.8 | 2.9 | 3.0 | 3.5 | 2.9 | 2.0 | 4.0 |
| Quercus alba | 3.5 | 2.5 | 2.3 | 2.3 | 3.0 | 3.0 | 1.0 | 1.9 | 2.3 | 1.5 | 2.3 | 3.3 | 0.5 | 1.3 | 1.3 |
| Potentilla simplex | 0.8 | - | - | - | 0.3 | - | - | - | - | - | 0.3 | - | - | - | 1.5 |
| Eurhynchium hians | - | - | 0.8 | - | - | - | - | - | - | - | - | - | - | - | - |
| Gaultheria procumbens | 1.5 | - | 2.5 | 2.3 | 2.5 | 0.8 | 2.3 | 1.0 | 2.0 | 1.5 | 1.3 | 2.5 | 2.0 | 0.8 | - |
| Epigaea repens | - | - | 2.0 | 0.3 | 0.3 | - | 0.8 | - | - | 0.5 | - | 0.5 | 0.5 | - | - |
| Pedicularis canadensis | - | - | - | - | 0.3 | - | - | - | - | - | - | 0.3 | - | - | - |
| Sassafras albidum | 3.5 | 3.3 | 3.5 | - | 3.0 | 2.3 | 2.8 | 0.3 | 3.3 | 3.3 | 3.3 | 3.3 | 2.3 | 3.3 | 4.0 |
| Pteridium aquilinium | 6.3 | 2.5 | 2.0 | 3.5 | 4.5 | 3.8 | 2.5 | 4.5 | 5.3 | 2.5 | 4.3 | 2.5 | 4.5 | 2.0 | 5.5 |
| Monotropa hypopithys | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - |

Table B.2. (cont.)

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rank order | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 |
| DCA score | 31 | 31 | 85 | 88 | 88 | 90 | 95 | 100 | 101 | 109 | 113 | 114 | 120 | 126 | 130 |
| Species | Stand | | | | | | | | | | | | | | |
| | 75 | 76 | 39 | 45 | 68 | 73 | 15 | 18 | 70 | 8 | 67 | 62 | 16 | 47 | 77 |
| Hamamelis virginiana | 2.3 | 2.3 | 7.0 | 2.5 | 3.0 | 3.0 | 0.3 | 2.3 | 4.3 | 2.0 | 2.5 | 0.3 | 0.5 | 1.8 | 1.0 |
| Callicladium haldanianum | - | - | 0.3 | 0.5 | - | - | 0.9 | 0.8 | - | 1.5 | - | - | 0.3 | 0.5 | - |
| Smilicina stellata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Amelanchier spp. | 2.0 | 1.5 | 2.0 | 2.0 | 2.5 | 2.0 | 1.3 | 2.0 | 3.5 | 2.3 | 2.8 | 2.3 | 1.5 | 1.0 | 3.0 |
| Polytrichum commune | - | - | 0.3 | 0.3 | - | - | - | 0.3 | 0.5 | 3.3 | - | - | - | - | - |
| Vitis aestivalis | - | 0.9 | - | - | - | 0.8 | - | - | - | - | - | - | - | - | 0.8 |
| Carex pensylvanica | 7.0 | 2.9 | 2.8 | 3.0 | 4.5 | 3.5 | 3.3 | 6.8 | 3.8 | 2.3 | 6.0 | 3.5 | 1.5 | 2.3 | 5.5 |
| Pyrola rotundifolia | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - |
| Acer rubrum | 2.3 | 2.0 | 2.3 | 1.5 | 2.3 | 3.3 | 1.8 | 1.8 | 3.0 | 1.5 | 2.3 | 2.5 | 2.3 | 2.5 | 4.0 |
| Desmodium spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4.8 |
| Populus grandidentata | 0.5 | - | - | - | - | 0.3 | - | 0.5 | 1.0 | 0.3 | - | 0.3 | 1.0 | 0.3 | 1.0 |
| Apocynum androsaemefolium | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Smilacina racemosa | 1.3 | 0.5 | 0.3 | 0.3 | 1.0 | 0.8 | 0.3 | 1.3 | 1.0 | 0.5 | 1.0 | 0.3 | 0.3 | 1.0 | 2.0 |
| Aster macrophyllum | 0.5 | - | 0.3 | - | 1.0 | - | 0.3 | - | 1.0 | - | 0.8 | 0.8 | 0.3 | - | 0.8 |
| Trientalis borealis | - | - | 1.8 | - | 0.8 | - | 1.5 | - | - | 0.5 | - | 0.3 | 1.0 | - | - |
| Desmodium nudiflorum | - | - | - | 0.5 | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Monotropa uniflora | - | - | 0.3 | - | - | - | 0.3 | 0.5 | - | - | - | 0.8 | 0.3 | - | 0.3 |
| Oryzopsis asperifolia | 2.0 | - | 1.0 | 0.8 | 0.3 | 1.5 | - | 1.8 | 1.5 | 1.3 | - | 1.5 | 0.8 | 2.0 | 1.8 |
| Rubus allegheniensis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.3 |
| Rubus idaeus | - | - | - | - | - | - | - | - | - | - | - | 0.3 | - | - | - |
| Polygala paucifolia | 0.3 | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Prunus serotina | 3.8 | 0.5 | 1.0 | 1.5 | 2.3 | - | - | 2.0 | 1.8 | 1.0 | 2.8 | 1.3 | 1.0 | 0.3 | 3.5 |
| Viburnum acerifolium | 0.5 | 0.8 | 1.3 | 1.3 | - | 2.5 | 1.3 | 1.3 | 2.8 | 1.0 | 1.8 | 3.3 | 2.8 | 1.3 | 3.8 |
| Panicum latifolium | 1.0 | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 |
| Conopholis americana | - | - | - | 0.3 | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Quercus rubra | - | - | 1.0 | 0.5 | - | 1.5 | 0.8 | 2.0 | 2.5 | 0.3 | 2.0 | 1.0 | 0.8 | 0.5 | 1.8 |
| Populus tremuloides | - | - | - | - | 1.3 | - | 0.5 | 0.8 | - | - | 0.3 | 0.3 | - | - | - |
| Lonicera canadense | 0.5 | 0.3 | 0.5 | - | - | 0.3 | - | - | 0.3 | - | 0.5 | - | - | - | - |
| Mnium spp. | - | - | 0.3 | - | - | - | 0.8 | - | - | 0.5 | - | - | - | - | - |
| Prenanthes alba | - | - | - | - | - | - | - | - | - | 0.3 | - | 0.3 | - | - | - |
| Geranium maculatum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 |
| Hystrix patula | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Aralia nudicaulis | - | - | 0.3 | - | 0.5 | - | - | - | 3.5 | 0.3 | - | 0.5 | - | 1.0 | 2.8 |
| Solidago caesia | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.5 | 0.5 |
| Fagus grandifolia | - | 0.5 | 0.3 | 1.3 | - | 0.5 | - | 0.5 | - | 0.3 | 2.5 | - | 0.8 | - | - |
| Viola pubescens | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mitchella repens | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - |
| Maianthemum canadense | - | - | 1.3 | - | 1.0 | - | 0.3 | - | - | - | - | 0.8 | 1.3 | 0.3 | 0.5 |
| Panicum latifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cornus florida | - | - | - | 0.8 | - | - | - | 0.5 | - | - | - | - | - | - | - |
| Viola sororia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

Table B.2. (cont.)

| Rank order | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 81 | 81 | 85 | 88 | 88 | 90 | 95 | 100 | 101 | 109 | 113 | 114 | 120 | 126 | 130 |
| Species / Stand | 75 | 76 | 39 | 45 | 68 | 73 | 15 | 18 | 70 | 8 | 67 | 62 | 16 | 47 | 77 |
| Medeola virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Campanula rotundifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Fraxinus americana | - | - | - | - | - | - | - | 0.8 | - | - | 0.5 | - | - | - | 2.5 |
| Polygonatum biflorum | - | - | - | - | - | - | - | - | - | - | - | 0.3 | - | 0.8 | - |
| Galium boreale | 0.8 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Epifagus virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium lucidulum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ostrya virginiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Galium triflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium obscurum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Acer saccharum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carpinus caroliniana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Trillium grandiflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Sambucus pubens | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Viola canadense | - | - | - | - | - | - | - | - | - | - | - | 0.3 | - | - | - |
| Carex pedunculata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ribes cynosbati | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Actaea alba | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Osmorhiza claytonii | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex dewevana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hepatica acutiloba | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dryopteris spinulosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Tilia americana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Epipactis helleborine | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex plantaginea | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Adiantum pedatum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Uvularia perfoliata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Botrychium virginianum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Caulophyllum thalictroides | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mitella diphylla | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Allium tricoccum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dicentra canadensis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Tiarella cordifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

Table B.2. (cont.)

| Species | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rank order | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 |
| DCA score | 132 | 139 | 141 | 141 | 144 | 164 | 177 | 183 | 184 | 189 | 192 | 197 | 197 | 206 | 222 |
| Stand | 30 | 20 | 17 | 13 | 64 | 14 | 69 | 72 | 44 | 5 | 60 | 10 | 4 | 74 | 7 |
| Andropogon gerardii | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pinus banksiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Arctostaphylos uva-ursi | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium tristachyum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cladina spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Quercus ellipsoidalis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Rubus hispidus | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Rudbeckia spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cladonia spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lupinus perennis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Crataegus spp. | 1.0 | - | - | - | - | - | - | 2.3 | - | - | - | - | - | - | - |
| Comptonia peregrina | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pleurozium schreberi | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polytrichum juniperinum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Comandra umbellata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Deschampsia flexuosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hieracium venosum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Galium circaezans | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polytrichum piliferum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Chimaphila umbellata | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - |
| Melampyrum lineare | 0.5 | - | - | - | - | 0.5 | - | - | - | - | - | - | - | - | - |
| Dicranum polysetum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.2 |
| Pinus resinosa | - | - | - | - | 1.3 | - | - | - | - | - | - | - | - | - | - |
| Gaylussacia baccata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Thuidium recognitum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dicranum scoparium | - | 0.5 | - | 0.5 | - | - | - | - | - | - | - | - | - | - | - |
| Quercus velutina | 1.0 | - | - | 0.3 | - | - | - | 0.5 | 2.0 | - | - | 0.8 | - | - | - |
| Cypripedium acaule | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Rosa spp. | 0.3 | - | - | - | 0.5 | - | 0.3 | 1.0 | - | - | - | - | - | - | - |
| Pinus strobus | - | 0.5 | 0.5 | 1.3 | 3.0 | 1.3 | 0.3 | - | - | - | - | 4.5 | - | - | - |
| Leucobryum glaucum | 0.5 | 0.3 | - | 0.8 | - | 0.3 | - | 0.3 | - | - | - | - | - | - | - |
| Vaccinium angustifoliun | 2.8 | 2.3 | 1.3 | 0.8 | 2.8 | 1.0 | 0.8 | 2.0 | 0.3 | 0.8 | 1.8 | 0.8 | - | - | - |
| Quercus alba | 2.5 | 1.5 | 0.8 | 0.5 | 2.0 | 1.0 | 1.8 | 2.5 | - | - | 2.3 | 0.8 | 0.3 | 0.3 | - |
| Potentilla simplex | - | - | - | - | - | - | - | 1.3 | 0.5 | 0.5 | - | - | 0.2 | - | - |
| Eurhynchium hians | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Gaultheria procumbens | 2.3 | 1.5 | 0.8 | 1.5 | 1.0 | 1.0 | 1.0 | 2.0 | 0.3 | 0.7 | 2.0 | 1.8 | 0.2 | - | - |
| Epigaea repens | - | 0.3 | - | 0.3 | - | 0.3 | - | - | - | - | - | - | - | - | - |
| Pedicularis canadensis | - | - | - | - | - | 0.5 | - | - | - | - | - | - | - | - | - |
| Sassafras albidum | 2.8 | 2.3 | 1.8 | - | 3.0 | 1.8 | 2.0 | - | 3.0 | 2.5 | 2.3 | 1.8 | 1.8 | - | - |
| Pteridium aquilinium | 4.8 | 1.5 | 2.0 | 1.8 | 2.5 | 1.8 | 4.3 | 3.8 | 2.8 | 4.0 | 3.0 | 2.8 | 3.0 | 1.0 | 3.7 |
| Monotropa hypopithys | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - |

Table B.2. (cont.)

| Species | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rank order | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 |
| DCA score | 132 | 139 | 141 | 141 | 144 | 164 | 177 | 183 | 184 | 189 | 192 | 197 | 197 | 206 | 222 |
| Stand | 80 | 20 | 17 | 13 | 64 | 14 | 69 | 72 | 44 | 5 | 60 | 10 | 4 | 74 | 7 |
| Hamamelis virginiana | 1.3 | 2.5 | 2.0 | - | 4.3 | 2.9 | 3.3 | 2.5 | 1.0 | 3.3 | 2.0 | 2.3 | 2.3 | - | - |
| Callicladium haldanianum | - | 0.3 | 0.8 | 0.5 | - | 0.3 | - | - | 0.5 | 0.3 | - | 1.0 | 0.3 | - | 0.3 |
| Smilicina stellata | - | - | - | - | - | 0.3 | - | - | - | 0.2 | - | - | - | - | - |
| Amelanchier spp. | 2.5 | 1.5 | 1.3 | 1.0 | 2.3 | 1.8 | 3.0 | 2.3 | 0.5 | 1.2 | 3.5 | - | 0.3 | 0.5 | 0.7 |
| Polytrichum commune | - | 0.3 | - | 0.3 | - | 0.3 | - | - | 0.3 | - | - | - | - | - | 0.7 |
| Vitis aestivalis | - | - | - | - | - | - | - | - | 0.5 | 0.2 | - | - | 1.2 | - | - |
| Carex pensylvanica | 5.3 | 1.3 | 3.3 | 1.8 | 3.3 | 1.0 | 4.5 | 4.3 | 2.5 | 1.5 | 2.0 | 2.0 | 0.3 | 3.0 | 1.0 |
| Pyrola rotundifolia | - | - | - | - | - | - | 0.3 | - | - | - | 0.5 | - | - | - | - |
| Acer rubrum | 2.8 | 1.0 | 2.0 | 1.0 | 2.0 | 2.3 | 2.8 | 4.9 | 5.0 | 4.8 | 4.5 | 2.0 | 2.8 | 2.5 | 1.0 |
| Desmodium spp. | 0.5 | - | - | - | 3.0 | - | 0.8 | 0.5 | - | - | - | - | - | 0.8 | - |
| Populus grandidentata | - | 0.3 | 0.8 | 0.8 | - | 0.3 | - | - | 0.8 | 0.2 | 0.5 | - | 0.5 | - | - |
| Apocynum androsaemefolium | - | - | - | - | - | - | - | - | 0.3 | - | - | - | 0.2 | - | - |
| Smilacina racemosa | 1.3 | 1.0 | 1.0 | 0.5 | 1.3 | 0.0 | 1.3 | 1.0 | 1.3 | 1.5 | 1.5 | 1.3 | 1.0 | 1.3 | - |
| Aster macrophyllum | 0.8 | 0.0 | 0.3 | - | 1.3 | 1.3 | 1.5 | 0.9 | 0.5 | 0.2 | 1.3 | 1.0 | - | 0.3 | - |
| Trientalis borealis | - | 1.0 | - | 0.5 | - | 1.0 | 0.8 | 0.8 | - | 0.5 | 2.5 | 1.5 | 0.5 | - | 0.2 |
| Desmodium nudiflorum | - | - | - | - | - | - | - | - | 2.8 | 2.3 | - | 0.5 | 0.8 | - | - |
| Monotropa uniflora | 0.5 | 0.5 | 0.3 | - | 0.3 | 0.3 | - | - | - | - | 0.3 | - | - | 0.5 | - |
| Oryzopsis asperifolia | 2.0 | 1.8 | 1.5 | 0.8 | 1.8 | 1.0 | 2.0 | 2.0 | 2.3 | 1.5 | 0.5 | 2.0 | 0.8 | 1.5 | 0.8 |
| Rubus allegheniensis | 0.5 | - | - | - | - | - | - | 1.8 | 2.5 | 2.3 | - | 0.3 | 0.2 | - | - |
| Rubus idaeus | - | - | - | - | - | - | - | 0.3 | - | - | 0.5 | - | - | 0.5 | - |
| Polygala paucifolia | - | 0.3 | - | 0.3 | - | 0.8 | - | - | - | - | 0.0 | - | - | - | - |
| Prunus serotina | 3.5 | 0.8 | 1.3 | - | 3.0 | 0.8 | 3.3 | 4.3 | 4.0 | 4.3 | 4.5 | 4.0 | 2.3 | 3.3 | 2.3 |
| Viburnum acerifolium | 2.3 | 0.8 | 0.3 | 0.8 | 4.3 | 4.0 | 3.3 | 4.0 | 3.5 | 3.5 | 4.0 | 1.5 | 2.0 | 2.8 | 0.2 |
| Panicum latifolium | - | 0.3 | - | - | - | - | - | 0.3 | 0.5 | 0.5 | - | 0.3 | - | - | 0.2 |
| Conopholis americana | - | 0.5 | 1.3 | 0.3 | - | - | - | - | 1.3 | 0.5 | 0.8 | - | 1.2 | - | - |
| Quercus rubra | 2.3 | 0.8 | - | 0.8 | 1.0 | - | 1.5 | 1.5 | 1.0 | 1.0 | 1.0 | - | 0.3 | 2.0 | 1.3 |
| Populus tremuloides | - | 0.3 | - | - | - | - | 0.3 | - | - | 0.2 | 0.3 | - | - | - | - |
| Lonicera canadense | - | - | - | - | - | 0.3 | 0.5 | 0.5 | - | - | 1.3 | - | - | - | - |
| Mnium spp. | - | - | - | - | - | 1.3 | - | - | - | - | - | 0.3 | - | - | 0.2 |
| Prenanthes alba | - | - | - | - | - | - | 0.5 | - | 0.3 | 0.2 | 0.5 | 1.3 | - | - | - |
| Geranium maculatum | - | - | - | - | - | - | 0.5 | 0.5 | 0.5 | 0.2 | - | 1.3 | - | - | - |
| Hystrix patula | - | - | - | - | - | - | - | - | 0.5 | - | - | - | - | - | - |
| Aralia nudicaulis | 0.5 | 0.3 | - | - | 1.0 | 2.0 | 2.0 | 1.5 | - | 0.5 | 1.3 | 0.8 | 0.3 | 0.3 | - |
| Solidago caesia | 0.3 | - | 0.3 | 0.3 | 0.3 | - | - | - | - | - | - | 0.3 | 0.2 | 0.8 | - |
| Fagus grandifolia | 1.5 | - | 1.0 | 2.0 | - | 1.3 | 2.3 | - | 1.8 | 0.7 | - | - | 1.2 | 3.8 | 1.0 |
| Viola pubescens | - | - | - | - | - | 0.8 | - | 2.0 | - | 0.8 | - | 1.3 | 0.7 | - | - |
| Mitchella repens | - | 0.5 | - | 0.5 | - | - | - | 1.3 | 0.5 | 0.2 | 0.8 | 2.0 | 0.3 | - | 0.3 |
| Maianthemum canadense | 1.3 | 1.0 | 1.3 | 0.8 | - | 0.5 | 1.0 | 2.0 | 0.3 | - | 2.0 | 1.8 | 1.0 | 1.0 | 1.3 |
| Panicum latifolia | - | - | - | - | - | - | - | - | 0.5 | - | - | - | - | - | - |
| Cornus florida | - | - | - | - | 5.8 | - | - | 3.5 | 6.0 | 1.0 | - | - | 6.3 | - | - |
| Viola sororia | - | - | - | - | - | 0.5 | - | - | - | - | - | 0.8 | - | - | 0.2 |

Table B.2. (cont.)

| Species | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 132 | 139 | 141 | 141 | 144 | 164 | 177 | 183 | 184 | 189 | 192 | 197 | 197 | 206 | 222 |
| Stand | 80 | 28 | 17 | 13 | 64 | 14 | 69 | 72 | 44 | 5 | 60 | 10 | 4 | 74 | 7 |
| Medeola virginiana | - | - | - | - | - | 1.0 | - | 1.5 | - | - | - | 0.3 | - | - | - |
| Campanula rotundifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Fraxinus americana | - | - | 0.3 | - | - | 0.8 | 3.0 | - | 0.3 | 1.0 | - | 1.5 | 1.2 | 3.0 | 1.5 |
| Polygonatum biflorum | - | 0.5 | - | 0.3 | - | 1.3 | 0.3 | - | - | 0.7 | - | - | 0.8 | 1.8 | 0.8 |
| Galium boreale | - | - | - | - | - | - | - | - | 0.5 | 0.3 | - | - | 0.7 | 0.3 | - |
| Epifagus virginiana | - | - | - | 0.5 | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium lucidulum | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - |
| Ostrya virginiana | 1.3 | - | - | - | - | 0.3 | 2.5 | 0.3 | - | 0.5 | 0.5 | - | - | 3.0 | 1.2 |
| Galium triflorum | - | - | - | - | 0.8 | - | - | 2.0 | 0.8 | 0.2 | 0.5 | 1.8 | 0.3 | - | - |
| Lycopodium obscurum | - | - | - | - | - | - | - | - | - | - | 0.5 | - | - | - | - |
| Acer saccharum | - | - | - | - | - | 0.3 | 0.5 | 0.5 | - | - | 0.5 | - | - | 2.8 | 1.8 |
| Carpinus caroliniana | - | - | - | - | - | - | - | 0.5 | - | - | - | - | 0.3 | - | - |
| Trillium grandiflorum | - | - | - | - | - | - | - | - | - | 0.2 | 0.3 | - | 0.2 | - | 0.5 |
| Sambucus pubens | - | - | - | - | - | 0.3 | - | - | - | - | - | - | 0.3 | - | - |
| Viola canadense | - | - | - | - | 0.3 | - | - | - | 1.0 | - | - | 0.3 | - | - | - |
| Carex pedunculata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.5 |
| Ribes cynosbati | - | - | - | - | - | - | - | 3.0 | - | - | 0.8 | 0.5 | - | - | - |
| Actaea alba | - | - | - | - | - | - | - | - | 0.3 | - | - | 0.3 | - | - | - |
| Osmorhiza claytonii | - | - | - | - | - | - | 0.3 | - | - | - | - | 0.8 | - | - | - |
| Carex deweyana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hepatica acutiloba | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dryopteris spinulosa | - | - | - | - | - | - | - | 0.5 | - | - | - | - | - | - | - |
| Tilia americana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Epipactis helleborine | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex plantaginea | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 |
| Adiantum pedatum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Uvularia perfoliata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Botrychium virginianum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Caulophyllum thalictroides | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mitella diphylla | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Allium tricoccum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dicentra canadensis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Tiarella cordifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

Table 8.2. (cont.)

| Rank order | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 234 | 244 | 245 | 249 | 265 | 282 | 282 | 284 | 285 | 295 | 295 | 297 | 305 | 321 | 321 |
| Species | Stand | | | | | | | | | | | | | | |
| | 2 | 21 | 35 | 31 | 41 | 48 | 56 | 57 | 23 | 32 | 26 | 42 | 25 | 6 | 36 |
| Andropogon gerardii | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pinus banksiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Arctostaphylos uva-ursi | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lycopodium tristachyum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cladina spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Quercus ellipsoidalis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Rubus hispidus | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Rudbeckia spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cladonia spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lupinus perennis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Crataegus spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Comptonia peregrina | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pleurozium schreberi | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polytrichum juniperinum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Comandra umbellata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Deschampsia flexuosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hieracium venosum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Galium circaezans | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polytrichum piliferum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Chimaphila umbellata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Melampyrum lineare | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dicranum polysetum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pinus resinosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Gaylussacia baccata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Thuidium recognitum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dicranum scoparium | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Quercus velutina | 0.2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cypripedium acaule | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Rosa spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pinus strobus | 0.2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Leucobryum glaucum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Vaccinium angustifolium | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Quercus alba | - | - | - | - | - | - | - | - | - | 0.5 | - | - | - | - | - |
| Potentilla simplex | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Eurhynchium hians | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Gaultheria procumbens | 0.2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Epigaea repens | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | 0.5 |
| Pedicularis canadensis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Sassafras albidum | 0.2 | - | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - |
| Pteridium aquilinium | 1.3 | 0.5 | 0.8 | - | - | 1.0 | 0.5 | - | - | - | - | - | - | - | - |
| Monotropa hypopithys | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 | - | - |

Table B.2. (cont.)

| Rank order | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 234 | 244 | 245 | 249 | 265 | 282 | 282 | 284 | 285 | 295 | 295 | 297 | 305 | 321 | 321 |
| Species | Stand | | | | | | | | | | | | | | |
| | 2 | 21 | 35 | 31 | 41 | 40 | 56 | 57 | 23 | 32 | 26 | 42 | 25 | 6 | 36 |
| Hamamelis virginiana | 0.3 | - | - | - | - | - | - | - | - | 0.5 | - | - | - | - | - |
| Callicladium haldanianum | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - |
| Smilicina stellata | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Amelanchier spp. | 0.2 | 0.3 | 0.8 | 0.5 | - | 1.0 | - | - | 0.3 | - | 0.3 | 0.3 | - | - | - |
| Polytrichum commune | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 | - | - |
| Vitis aestivalis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Carex pensylvanica | - | 1.0 | - | 1.8 | - | - | - | - | 1.3 | 3.5 | 0.8 | - | 2.0 | 0.5 | - |
| Pyrola rotundifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Acer rubrum | 0.8 | 0.3 | 1.8 | 1.0 | 1.5 | 0.5 | 1.8 | 0.3 | - | 1.0 | 0.5 | 1.5 | - | - | - |
| Desmodium spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Populus grandidentata | 0.2 | 0.3 | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - |
| Apocynum androsaemefolium | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.2 | - |
| Smilacina racemosa | - | - | - | - | 0.5 | - | 0.3 | - | - | - | - | 0.8 | - | 2.0 | 0.5 |
| Aster macrophyllum | 0.7 | - | - | - | 0.3 | - | - | - | - | 0.3 | - | - | - | - | - |
| Trientalis borealis | 0.5 | - | 1.8 | - | - | - | - | - | - | - | - | - | - | - | - |
| Desmodium nudiflorum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Monotropa uniflora | - | 0.3 | 0.8 | 0.5 | 0.3 | - | - | 0.3 | - | - | - | - | 0.3 | - | 0.3 |
| Oryzopsis asperifolia | 3.0 | 0.5 | - | 0.3 | 0.5 | 1.3 | 0.5 | 2.5 | 0.5 | 1.3 | - | - | 0.3 | - | - |
| Rubus allegheniensis | - | - | - | - | - | - | - | - | - | 0.3 | 0.5 | - | - | 0.2 | - |
| Rubus idaeus | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polygala paucifolia | 0.3 | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - |
| Prunus serotina | 2.2 | 1.5 | 2.0 | 1.0 | 2.0 | 1.8 | 2.5 | 2.5 | 1.8 | 3.0 | 1.8 | 2.0 | 2.0 | 0.7 | 2.0 |
| Viburnum acerifolium | 1.5 | 1.8 | 2.0 | - | - | - | - | 2.0 | 0.3 | 2.3 | - | - | - | 0.3 | - |
| Panicum latifolium | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Conopholis americana | - | - | 0.3 | 1.0 | - | - | - | - | - | - | - | - | - | - | - |
| Quercus rubra | - | 0.3 | - | 0.8 | 0.8 | 0.8 | 0.3 | 0.5 | - | 1.3 | 0.8 | - | 0.5 | 0.7 | 0.8 |
| Populus tremuloides | 0.3 | 0.8 | - | - | 0.3 | 0.5 | - | - | 0.3 | 0.3 | - | - | - | - | - |
| Lonicera canadense | 0.2 | - | 0.3 | - | 0.5 | 0.3 | 0.5 | 0.3 | - | - | 0.5 | 0.3 | 0.3 | 0.5 | - |
| Mnium spp. | 0.8 | - | - | - | - | - | - | - | - | 3.5 | - | - | - | - | - |
| Prenanthes alba | 1.7 | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - |
| Geranium maculatum | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.2 | - |
| Hystrix patula | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - |
| Aralia nudicaulis | 1.0 | 0.5 | 0.5 | - | 0.5 | - | 1.3 | 0.3 | - | - | - | - | - | 1.8 | 0.5 |
| Solidago caesia | 3.8 | 0.3 | - | 0.5 | - | - | - | 2.3 | - | 1.0 | - | - | - | - | - |
| Fagus grandifolia | 0.3 | 3.5 | 1.8 | 0.5 | 2.3 | 3.0 | 3.3 | - | 4.8 | 1.8 | 1.3 | 2.0 | 2.5 | - | 2.0 |
| Viola pubescens | 1.0 | - | - | - | - | - | - | - | - | - | - | - | - | 1.3 | - |
| Mitchella repens | 0.5 | 0.5 | 0.8 | 0.5 | - | 0.5 | 0.5 | - | - | 0.5 | 0.3 | 0.8 | - | - | - |
| Maianthemum canadense | 2.0 | 1.0 | 1.5 | 1.0 | 0.5 | 0.5 | 2.3 | 2.3 | 1.5 | 1.3 | 1.5 | 1.0 | 0.5 | 2.0 | 2.3 |
| Panicum latifolia | - | - | - | - | - | - | 0.5 | - | - | 0.5 | - | - | - | - | 0.5 |
| Cornus florida | - | - | - | - | - | - | - | - | 0.3 | - | - | - | - | 1.2 | - |
| Viola sororia | 0.2 | - | - | - | - | - | - | - | - | - | - | - | - | 1.7 | - |

Table B.2. (cont.)

| Rank order | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DCA score | 234 | 244 | 245 | 249 | 265 | 282 | 282 | 284 | 285 | 295 | 295 | 297 | 305 | 321 | 321 |
| Species | ---------- | | | | | | | Stand | | | | | | | ---------- |
| | 2 | 21 | 35 | 31 | 41 | 40 | 56 | 57 | 23 | 32 | 26 | 42 | 25 | 6 | 36 |
| Medeola virginiana | - | 0.5 | - | - | - | - | - | - | - | 0.3 | - | 1.0 | - | - | - |
| Campanula rotundifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Fraxinus americana | 1.2 | 1.0 | 1.8 | - | 1.8 | 2.3 | 1.8 | 2.0 | 1.5 | 2.5 | 2.0 | 0.8 | 1.8 | 3.3 | 1.0 |
| Polygonatum biflorum | 0.2 | 0.3 | 1.3 | 0.3 | 0.5 | 0.3 | 0.3 | 2.3 | 0.3 | 0.5 | - | 0.5 | 0.8 | 1.7 | 1.5 |
| Galium boreale | 0.5 | - | 0.3 | - | - | 0.3 | - | 0.5 | - | 1.0 | - | - | - | 1.2 | - |
| Epifagus virginiana | - | 0.3 | - | - | 0.3 | - | 0.5 | - | 0.5 | - | - | 1.3 | 0.3 | - | - |
| Lycopodium lucidulum | - | 0.5 | - | - | - | - | 0.3 | - | 0.5 | - | - | 0.5 | 0.5 | - | - |
| Ostrya virginiana | 2.7 | 0.5 | 2.3 | 1.5 | 2.5 | 5.3 | 3.0 | 1.8 | 1.0 | 5.0 | 1.5 | 0.5 | 2.0 | 1.8 | 0.8 |
| Galium triflorum | - | - | - | - | - | 0.3 | - | - | - | 0.3 | 0.5 | - | 0.3 | 1.8 | - |
| Lycopodium obscurum | - | 0.5 | - | - | - | 0.3 | 2.0 | - | 1.5 | - | - | 1.3 | 0.5 | - | - |
| Acer saccharum | 1.3 | 2.5 | 2.5 | 1.0 | 3.5 | 2.0 | 3.0 | 3.0 | 3.5 | 2.5 | 2.3 | 2.8 | 3.5 | 3.5 | 5.0 |
| Carpinus caroliniana | 0.2 | - | - | - | - | - | - | - | - | 1.3 | - | - | - | 1.2 | - |
| Trillium grandiflorum | 1.2 | - | 0.3 | - | - | - | - | 0.3 | 0.3 | - | 0.5 | - | 0.5 | 2.0 | - |
| Sambucus pubens | - | - | - | - | - | - | - | - | - | - | 0.5 | 0.3 | - | - | - |
| Viola canadense | - | - | - | 1.0 | - | 0.3 | - | - | - | 1.5 | 0.8 | - | 0.3 | 1.3 | 0.5 |
| Carex pedunculata | - | - | - | - | 0.8 | - | 1.5 | 0.5 | - | 0.3 | 0.3 | 0.5 | 0.5 | - | - |
| Ribes cynosbati | 0.5 | - | 0.3 | - | - | - | - | - | 0.5 | 0.3 | 0.8 | - | 0.3 | 2.0 | - |
| Actaea alba | 1.2 | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 | - |
| Osmorhiza claytonii | 0.3 | - | - | - | - | - | - | - | 0.3 | 1.3 | 1.5 | - | 0.5 | 3.8 | 0.5 |
| Carex deweyana | - | - | - | 0.8 | 0.8 | 0.8 | 1.0 | 0.5 | - | 0.3 | - | 0.8 | 0.3 | 1.3 | 0.8 |
| Hepatica acutiloba | 0.3 | - | - | 0.3 | - | - | - | - | - | 0.5 | - | - | - | - | 0.3 |
| Dryopteris spinulosa | - | - | - | - | - | - | 0.3 | - | 0.8 | - | - | 2.5 | - | - | 1.8 |
| Tilia americana | 0.3 | - | - | 0.3 | - | - | 0.3 | - | - | 1.5 | 0.3 | - | 0.8 | - | - |
| Epipactis helleborine | - | - | - | 0.5 | - | - | - | 0.5 | - | - | - | - | 0.3 | - | - |
| Carex plantaginea | - | 0.5 | - | - | - | - | - | 0.5 | - | 1.5 | 0.5 | - | - | 1.7 | 0.3 |
| Adiantum pedatum | 1.0 | - | - | - | - | - | - | - | - | 0.3 | - | - | - | 0.5 | - |
| Uvularia perfoliata | 1.3 | - | - | - | - | - | - | - | - | 0.3 | - | - | - | - | 0.3 |
| Botrychium virginianum | 0.3 | - | - | - | - | - | - | - | - | - | - | - | 0.3 | 1.0 | - |
| Caulophyllum thalictroides | - | - | - | - | - | - | - | - | - | 0.3 | - | - | - | 1.2 | 0.3 |
| Mitella diphylla | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.7 | 0.3 |
| Allium tricoccum | - | - | - | - | - | - | - | - | - | 0.5 | - | - | - | 3.3 | - |
| Dicentra canadensis | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 | - | - |
| Tiarella cordifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.7 | - |

Table B.2. (cont.)

| Rank order | 76 | 77 | 78 | 79 | 80 |
|---|---|---|---|---|---|
| DCA score | 329 | 335 | 336 | 347 | 365 |
| Species | -----Stand | | | | |
| | 24 | 27 | 43 | 22 | 37 |
| Andropogon gerardii | - | - | - | - | - |
| Pinus banksiana | - | - | - | - | - |
| Arctostaphylos uva-ursi | - | - | - | - | - |
| Lycopodium tristachyum | - | - | - | - | - |
| Cladina spp. | - | - | - | - | - |
| Quercus ellipsoidalis | - | - | - | - | - |
| Rubus hispidus | - | - | - | - | - |
| Rudbeckia spp. | - | - | - | - | - |
| Cladonia spp. | - | - | - | - | - |
| Lupinus perennis | - | - | - | - | - |
| Crataegus spp. | - | - | - | - | - |
| Comptonia peregrina | - | - | - | - | - |
| Pleurozium schreberi | - | - | - | - | - |
| Polytrichum juniperinum | - | - | - | - | - |
| Comandra umbellata | - | - | - | - | - |
| Deschampsia flexuosa | - | - | - | - | - |
| Hieracium venosum | - | - | - | - | - |
| Galium circaezans | - | - | - | - | - |
| Polytrichum piliferum | - | - | - | - | - |
| Chimaphila umbellata | - | - | - | - | - |
| Melampyrum lineare | - | - | - | - | - |
| Dicranum polysetum | - | - | - | - | - |
| Pinus resinosa | - | - | - | - | - |
| Gaylussacia baccata | - | - | - | - | - |
| Thuidium recognitum | - | - | - | - | - |
| Dicranum scoparium | - | - | - | - | - |
| Quercus velutina | - | - | - | - | - |
| Cypripedium acaule | - | - | - | - | - |
| Rosa spp. | - | - | - | - | - |
| Pinus strobus | - | - | - | - | - |
| Leucobryum glaucum | - | - | - | - | - |
| Vaccinium angustifolium | - | - | - | - | - |
| Quercus alba | - | - | - | - | - |
| Potentilla simplex | - | - | - | - | - |
| Eurhynchium hians | - | - | - | - | - |
| Gaultheria procumbens | - | - | - | - | - |
| Epigaea repens | - | - | - | - | - |
| Pedicularis canadensis | - | - | - | - | - |
| Sassafras albidum | - | - | - | - | - |
| Pteridium aquilinium | - | - | - | - | - |
| Monotropa hypopithys | - | - | - | - | - |

Table 8.2. (cont.)

| Species | Rank order 76 | 77 | 78 | 79 | 80 |
|---|---|---|---|---|---|
| | DCA score 329 | 335 | 336 | 347 | 365 |
| | Stand 24 | 27 | 43 | 22 | 37 |
| Hamamelis virginiana | - | - | - | - | - |
| Callicladium haldanianum | - | - | 0.3 | - | - |
| Smilicina stellata | - | - | - | - | - |
| Amelanchier spp. | - | - | 1.3 | - | - |
| Polytrichum commune | - | - | - | - | - |
| Vitis aestivalis | - | - | - | - | - |
| Carex pensylvanica | 2.0 | 1.5 | - | - | - |
| Pyrola rotundifolia | - | - | - | - | - |
| Acer rubrum | - | - | - | 0.3 | - |
| Desmodium spp. | - | - | - | - | - |
| Populus grandidentata | 0.3 | - | - | - | - |
| Apocynum androsaemefolium | - | - | - | - | - |
| Smilacina racemosa | - | 0.3 | 1.5 | 2.0 | 1.0 |
| Aster macrophyllum | - | - | 0.5 | - | - |
| Trientalis borealis | - | - | - | - | - |
| Desmodium nudiflorum | - | - | - | - | - |
| Monotropa uniflora | - | - | - | - | - |
| Oryzopsis asperifolia | 0.3 | - | - | - | - |
| Rubus allegheniensis | - | 0.5 | - | - | - |
| Rubus idaeus | - | - | - | - | - |
| Polygala paucifolia | - | - | - | - | - |
| Prunus serotina | 2.0 | 2.5 | 2.5 | 1.5 | 1.5 |
| Viburnum acerifolium | 2.0 | 0.5 | - | 0.8 | - |
| Panicum latifolium | 1.5 | - | - | - | - |
| Conopholis americana | - | - | - | - | - |
| Quercus rubra | 1.0 | 0.8 | - | 0.3 | - |
| Populus tremuloides | - | - | - | - | - |
| Lonicera canadense | 1.5 | 2.0 | 0.3 | - | - |
| Mnium spp. | - | 0.8 | 0.3 | - | - |
| Prenanthes alba | 0.3 | - | - | - | - |
| Geranium maculatum | - | - | - | - | - |
| Hystrix patula | 0.5 | - | - | 0.5 | - |
| Aralia nudicaulis | 2.0 | 1.0 | 0.3 | 2.0 | - |
| Solidago caesia | - | - | 0.5 | 2.5 | - |
| Fagus grandifolia | 0.3 | 0.5 | 0.3 | 1.0 | 0.3 |
| Viola pubescens | - | - | - | - | - |
| Mitchella repens | - | - | 0.8 | - | - |
| Maianthemum canadense | 2.0 | 1.0 | 2.0 | 0.5 | 2.0 |
| Panicum latifolia | - | - | 2.3 | - | 0.5 |
| Cornus florida | 0.5 | 1.0 | 0.3 | - | - |
| Viola sororia | - | - | - | - | - |

Table B.2. (cont.)

| Species | Rank order | 76 | 77 | 78 | 79 | 80 |
|---|---|---|---|---|---|---|
| | DCA score | 329 | 335 | 336 | 347 | 365 |
| | -----Stand | | | | | |
| | | 24 | 27 | 43 | 22 | 37 |
| Medeola virginiana | | - | - | - | - | - |
| Campanula rotundifolia | | 0.3 | - | 0.3 | 0.8 | 0.3 |
| Fraxinus americana | | 3.3 | 2.5 | 2.0 | 2.5 | 1.5 |
| Polygonatum biflorum | | 0.8 | 0.3 | 1.5 | 2.0 | 0.8 |
| Galium boreale | | 1.3 | 0.8 | - | 1.5 | - |
| Epifagus virginiana | | - | - | - | - | - |
| Lycopodium lucidulum | | - | - | - | - | - |
| Ostrya virginiana | | 3.0 | 3.0 | 2.5 | 3.0 | 1.8 |
| Galium triflorum | | 2.3 | 1.8 | 1.0 | 0.3 | 0.5 |
| Lycopodium obscurum | | - | - | - | - | - |
| Acer saccharum | | 3.5 | 3.8 | 3.3 | 4.0 | 6.8 |
| Carpinus caroliniana | | 0.3 | 0.5 | - | - | - |
| Trillium grandiflorum | | 2.0 | 1.3 | 0.8 | 1.3 | - |
| Sambucus pubens | | - | 1.0 | - | - | 0.5 |
| Viola canadense | | 2.0 | 2.3 | 0.3 | 1.3 | 1.3 |
| Carex pedunculata | | 0.3 | - | - | - | - |
| Ribes cynosbati | | 1.5 | 1.0 | 0.5 | 1.0 | 0.3 |
| Actaea alba | | 0.3 | - | 0.3 | 0.3 | 0.5 |
| Osmorhiza claytonii | | 2.8 | 4.3 | 1.5 | 3.0 | 4.0 |
| Carex deweyana | | - | - | 1.6 | 0.3 | 0.3 |
| Hepatica acutiloba | | 1.3 | 0.3 | - | 0.5 | - |
| Dryopteris spinulosa | | 0.3 | 1.3 | 0.3 | - | 0.8 |
| Tilia americana | | 0.8 | 1.0 | 0.5 | 1.0 | 0.3 |
| Epipactis helleborine | | 0.3 | - | 0.3 | 0.8 | - |
| Carex plantaginea | | 1.8 | 1.0 | 0.8 | 1.8 | 0.3 |
| Adiantum pedatum | | 1.3 | - | - | 0.3 | 0.5 |
| Uvularia perfoliata | | - | 1.5 | 1.0 | 2.0 | 2.0 |
| Botrychium virginianum | | 1.0 | 1.3 | 1.0 | 0.8 | 0.3 |
| Caulophyllum thalictroides | | 2.0 | 0.5 | 0.5 | 1.3 | 0.5 |
| Mitella diphylla | | 1.5 | 2.0 | 1.0 | 2.0 | - |
| Allium tricoccum | | 2.5 | 0.5 | 0.5 | 2.0 | 0.3 |
| Dicentra canadensis | | 0.5 | 1.0 | 0.3 | 0.3 | 1.5 |
| Tiarella cordifolia | | 2.0 | 1.5 | 0.3 | 1.3 | 0.3 |

## APPENDIX C

Table C.1. Physical and chemical soil properties, summarized by stand.

| | 0 - 10 cm | | 45 - 55 cm depth | | | | 95 - 105 cm depth | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| STAND | % Organic Carbon | pH | % coarse and medium sand | % very fine and fine sand | % silt + clay | mean weighted particle diameter | % coarse and medium sand | % very fine and fine sand | % silt + clay | mean weighted particle diameter |
| 1 | 1.89 | 4.00 | | | | | | | | |
| 2 | 2.90 | 4.86 | 55.1 | 19.6 | 14.7 | 0.279 | 13.0 | 41.0 | 20.7 | 0.158 |
| 3 | 2.46 | 3.93 | 73.4 | 4.1 | 3.6 | 0.348 | 71.1 | 6.7 | 6.4 | 0.332 |
| 4 | 2.69 | 4.13 | 29.0 | 38.5 | 26.7 | 0.203 | 54.0 | 14.0 | 12.5 | 0.309 |
| 5 | 2.29 | 4.17 | 40.7 | 22.2 | 18.1 | 0.278 | 34.4 | 42.1 | 37.2 | 0.201 |
| 6 | 2.60 | 5.53 | 42.4 | 18.7 | 13.3 | 0.251 | 22.5 | 28.3 | 15.1 | 0.199 |
| 7 | 2.73 | 4.20 | 56.0 | 6.0 | 4.9 | 0.280 | 63.2 | 2.0 | 1.4 | 0.304 |
| 8 | 1.76 | 3.87 | 57.7 | 6.9 | 4.9 | 0.300 | | | | |
| 9 | 2.79 | 3.84 | 79.4 | 6.4 | 6.1 | 0.366 | 80.4 | 0.2 | 0.1 | 0.352 |
| 10 | 2.93 | 4.46 | 15.0 | 61.2 | 51.9 | 0.127 | 23.7 | 41.3 | 24.7 | 0.182 |
| 11 | 2.15 | | 56.1 | 2.0 | 1.0 | 0.289 | 73.1 | 0.7 | 0.6 | 0.337 |
| 12 | 1.76 | 4.00 | 59.9 | 6.2 | 5.5 | 0.319 | 57.0 | 5.6 | 4.3 | 0.313 |
| 13 | 2.04 | 3.93 | 60.6 | 6.3 | 5.6 | 0.299 | 59.1 | 4.6 | 2.3 | 0.318 |
| 14 | 2.23 | 4.42 | 50.4 | 9.9 | 7.0 | 0.288 | 56.8 | 5.1 | 3.4 | 0.306 |
| 15 | 2.39 | 3.89 | 72.5 | 5.7 | 5.2 | 0.361 | 79.7 | 1.4 | 1.3 | 0.367 |
| 16 | 2.26 | 3.92 | 54.8 | 19.7 | 16.2 | 0.294 | 41.3 | 30.1 | 15.7 | 0.253 |
| 17 | 1.93 | 4.20 | | | | | 24.5 | 42.2 | 24.7 | 0.184 |
| 18 | 2.35 | 4.13 | 78.5 | 4.1 | 3.9 | 0.390 | 67.2 | 5.3 | 4.4 | 0.359 |
| 19 | 2.84 | 3.76 | 77.4 | 4.0 | 3.7 | 0.389 | 76.2 | 2.9 | 2.8 | 0.368 |
| 20 | 2.41 | 4.07 | 88.1 | 3.8 | 3.6 | 0.474 | 88.3 | 3.3 | 3.0 | 0.477 |
| 21 | 1.62 | 4.18 | 58.1 | 5.8 | 4.2 | 0.311 | 28.5 | 14.5 | 5.5 | 0.226 |
| 22 | 6.41 | 5.76 | 78.9 | 6.9 | 6.3 | 0.381 | 76.0 | 3.9 | 3.7 | 0.375 |
| 23 | 1.69 | 3.33 | 57.8 | 2.7 | 1.2 | 0.292 | 82.2 | 0.8 | 0.8 | 0.389 |
| 24 | 4.12 | 5.48 | 33.3 | 16.2 | 6.8 | 0.234 | 28.8 | 13.5 | 9.1 | 0.225 |
| 25 | 2.49 | 4.25 | 45.7 | 8.2 | 4.3 | 0.272 | 26.7 | 8.1 | 3.9 | 0.223 |
| 26 | 2.05 | 4.56 | 48.4 | 10.2 | 7.2 | 0.277 | 63.4 | 3.0 | 2.0 | 0.334 |
| 27 | 3.24 | 5.58 | 62.3 | 8.2 | 6.6 | 0.319 | 53.3 | 25.6 | 24.4 | 0.256 |
| 28 | 1.90 | 3.74 | 75.7 | 5.0 | 5.1 | 0.399 | 90.6 | 2.3 | 2.3 | 0.439 |
| 29 | | 4.14 | 50.5 | 18.3 | 7.4 | 0.285 | 69.1 | 4.8 | 4.2 | 0.352 |
| 30 | 2.00 | 4.12 | 87.3 | 3.6 | 3.5 | 0.403 | 90.8 | 1.1 | 1.0 | 0.378 |
| 31 | 2.26 | 4.53 | 52.4 | 17.0 | 8.8 | 0.278 | 54.7 | 10.3 | 7.1 | 0.306 |
| 32 | 2.91 | 4.59 | | | | | 55.6 | 9.6 | 5.1 | 0.316 |
| 33 | 1.86 | 3.57 | 65.2 | 2.4 | 1.0 | 0.312 | 52.2 | 3.6 | 2.0 | 0.283 |

Table C.1. (cont.)

| STAND | 0 - 10 cm % Organic Carbon | 0 - 10 cm pH | 45 - 55 cm depth % coarse and medium sand | 45 - 55 cm depth % very fine and fine sand | 45 - 55 cm depth % silt + clay | 45 - 55 cm depth mean weighted particle diameter | 95 - 105 cm depth % coarse and medium sand | 95 - 105 cm depth % very fine and fine sand | 95 - 105 cm depth % silt + clay | 95 - 105 cm depth mean weighted particle diameter |
|---|---|---|---|---|---|---|---|---|---|---|
| 34 | 1.55 | 3.95 | 70.1 | 6.0 | 4.3 | 0.348 | 78.9 | 1.6 | 1.6 | 0.373 |
| 35 | 1.93 | 4.29 | 62.3 | 12.0 | 10.3 | 0.324 | 56.4 | 12.3 | 9.6 | 0.305 |
| 36 | 1.80 | 4.40 | 71.5 | 6.4 | 5.8 | 0.346 | 69.9 | 2.5 | 1.9 | 0.353 |
| 37 | 5.06 | 5.30 | 55.7 | 13.3 | 9.8 | 0.303 | 51.6 | 20.1 | 16.6 | 0.289 |
| 38 | 2.16 | 4.00 | 78.4 | 3.2 | 3.0 | 0.374 | 81.1 | 1.0 | 0.9 | 0.387 |
| 39 | 2.67 | 3.99 | 66.4 | 3.9 | 3.3 | 0.348 | 59.5 | 4.2 | 3.2 | 0.325 |
| 40 | 2.25 | 4.27 | | | | | | | | |
| 41 | 2.19 | 3.93 | | | | | | | | |
| 42 | 2.52 | 3.37 | 82.5 | 2.2 | 2.0 | 0.382 | 70.3 | 1.3 | 1.1 | 0.332 |
| 43 | 4.54 | 4.23 | | | | | | | | |
| 44 | 2.70 | 4.27 | 39.4 | 22.8 | 14.7 | 0.234 | 8.7 | 59.0 | 29.9 | 0.126 |
| 45 | 2.21 | 4.08 | 57.7 | 3.7 | 2.0 | 0.297 | 55.3 | 3.5 | 1.7 | 0.288 |
| 46 | 1.67 | 3.97 | 67.4 | 3.4 | 2.5 | 0.342 | 59.7 | 4.5 | 2.5 | 0.323 |
| 47 | 2.66 | 4.07 | 62.7 | 5.6 | 4.0 | 0.319 | 76.1 | 1.0 | 0.2 | 0.341 |
| 48 | 1.88 | 4.29 | 65.2 | 7.1 | 4.3 | 0.345 | 57.5 | 3.2 | 2.7 | 0.309 |
| 49 | 2.11 | 3.94 | 53.3 | 4.5 | 3.5 | 0.300 | 52.7 | 2.5 | 1.8 | 0.288 |
| 50 | 2.09 | 4.33 | 84.6 | 2.5 | 2.4 | 0.407 | 93.1 | 0.9 | 0.9 | 0.416 |
| 51 | 2.08 | 4.20 | 46.5 | 9.4 | 8.3 | 0.270 | 45.0 | 7.7 | 6.3 | 0.276 |
| 52 | 2.70 | 3.99 | 64.5 | 1.6 | 1.3 | 0.316 | 45.4 | 15.2 | 13.1 | 0.266 |
| 53 | 2.02 | 3.82 | 90.0 | 5.6 | 5.4 | 0.469 | 93.5 | 1.5 | 1.4 | 0.438 |
| 54 | 1.91 | 3.63 | 80.3 | 6.3 | 6.2 | 0.407 | 82.4 | 3.0 | 2.8 | 0.443 |
| 55 | 2.16 | 4.07 | 87.1 | 2.2 | 2.2 | 0.412 | 86.9 | 1.0 | 1.0 | 0.394 |
| 56 | 2.54 | 4.04 | 77.5 | 2.0 | 1.7 | 0.386 | 61.6 | 2.5 | 2.1 | 0.314 |
| 57 | 2.32 | 4.21 | 37.8 | 25.8 | 18.0 | 0.236 | 53.6 | 7.2 | 4.5 | 0.301 |
| 58 | 2.47 | 3.91 | 65.6 | 5.1 | 4.2 | 0.335 | 65.4 | 6.3 | 4.9 | 0.333 |
| 59 | 2.29 | 3.98 | 64.0 | 4.0 | 3.5 | 0.332 | 60.7 | 2.0 | 1.8 | 0.311 |
| 60 | 1.35 | 4.09 | 61.6 | 7.8 | 6.2 | 0.321 | 53.5 | 10.7 | 6.5 | 0.295 |
| 61 | 2.41 | 4.17 | 71.9 | 6.4 | 5.9 | 0.349 | 77.4 | 1.9 | 1.5 | 0.372 |
| 62 | 1.45 | 4.19 | 58.5 | 11.3 | 8.9 | 0.309 | 68.2 | 4.3 | 2.8 | 0.351 |
| 63 | 1.60 | 4.26 | 70.3 | 8.1 | 7.2 | 0.352 | 74.0 | 2.1 | 1.8 | 0.357 |
| 64 | 1.56 | 4.55 | 65.3 | 10.7 | 8.7 | 0.341 | 52.4 | 20.1 | 16.7 | 0.279 |
| 65 | 2.17 | 4.00 | | | | | | | | |
| 66 | 2.33 | | 72.3 | 8.1 | 6.9 | 0.343 | 80.0 | 2.2 | 1.5 | 0.373 |
| 67 | 1.04 | 4.19 | 65.2 | 10.2 | 7.7 | 0.335 | 81.7 | 5.4 | 4.0 | 0.398 |
| 68 | 1.72 | 4.10 | | | | | 66.3 | 8.4 | 4.0 | 0.309 |
| 69 | 1.13 | 4.43 | 48.4 | 17.9 | 15.0 | 0.266 | 51.0 | 26.4 | 23.1 | 0.253 |
| 70 | 1.42 | 4.10 | 57.0 | 10.3 | 7.0 | 0.305 | 68.2 | 9.2 | 6.4 | 0.331 |
| 71 | 1.04 | 4.46 | 64.8 | 6.0 | 4.0 | 0.318 | 82.1 | 2.7 | 2.2 | 0.375 |

Table C.1. (cont.)

| | 0 - 10 cm | | 45 - 55 cm depth | | | | 95 - 105 cm depth | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| STAND | % Organic Carbon | pH | % coarse and medium sand | % very fine and fine sand | % silt + clay | mean weighted particle diameter | % coarse and medium sand | % very fine and fine sand | % silt + clay | mean weighted particle diameter |
| 72 | 2.22 | 4.10 | 36.5 | 47.1 | 42.6 | 0.209 | 63.0 | 31.5 | 31.4 | 0.321 |
| 73 | 1.88 | 4.07 | 49.0 | 9.3 | 6.3 | 0.289 | 65.3 | 4.4 | 2.4 | 0.343 |
| 74 | 1.24 | 4.43 | 62.0 | 8.1 | 6.6 | 0.330 | 75.8 | 3.1 | 2.1 | 0.360 |
| 75 | 1.43 | 4.41 | 65.6 | 8.4 | 7.2 | 0.348 | 82.9 | 4.3 | 4.0 | 0.426 |
| 76 | 1.84 | 3.94 | 77.5 | 5.0 | 4.7 | 0.374 | 74.0 | 3.1 | 2.4 | 0.354 |
| 77 | 1.17 | 4.45 | 41.8 | 7.8 | 4.7 | 0.255 | 55.3 | 8.7 | 6.8 | 0.285 |
| 78 | 1.09 | 4.09 | 61.2 | 8.8 | 7.4 | 0.305 | 67.8 | 2.1 | 0.7 | 0.329 |
| 79 | 1.68 | 4.24 | 70.1 | 7.7 | 7.0 | 0.367 | 85.1 | 2.2 | 2.1 | 0.424 |
| 80 | 1.87 | 4.15 | 37.9 | 10.3 | 10.0 | 0.250 | 42.4 | 10.3 | 9.5 | 0.240 |